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Taphonomy of the fossil insects of the middle Eocene Kishenehn Formation

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The lacustrine oil shales of the Coal Creek Member of the Kishenehn Formation in northwestern Montana comprise a relatively unstudied middle Eocene fossil insect locality. Herein, we detail the stratigraphic position of the fossiliferous unit, describe the insect fauna of the Coal Creek locality and document its bias towards very small but remarkably preserved insects. In addition, the depositional environment is examined and the mineral constituents of the laminations that comprise the varves of the Kishenehn oil shale are defined. Fifteen orders of insects have been recorded with the majority of all insects identified as aquatic with the families Chironomidae (Diptera) and Corixidae (Hemiptera) dominant. The presence of small aquatic insects, many of which are immature, the intact nature of >90% of the fossil insects and the presence of *Daphnia* ephippia, all indicate that the depositional environment was the shallow margin of a large freshwater lake. The fossil insects occur within fossilized microbial mat layers that comprise the bedding planes of the oil shale. Unlike the fossiliferous shales of the Florissant and Okanagan Highlands, the mats are not a product of diatomaceous algae nor are diatom frustules a component of the sediments or the varve structure. Instead, the varves are composed of very fine eolian siliciclastic silt grains overlaid with non-diatomaceous, possibly cyanobacteria-derived microbial mats which contain distinct traces of polyaromatic hydrocarbons. A distinct third layer composed of essentially pure calcite is present in the shale of some exposures and is presumably derived from the seasonal warming-induced precipitation of carbonate from the lake's waters. The Coal Creek locality presents a unique opportunity to study both very small middle Eocene insects not often preserved as compression fossils in most Konservat-Lagerstätte and the processes that led to their preservation.

Key words: Diptera, Hemiptera, taphonomy, varve, depositional environment, Eocene, USA, Montana.

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Introduction

As a result of their small size and often delicate structure, fossil insects are relatively uncommon. Searches of the EDNA fossil insect database and the Paleobiology Database yielded 22 618 valid species designations and 24 768 "occurrences" respectively (Clapham 2013; Mitchell 2013). These numbers are miniscule relative to the millions of species of both extant insects and those that have existed through deep time. Nonetheless, their discovery and study have provided numerous and important insights into the evolution and spectacular success of this clade. The preservation of fossil insects occurs via a number of different mechanisms that yield various degrees of preserved detail. Amber inclusions are recognized as providing the most well-preserved fossils and numerous studies have been published on region-specific amber inclusions (Poinar et al. 1999; Grimaldi et al. 2000, 2002; Penney 2010). Most insect fossils, however, occur in rocks such as

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laminar or nodular limestone (e.g., the Solnhofen, Crato, and Santana formations), ironstone concretions (e.g., siderite casts from Mazon Creek), laminated shale (e.g., the shales of the Messel and Eckfelder maars, and the Florissant Formation) and other rock types. This topic has been extensively reviewed by Lutz (1997) and Martinez-Delclòs et al. (2004). Although a lacustrine depositional environment is most common, there is no consensus on the exact mechanism(s) by which the fossilization process is initiated (Martinez-Delclòs et al. 2004; Smith 2012).

The North American west contains several very productive Eocene fossil insect localities. These include the Green River Formation of Colorado and Utah, the Okanagan Highlands in British Columbia and Washington and, at the Eocene–Oligocene boundary, the Florissant Formation in Colorado (Wilson 1978; Grimaldi and Engel 2005). The Florissant insects are by far the most studied and most diverse with 18 orders and nearly 200 families identified; more than a thousand species of fossil insects have been described from the Florissant alone. Although relatively less studied, the insect fauna of the Green River and Okanagan Highlands sites are quite diverse with 14 orders and nearly 100 families and 13 orders and 40 families described respectively (Meyer 2003; Grimaldi and Engel 2005). The Coal Creek Member of the Kishenehn Formation in northwestern Montana is an emerging Konservat Lagerstätte of middle Eocene insects. Recent descriptions of fossil insects from the Coal Creek Member include the first fairy wasps (Hymenoptera: Mymaridae) to be described from shale, a feather-winged beetle (Coleoptera: Ptiliidae) only 670 mm in length, a katydid (Orthoptera: Tettigoniidae) with an intact stridulatory apparatus and the first fossil of a blood-engorged mosquito, the abdomen of which was shown to contain porphyrins derived from the heme prosthetic group of hemoglobin (Huber and Greenwalt 2011; Greenwalt et al. 2013; Shockley and Greenwalt 2013; Greenwalt and Rust 2014). Given the uncommonly high quality of preservation of very small insects in the oil shale of the Coal Creek Member, it is of interest to better understand both the depositional environment and the taphonomic processes involved in the production of these fossils.

Institutional abbreviations.—USNM, Department of Paleobiology, NMNH, Smithsonian Institution in Washington, D.C., USA.

Geological setting

The Kishenehn Basin of northwestern Montana is a narrow 150 km long half-graben which formed along the Flathead fault system and today contains the North and Middle Forks of the Flathead River. In the Middle Fork region of the basin, the Kishenehn Formation consists of two members, the Coal Creek Member, which is estimated to be 46.2 ± 0.4 Ma (middle Eocene) by $^{40}Ar/^{39}Ar$ analysis and 43.5 ± 4.9 Ma by fission-track analysis, and the overlying Pinchot Conglomerate Member (Constenius 1996). The Coal Creek Member consists of a 1150 m thick heterogeneous basin fill consisting primarily of sandstone, siltstone, lignite and oil shale (Constenius et al. 1989). Fossil insects are found in lacustrine oil shale at the very base of the middle sequence of the Coal Creek Member, intercalated with lacustrine sandstone, siltstone, mudstone and marlstone, that have an aggregate thickness of about 100 m, with individual beds ranging in thickness from 0.5–10 m (Fig. 1).

The depositional environment of the Coal Creek Member is thought to have been profundal and marginal lacustrine, paludal, lacustrine deltaic and fan delta (Constenius et al. 1989; Pierce and Constenius 2014). Data from several studies suggest that the climate of the Middle Fork region of the Kishenehn Basin 46 million years ago was tropical with a mean annual temperature as much as 15°C higher than the region's current temperatures (Wolfe 1995; Zachos et al. 2001; Huber and Caballero 2011). In a study of the molluscan fauna of the Kishenehn Formation in the Middle Fork region, Pierce and Constenius (2001) divided these invertebrates into four different paleoenvironmental groups, the first exemplified by *Gastrocopta miniscula*. The species *Gastrocopta pellucida*, selected as the extant analog of *G. miniscula*, lives in a humid tropical environment characterized by a mean annual temperature of 25–27°C. The early arboreal primate *Tarkadectes montanensis*, originally described from the Coal Creek member and recently assigned to the extinct family Omomyidae, is closely related to the extant insectivorous Tarsiidae that are restricted to islands of Southeast Asia (McKenna 1990; Groves and Shekelle 2010; Ni et al. 2010). Perhaps more important than temperature per se, however, is the low temperature seasonality that existed throughout the Eocene epoch and is thought to be responsible for the very high degree of insect diversity—similar to that of modern tropical forests—that existed during that time period (Archibald et al. 2010, 2013).

Material and methods

Specimens were collected from the middle sequence of the Coal Creek Member of the Kishenehn Formation in northwestern Montana under the auspices of USFS Permit HUN281. A total of 2746 pieces of shale and 7469 fossil insects were collected in 2009 and 2010 in a non-biased fashion (i.e., no specimens, regardless of their degree of fragmentation or state of preservation, were discarded) and are currently housed at the Department of Paleobiology, NMNH, Smithsonian Institution in Washington, D.C. Non-insect specimens (fish, snails, ostracods, etc.) were collected only en passant. Fossil specimens were collected from the Park (USNM 553696, 559597, and 560104), Deep Ford (USNM 559598), Spring (USNM 593436 and 593437) and Disbrow Creek (USNM 595136) sites. In addition, shale samples were collected from the Dakin (USNM 560100 and 560101), Pi-

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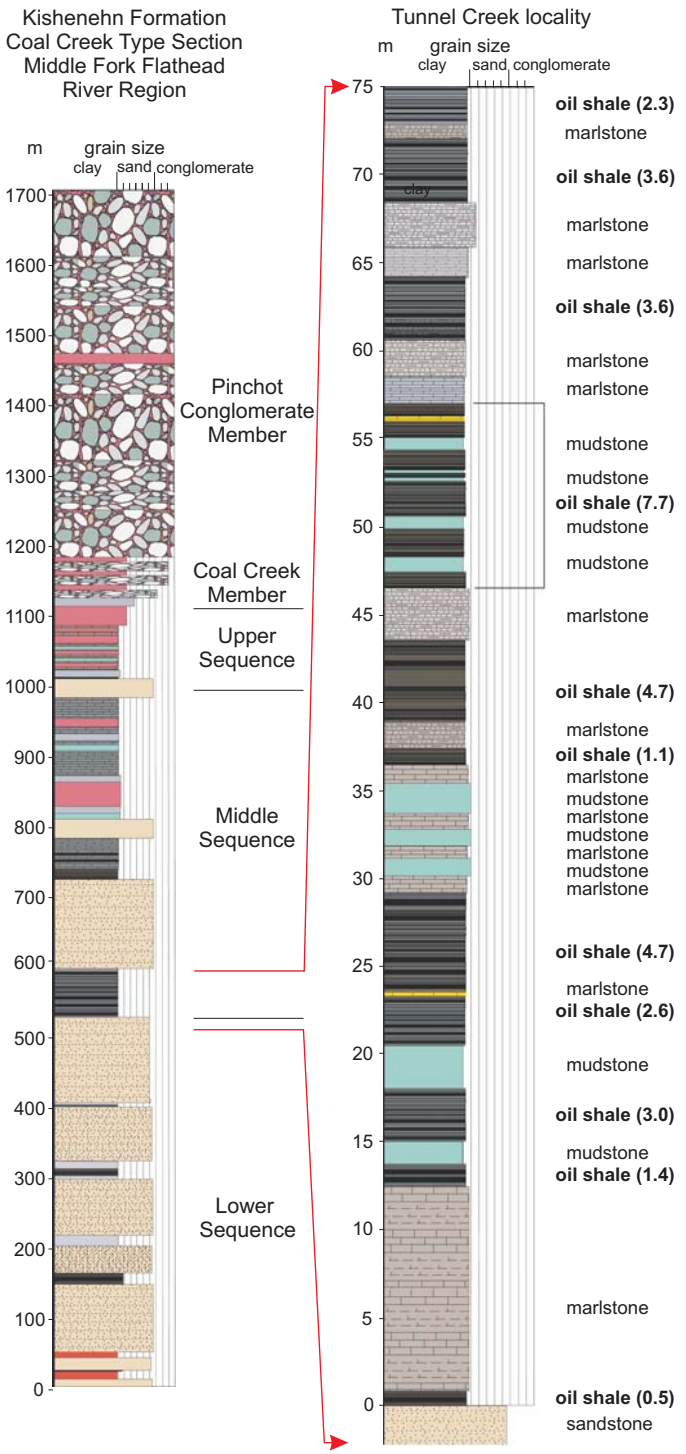


Fig. 1. Stratigraphy of the middle Eocene Kishenehn Formation from the type area at Coal Creek, Middle Fork of Flathead River region, shown in relation to the measured section at the Tunnel Creek locality—oil shale stratigraphy is representative of the other insect localities and demonstrates the heterogeneous lithologic makeup of the lower sequence of the Coal Creek Member. The thicknesses of the oil shale beds in meters is shown in parentheses. For the interval with numerous interbeds of marlstone and mudstone denoted by the bracket, the composite thickness of oil shale is listed. The oil shale within this bracket contains fossil insects.

sces (560099), Park (USNM 560103, 593433, and 595137) and Deep Ford (USNM 560102) sites.

Distributions of total body lengths of the Curculionidae (Coleoptera) from the Coal Creek and Green River collections were determined from 55 of the 67 Coal Creek weevil specimens collected in 2009 and 2010 and 110 specimens of Curculionidae from both the Labandeira and Kohl sites of the USNM Green River fossil insect collection (55 specimens randomly selected from each site); 12 Coal Creek specimens were not measured due to an inability to define the posterior or anterior extremity of the fossil. Body lengths were measured from the posterior of the abdomen to the anterior base of the rostrum.

The fossils, when dry, were often invisible due to a thin overlying surface layer of silicates. When immersed in ethanol or water, the silicate layer became translucent and the fossils visible. Occasionally, this layer was removed through use of a Faber-Castell eraser pencil (#185698). Fossils were immersed in 95% ethanol for examination and photographed with an Olympus SZX12 microscope equipped with a Q-Color5 Olympus camera. Image-Pro Plus 7.0 software was used to capture and record the images and measurements. To prepare thin-sections, pieces of shale were embedded at room temperature in Epotek-301 epoxy (Epoxy Technology. Inc. Billarica, MA) and pumped to ~30 torr twice to remove air bubbles. The hardened block of epoxy was ground smooth on one side to expose a horizontal section of the shale. The block was then affixed to a 1”×2” glass slide with Epotek-301 and the specimen was cut off and ground to ~20 mm with a Hillquist thin-sectioning machine. Final grinding to optical thickness was done by hand with silicon carbide sandpaper and tin oxide as a polishing medium. In some cases, edges of unembedded shale samples were ground smooth with use of a series of sandpapers.

Microanalysis and imaging were performed at the NMNH Department of Mineral Sciences. Elemental analyses were done on uncoated samples using an FEI NOVA NanoSEM 600 FEG Variable Pressure Analytical Scanning Electron Microscope (SEM) outfitted with a ThermoNoran energy dispersive spectrometer (EDS). Standardless EDS analyses were performed on thin sections and at 15 kV and 1–2 nA and have an analytical uncertainty of less than 5%. Mass spectrometry analyses were done with a ToF-SIMS IV (ION-TOF GmbH) time of flight secondary ion mass spectrometer. A fresh sample surface was prepared by splitting the sample immediately prior to ToF-SIMS analysis and then mounting the sample as a cross-section in a laminar flow hood. Ion imaging was done using a 25 keV Bi^{+3} beam at a pulsed current of 0.3 pA, rastered over the area of ~150×150 μm^2 to 500×500 μm^2 for 180–600 seconds. The accumulated primary ion dose never exceeded 8×10^{11} ions per cm^2, which is below the static limit (the point where the same location is statistically sampled more than once) of 10^{12} ions per cm^2 for organic molecules. Analyses were performed with the instrument optimized for high mass resolution (bunched mode: m/Δm of at least ~2000 at m/z 30).

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Fig. 2. Photograph of the Kishenehn Formation (Coal Creek Member) Dakin and Pisces sites. The beds (parallel ridges) can be traced beneath water level to connect the two sites. Map data ©2014 Google.

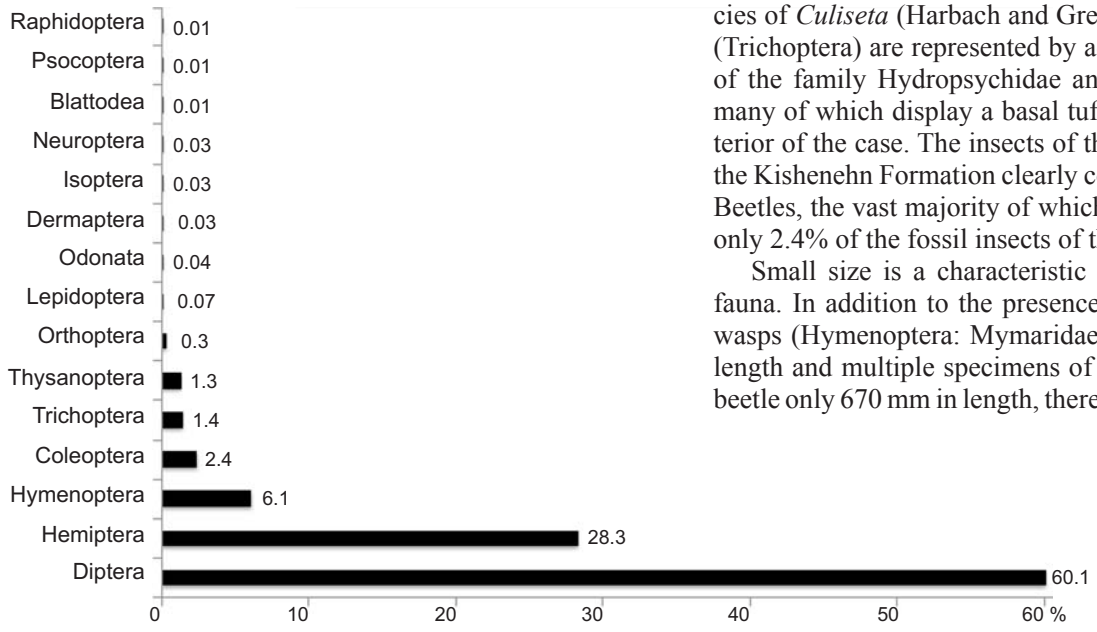


Fig. 3. Distribution of fossil insect orders from the Coal Creek member of the Kishenehn Formation. Percentages of the total insect fossils for each order are given to the right of each horizontal bar. Insects not identifiable to order (8.38% of the total) are not included in the graph. Within Diptera and Hemiptera, the families Chironomidae (nonbiting midges) and Corixidae (water boatmen) respectively, make up the majority of the specimens.

Results

Analyses of the fossil insects.—Ten different Coal Creek Member collection sites are distributed over approximately seven miles of the Flathead River although, due to the meandering nature of the river, some sites consist of stratigraphically similar sediments (e.g., the Pisces and Dakin sites; Fig. 2). Most sites vary relative to their fossil insect fauna. For example, trichopteran larval cases occur 15 times more frequently at the Spring site than at the Dakin site, an indication that the former may represent deposition adjacent to flowing water versus still water at the Dakin site. Fifteen different insect orders and the entognathous Collembola are currently represented (Fig. 3). The orders Collembola, Blattodea, Raphidioptera, and Psocoptera are each represented by a single specimen. The orders Dermaptera, Isoptera and Neuroptera are each represented by only two specimens; Odonata and Lepidoptera are represented by three and five specimens respectively. Larger specimens are usually poorly preserved (Lepidoptera and Orthoptera) and/or found as isolated wings or legs (Odonata and Orthoptera). Most (60.1%) of all specimens are Diptera and another 28.3% of all specimens are in the order Hemiptera; 84.1% of all Diptera are from a single family of midges (Chironomidae), and 55.7% of all the Hemiptera are water boatmen (Corixidae). A small percentage of the fossil insects (8.38%) were not identifiable to order. Large numbers of Chironomide pupae, which consisted only of the cephalothorax, were not counted in the inventory of total insects. Many intact culicomorphan (Diptera: Nematocera: Culicomorpha: Culicoidea + Chironomoidea) pupae were well preserved, however, and accounted for 19.2% of the total Chironomidae + Culicidae. To date, 40 adult fossil mosquitoes have been collected including two new species of *Culiseta* (Harbach and Greenwalt 2012). Caddisflies (Trichoptera) are represented by adults, a single intact larva of the family Hydropsychidae and numerous larval cases, many of which display a basal tuft extending from the posterior of the case. The insects of the Coal Creek Member of the Kishenehn Formation clearly constitute an aquatic fauna. Beetles, the vast majority of which are terrestrial, constitute only 2.4% of the fossil insects of the Coal Creek fauna.

Small size is a characteristic of the Coal Creek insect fauna. In addition to the presence of numerous fossil fairy wasps (Hymenoptera: Mymaridae) approximately 1 mm in length and multiple specimens of a single species of ptiliid beetle only 670 mm in length, there are large numbers—near-

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ly 1% of the Coal Creek total—of tiny wasps of the single subfamily Belytinae (Hymenoptera: Diapriidae). Similarly, 17% of all Coal Creek Hymenoptera are in the superfamily Chalcidoidea, a group of parasitic wasps usually 1 to 2 mm or less in length. There are approximately 22 000 known extant species within the superfamily Chalcidoidea and their presence in the Coal Creek fauna may not be unexpected except for the fact that their small size usually constitutes a strong negative taphonomic filter. Most Coal Creek fossil beetles are also very small. For example, 83.6% of the weevils (Coleoptera: Curculionidae), a family that constitutes 33.5% of all the Coal Creek fossil beetles, were 3 mm or less in length. In contrast, only 19.1% of a randomly chosen subset of weevils in the NMNH's Green River fossil insect collection were 3 mm or less in length. The Coal Creek Member depositional environment was such that, not only were very tiny insects preserved, nearly all were fully articulated. Only 3.2% of all fossil insect specimens were isolated wings or legs.

Varve structure and composition.—In an attempt to understand the basis of the exceptional preservation of the Coal Creek insect fauna, the structure of the oil shale of the Coal Creek Member was examined. Micrographs of cross-sections of pieces of shale from the Pisces and Dakin sites show well-defined parallel rhythmites that vary in thickness from approximately 100 to 500 μm (Fig. 4). Although there is occasional undulation of the layers, anastomosis of the layers is absent. Each rhythmite in Fig. 4A is a couplet, comprised of two layers, a lower and thicker light gray layer and an overlying thinner black layer. Some samples of shale from the Dakin site (Fig. 4B), however, contain three distinct layers with an additional tan layer of intermediate thickness that is interposed between the thick gray and thin black layers. These layers can vary in thickness relative to one another and, in other examples of Coal Creek oil shale, rhythmites containing either two or three layers can be found adjacent to one another. Scanning electron microscopy was used to detail the microstructure of the three-layered rhythmites (Fig. 5). The uppermost thin black layer is made up of small (<2 μm) subspherical particles and a heterogeneous mixture of larger angular silt grains interspersed within a layered black matrix (Fig. 5B). The underlying middle layer is a nearly homogeneous zone of small subspherical particles with only a rare occurrence of larger angular silt grains (Fig. 5C). The bottom thick layer is composed almost entirely of large (2–20 μm) angular siliciclastic silt grains with very few of the smaller crystals and none of the black matrix characteristic of the middle and uppermost layers respectively (Fig. 5D).

Elemental analysis of the shale by energy dispersive X-ray spectroscopy reveals the geochemical composition of the laminae that comprise the rhythmites (Fig. 6). The black matrix of the uppermost layer is carbon. This and the undulating form of this carbonaceous component suggest that it is derived from an algal or microbial mat (Fig. 6B; see Discussion). The small amorphous particles characteristic of the middle layer are calcite ($CaCO_3$) (Fig. 6C). This layer is

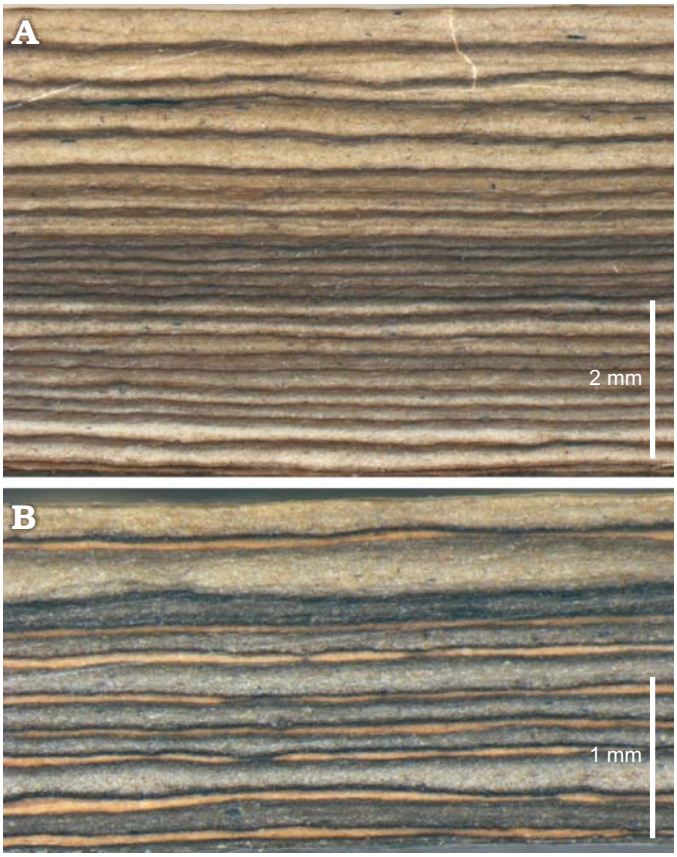


Fig. 4. Micrographs of cross-sections of two pieces of oil shale from the Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA. **A**. Shale (USNM 560099), 6 mm thick, from the Pisces site showing rhythmite couplets of varying thickness. **B**. Shale (USNM 560100), 2 mm thick, from the Dakin site showing rhythmites comprised of three distinct layers: A lower thick gray layer of siliciclastic particles, an adjacent thin tan layer of calcite and an uppermost black carbonaceous mat.

interpreted as the result of calcium carbonate precipitation induced by warming spring temperatures, possibly concomitant with an algal or microbial bloom (see Discussion). This interpretation is supported by the homogeneity of the layer which itself suggests that the precipitation of calcite took place relatively quickly, over a short period of time. In some instances, a thin layer of carbonaceous mat underlies as well as overlies the calcite layer. No diatom frustules or fragments of frustules were observed in any of the rhythmites examined. The thick bottommost layer is composed of a heterogeneous mixture of siliciclastic particles, occasional crystals of calcite, and other minor minerals. The major components of this layer are large angular to subangular crystals of quartz and potassium and sodium feldspars (Fig. 6D, E). The source of these minerals may have been tephra from ash plumes or loess derived from the adjacent volcanic landscape. The angular nature of these crystals suggests that they are windblown and not deposited in the lake by fluvial processes. Other minerals found in the clastic layer of the rhythmites include barite, pyrite and mica. The rhythmites are interpreted as annual varves (annually laminated deposits/rhythmites with annual periodicity) in which the bottom thick layer of

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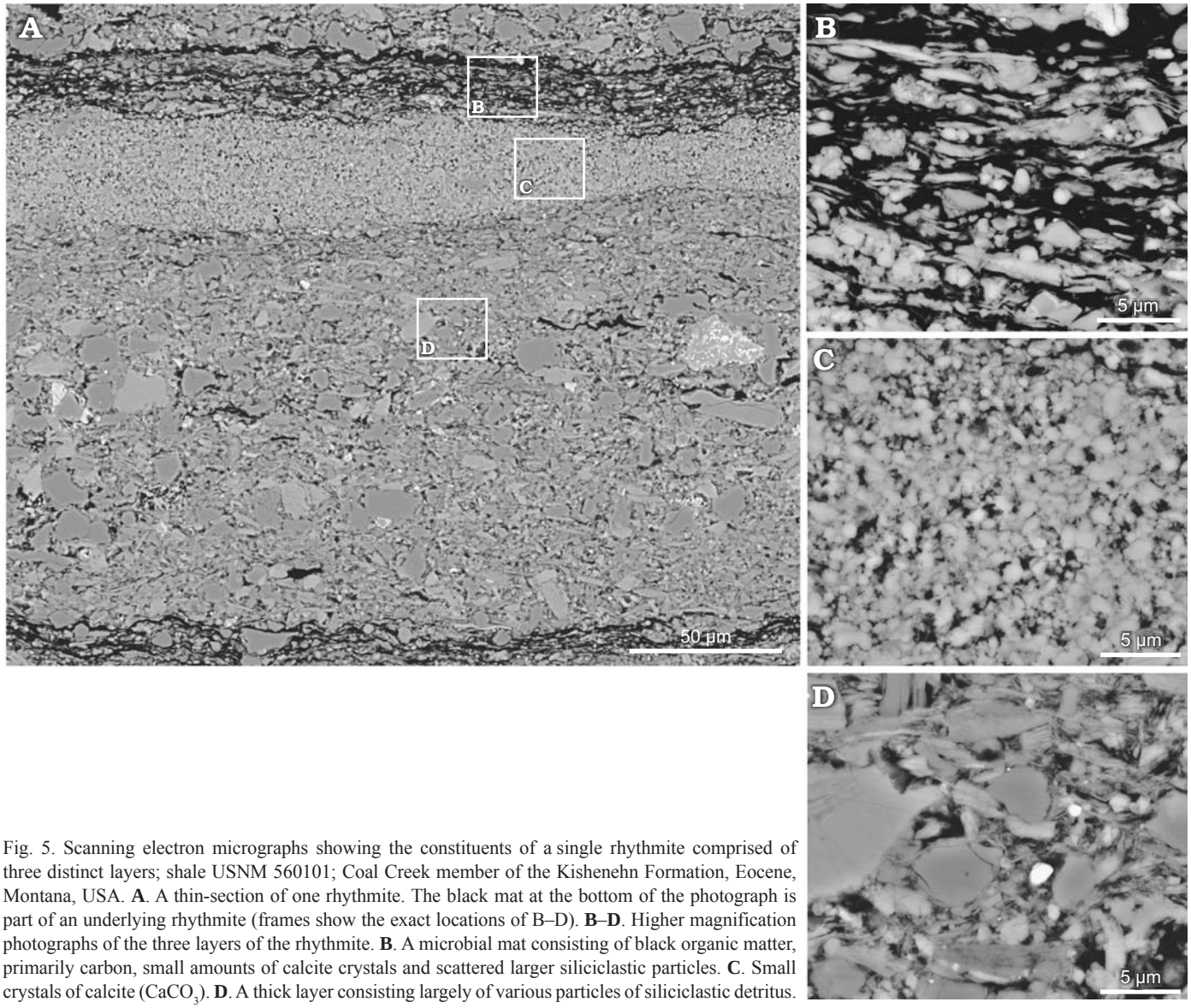


Fig. 5. Scanning electron micrographs showing the constituents of a single rhythmite comprised of three distinct layers; shale USNM 560101; Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA. **A**. A thin-section of one rhythmite. The black mat at the bottom of the photograph is part of an underlying rhythmite (frames show the exact locations of B–D). **B**–**D**. Higher magnification photographs of the three layers of the rhythmite. **B**. A microbial mat consisting of black organic matter, primarily carbon, small amounts of calcite crystals and scattered larger siliciclastic particles. **C**. Small crystals of calcite ($CaCO_3$). **D**. A thick layer consisting largely of various particles of siliciclastic detritus.

windblown clastic material accumulated during a period of reduced insolation, the calcite layer accumulated over a short period of several days in the warming spring and the uppermost carbonaceous microbial mats accumulated over the spring and/or summer. The microbial mat layer is composed of several individual carbon-rich laminae that may correspond to separate microbial blooms (Fig. 7). Interposed between the individual carbonaceous laminae are eolian siliciclastic components indicating that the deposition of the carbonaceous layers took place over a relatively long period of time (i.e., spring and summer). In ToF-SIMS analysis of a cross-section of freshly fractured shale, hydrocarbons (C_xH_x) are localized to the microbial mat layers (Fig. 8). Spectra retrieved from the mat specifically contain peaks from m/z 77.04 (C_6H_5) all the way up to at least m/z 300.07 ($C_{24}H_{12}$) (Fig. 8D) that can be assigned to aromatic moieties (Stephan et al. 2003). Similar aromatic patterns have been identified in ToF-SIMS spectra of crude oils and microfossils (Ivarsson et al. 2013; Siljeström 2013). Other identified organic peaks in the spectra of the shale include nitrogen containing compounds at m/z 18.03 (NH_4), m/z 30.04 (CH_4N), and m/z 44.05 (C_2H_6N). However, these latter peaks do not localize to the microbial mat. Peaks that can be assigned to biomarkers such as steranes and hopanes (Siljeström et al. 2009) were not found in the spectra of the shale.

Non-insect fossils.—The varves remain intact over large distances (>10 feet) with little evidence of bioturbation. The shale contains rare and small specimens of both snails and fish. A total of 64 specimens of fish were collected, all of which were 10 cm or less in length and fully articulated. Although the pieces of shale containing fossil fish were larger than average, only nine such pieces also contained fossil insects and these contained only an average of 1.4 insects/piece of shale. The fish-containing shale from the Park site, which produced 44% of all the fossil fish, was distinctly dif-

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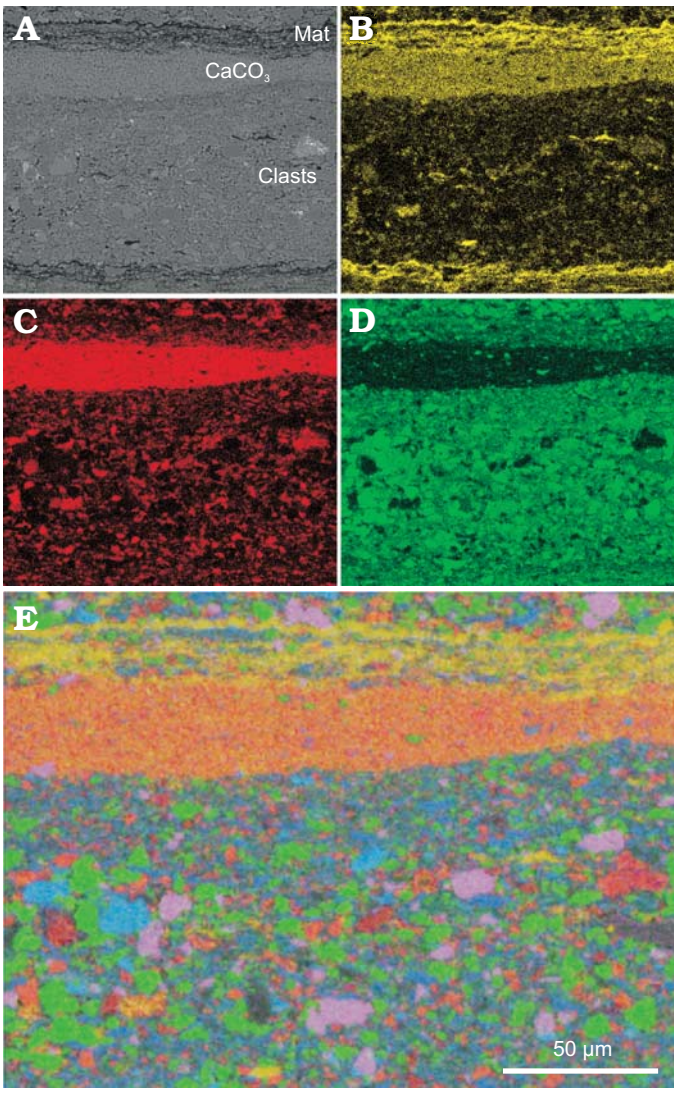


Fig. 6. Energy dispersive spectroscopy X-ray ion image maps of individual elements within a single rhythmite from the Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA. **A**. A scanning electron micrograph of a cross-section of a single rhythmite showing the mat, calcite ($CaCO_3$) and siliciclastic (clastic) layers. **B**–**D**. X-ray ion image maps of the elements carbon, calcium and silica respectively. **E**. A composite ion image energy dispersive X-ray map showing the localization of the elements carbon (yellow), calcium (red), silica (green), potassium (blue), and sodium (pink). The large blue crystals are potassium feldspar, the pink crystals are sodium feldspar and the green crystals are quartz.

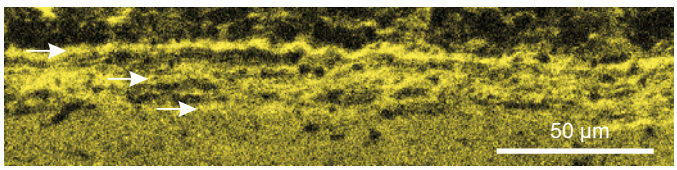


Fig. 7. A close-up of the microbial mat in Fig. 6B. The arrows point to individual carbon-rich laminae.

ferent from the shales pictured in Fig. 4 (Fig. 9). While this "fish shale" contained multi-component varves, the clastic layers were much more sapropelic in nature with numerous large (100–200 µm) clasts and occasional very large carbonized inclusions. The majority (79%) of the 57 specimens of fish coprolites were also small with diameters of ≤2 mm and frequently contained contents identifiable as insect remnants (Fig. 10). Snail fossils were locally numerous but only in siltstone or, most commonly, shale that did not contain insect fossils. The only other aquatic non-insect fauna collected were, rarely, ostracods (in 0.23% of all pieces of shale) and, more commonly, numerous ephippia (egg cases) of cladocerans of the subgenus *Ctenodaphnia*. These latter fossils were present at the Dakin, Disbrow Creek, Tunnel Creek, and Deep Ford sites. No other fossil benthic fauna were found. Small (<1 cm) seeds were found in the oil shale but larger leaves were very rare, the vast majority occurring in siltstone and sandstone. Fossil leaves of the family Pinaceae, Cupressaceae, and Platanaceae were collected, primarily at the Disbrow Creek and Brown's Hole sites, within deposits of siltstone and sandstone intercalated with the oil shales. Other leaf fossils remain to be identified but, in general, they are uncommon.

Taphonomically important fossils.—The Coal Creek shale weathers to continuous parallel laminae that vary from 1 to several millimeters in thickness (Fig. 11A). When these layers are split, they invariably do so within a fossilized mat (Fig. 11A, B); the shale never splits within the siliciclastic layer. The siliceous nature and glass-like appearance of the fossilized mat surfaces contrast markedly with the texture of the basal clastic layer of the varves. The fossilized mat surfaces can be light or dark gray but frequently range in color from to yellow to purple. The mat layer is also where the fossil insects reside. Figure 12 depicts an adult corixid fossil 2.3 mm in width preserved within a microbial mat. The thickness of the fossil insect and the enclosing mat is approximately 15 µm and does not differ substantially from the thickness of either the adjacent mat or the mats of the underlying varves (Fig. 12C). The Coal Creek fossils do not include specimens that consist of both part and counterpart. Rather, in very rare cases, the fossil will tear such that, for example, the anterior portion will be on one surface and the posterior portion on the other.

Several Coal Creek fossils preserve, directly or indirectly, examples of insect behavior that may relate to our understanding of taphonomic processes. Figure 13A depicts an adult corixid within a group of eight corixid nymphs. Such groupings are common, with a total of 58 pieces of shale with five or more corixids/piece of shale, collected from six different sites. The nymphs lack a head and display an anterior to posterior rift in the thorax along the ecdysial line and are probably exuvia. This grouping is not characteristic of "rafting" in which relatively large numbers of insects are swept together by surface water currents to form a tightly packed aggregation of insects. The corixids are separate one from another and constitute a grouping, characteristic of a dense population, that would not form if they sank from the surface of deep water where individual insects would be expected to disperse laterally before they reached the bottom. Figure 13B depicts a rove beetle (Coleoptera: Staphylinidae) on the surface of

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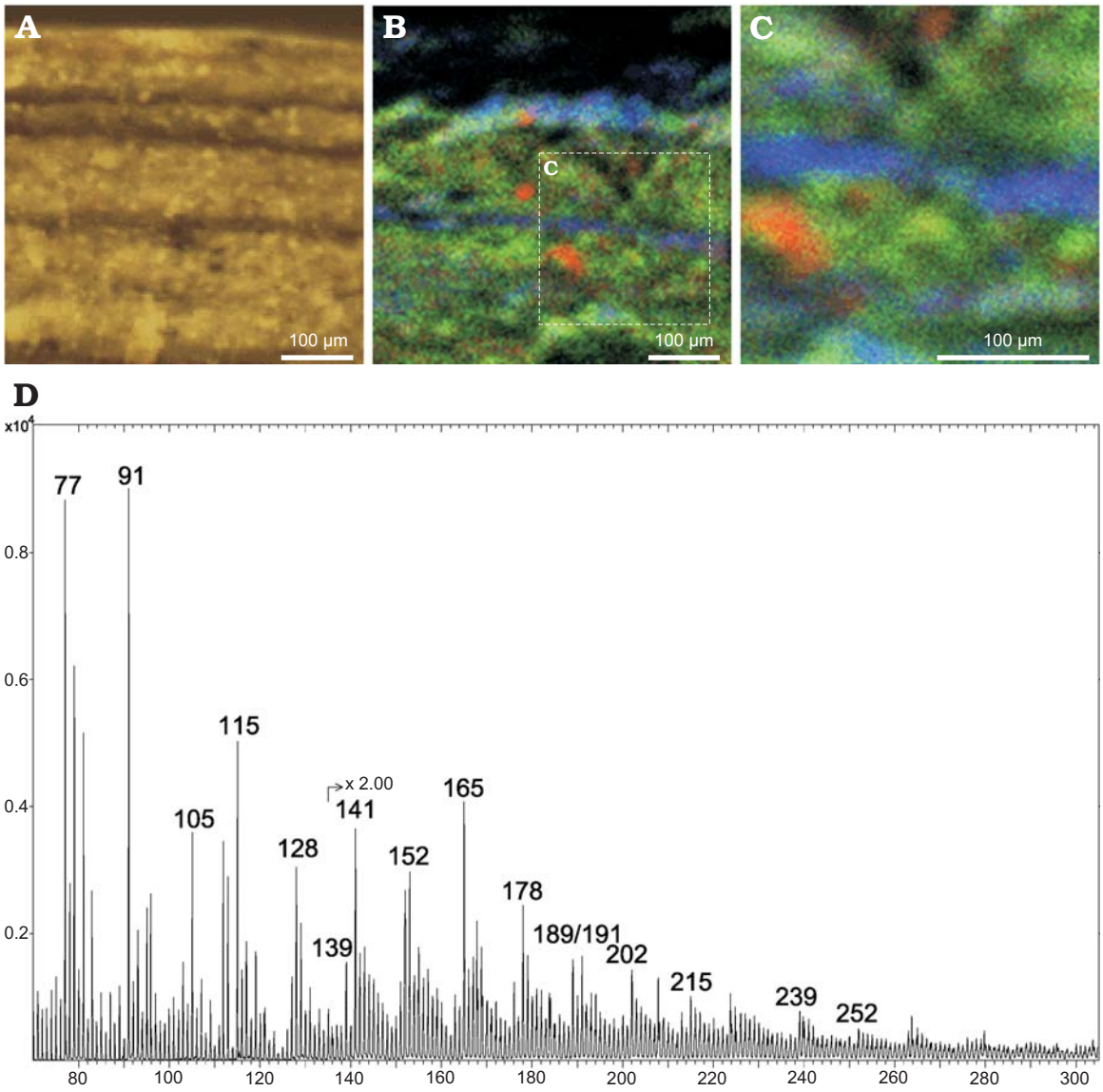


Fig. 8. ToF-SIMS ion images and spectrum of an oil shale rhythmite (USNM 593433) from the Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA. **A**. Micrograph of shale. **B**. Composite ion image with silica (green), calcium (red), and combined polyaromatic hydrocarbons (blue) imaged. **C**. Ion image of the polyaromatic hydrocarbon rich microbial mat layer. **D**. Positive ToF-SIMS spectrum of blue area in C. Numbers indicate aromatics at m/z 77.04 (C_6H_5), 91.05 (C_7H_7), 105.09 (C_8H_9), 115.05 (C_9H_7), 128.05 ($C_{10}H_8$), 141.06 ($C_{11}H_9$), 152.05 ($C_{12}H_8$), 165.06 ($C_{13}H_9$), 178.06 ($C_{14}H_{10}$), 189.05 ($C_{15}H_9$), 202.06 ($C_{16}H_{10}$), 215.07 ($C_{17}H_{11}$), 239.05 ($C_{19}H_{11}$).

a fossilized algal/microbial mat. The legs of the beetle have been displaced posteriorly and setae that have been pulled from the posterior end of its abdomen outline movement of the beetle. This configuration may be interpreted as the result of the beetle's attempt to escape the mucilaginous trap of a mat's surface. Figure 13C depicts the process of eclosion wherein a chironomid midge exits its pupal exuvium. Adults use the surface tension of calm shallow water to stay suspended when they emerge from pupal cases and dry their wings. Such insects would not be expected to exist in or be transported to deep water. Figure 13D depicts fossils of the chitinous egg cases or ephippia of *Daphnia*. These egg cases are produced during unfavorable environmental conditions (e.g., reduced rainfall and/or insolation) and can enter diapause until conditions improve (Stross and Hill 1965; Kleiven et al. 1992). Morphological characteristics of the fossil ephippia such as a D-shaped case and eggs with their axes sub-parallel to the ephippium's dorsal margin identify these specimens as *Ctenodaphnia* (Benzie 2005). This subgenus prefers shallow, even temporary waters although exceptions exist (Colbourne et al. 1997; Richter and Wedmann 2005).

Discussion

Insect fossils and their depositional environment.—Knowledge of the depositional environment of the Coal Creek Member fossil insect assemblage is critical in understanding both the compositional basis of the insect fauna and

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the processes responsible for their remarkable preservation. The Coal Creek insects are characteristic of an aquatic environment in and around a large relatively shallow lake or the shallow margins of a deep lake. This conclusion is supported by the preponderance of autochthonous adult, larval and pupal chironomide midges, corixid adults and nymphs, trichopteran adults and larvae and adult culicids in relatively large numbers. Given the lacustrine environment, this is not unexpected; several insect Lagerstätte have fauna dominated by aquatic insects. The Triassic Solite and the Miocene Biocorb Basin insect fauna are dominated by giant water bugs (Hemiptera: Belostomatidae)—mostly nymphs, and chironomid pupal exuvia respectively (Liutkus et al. 2010; Peñalver and Gaudant 2010). However, there are several exceptions. The fossil insect fauna at the Horsefly River and other Okanagan Highlands sites is dominated by march flies (Diptera: Bibionidae) (Wilson 1996). The Green River, McAbee, Maiz Gordo, Eckfelder Maar, and Messel insect fauna are all dominated by beetles (Scudder 1890a, b; Lutz 1988, 1997; Wappler 2003; Petrulevicius 2005; Archibald et al. 2010)—this is in great contrast to the Coal Creek insect fauna, of which only 2.4% are beetles. Although beetles are the most diverse group of extant insects, the vast majority are terrestrial; their presence or absence in the sediments is controlled by an array of site-specific taphonomic windows and filters. In studies of six different sites in the Okanagan Highlands, Wilson (1996) concluded that the depositional environment, not the composition of the local insect fauna, was the most important factor in determining which insects were preserved as fossils.

The Coal Creek insects, the vast majority of which are either chironomids or corixids, represent only a small percentage of the total insect fauna that existed in and around the waters of Lake Kishenehn. Most terrestrial insects immediately adjacent to various bodies of water would not be expected to be represented in the fossil assemblage. In experiments designed to quantify this seemingly intuitive assumption, Smith (2000) determined that only 7.3% of the extant beetle genera known to populate the area adjacent to Wilcox Playa in Arizona were represented amongst those buried in lakeshore sediments. Large insects were rarely found in the sediments. Beetles less than 5 mm in length were five times more likely to be buried than those longer than 5 mm despite the fact that 74% of the living beetles sampled at the site were in the larger category. Insect size is a powerful taphonomic factor. Small insects with a wing span less than 5 mm have been shown to be more likely to be trapped on and unable to escape from the water's surface (Martinez-Delclòs and Martinell 1993). Smith (2006) demonstrated that small (4 mm) subspherical weevils (Coleoptera: Curculionidae) tended to sink more quickly and disarticulate less than most other beetles; they were also the most common family of beetles collected at the Florissant. Similarly, weevils are by far the most common beetle found in the Coal Creek fauna and the vast majority of them are very small (<3 mm). In contrast, the much larger dragonflies (Odonata: Anisoptera), most of

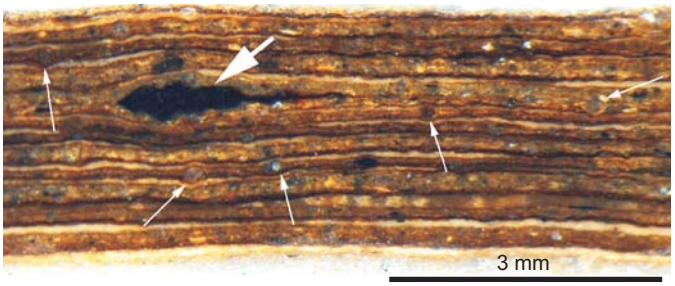


Fig. 9. Rhythmite structure of Park site oil shale (USNM 595137) from the Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA, that is a source of numerous small (<10 cm) fish fossils. Note the dark colored, organic-rich sapropelic nature of the shale and the small clastic (small arrows) and large (large arrow) organic inclusions.

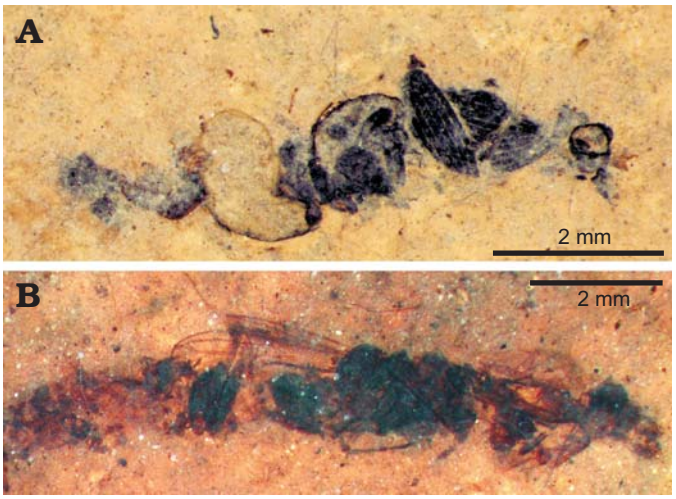


Fig. 10. Fossil coprolites in oil shale from the Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA. **A**. USNM 593436, coprolite composed entirely of beetle elytra. **B**. USNM 593437, coprolite that contains a heterogeneous accumulation of insect parts including dipteran wings.

which spend at least a portion of their life in or near an aquatic environment, are represented in the Coal Creek insect fauna by a single wing fragment. In a manner analogous to insects that evade entrapment in tree resins, large insects strong enough to escape from the water's surface can avoid entrapment and death. The water's surface, tree resins and the adherent mucopolysaccharides on the surface of algal and microbial mats (see below) all represent strong taphonomic filters that result in a bias towards the preservation of small insects. This is particularly the case for the Coal Creek insect fauna where insects 1 mm or less in length (e.g., Mymaridae and Ptiliidae) are found as highly detailed fossils. These particular families are not represented in the Green River, Florissant, and Messel Lagerstätte. At the McAbee site in the Okanagan highlands, no fossils less than 2 mm in length were found (Archibald et al. 2010). Of course, factors other than those mentioned above may be responsible for the unique makeup of the Coal Creek fauna. The unusually large numbers of belytinid wasps, both in sheer numbers and different morphotypes, may be the result of the very large numbers of nematoceran flies recorded in the Coal Creek

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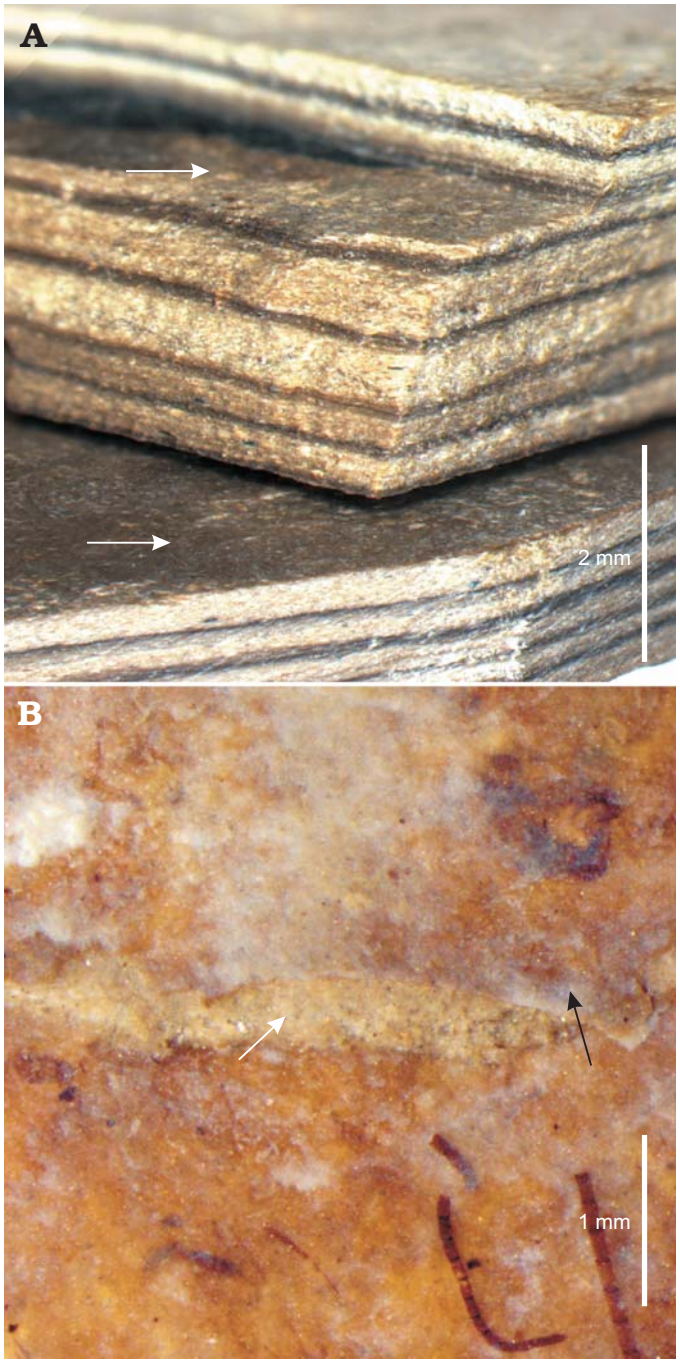


Fig. 11. Splitting of the oil shale from the Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA, exposes the fossil-containing microbial mat layer. **A**. A piece (USNM 560103) that consists of 12 rhythmite couplets. Note that the shale naturally splits (arrows) within the dark microbial mat layer. **B**. A micrograph of the siliceous surfaces of two rhythmites (USNM 560102). Note the glass-like appearance of the uppermost fossilized mat (black arrow) overlying the thicker clastic basal layer (white arrow). The reddish linear structures at the bottom right of the photograph are fragments of fossil insect antennae on the surface of the mat of the lowermost varve.

Member as Huggert (1979) has made the observation that belytinid wasps parasitize nematoceran pupae. It is of interest to note that minute fossil parasitic wasps and chironomide pupal exuviae have been described from the Early Miocene Rubielos de Mora and Bicorb Basins respectively that closely resemble the Coal Creek fossils in their appearance. The fossils were described as being composed of "carbonaceous films" and covered with "sediment (that) became translucent under alcohol" in a manner similar to the Coal Creek fossils (Peñalver and Engel 2006; Peñalver and Gaudant 2010).

Other physical characteristics of insects have been shown to affect their fossilization potential. Lepidopterans, when dead and on the water's surface, tend to float and remain on the surface for very long periods of time (Martinez-Delclòs and Martinell 1993). Their propensity to float, due to both the large surface area of their wings and the hydrophilic scales that cover their wings, subjects these insects to greater chances of predation, fragmentation and decay (Martinez-Delclòs and Martinell 1993; Wagner et al. 1996: 3). These factors may well be responsible for the rarity of lepidopteran fossils both in the Kishenehn Formation and most other Lagerstätte, as has been previously suggested by Archibald et al. (2010). Where lepidopteran and large-winged neuropteran fossils do exist, their preservation has been ascribed to the ameliorative effects of cyanobacterial or algal mat-mediated stabilization processes (Martinez-Delclòs et al. 2004; Archibald and Makarkin 2006).

Insect size and flying ability are also important factors in determining the type of environment in which fossilization takes place. Several studies have documented a bias towards preservation of allochthonous insects that are larger in size and strong flyers (e.g., winged ants) in deep offshore locations and smaller weaker or non-flyers such as adult Culicomorpha, immature stages such as larvae and pupae and small beetles in shallow nearshore locations (Wilson 1980, 1988; Smith and Moe-Hoffman 2007). The preponderance of large insects and the relative absence of immature insects at McAbee is ascribed to the former's aerial transport to deep water; the fossils at Solite, which are mostly wingless belostomatid nymphs, are thought to have been deposited in shallow water (Archibald et al. 2010; Liutkus et al. 2010). The fossil insects of the Bicorb Basin, 80% of which are pupal exuvia, may also have been deposited in shallow water (Peñalver and Gaudant 2010).

Increased diversity and the extent of disarticulation are also thought to correlate with shallow/nearshore environments (Wilson 1980, 1982, 1988; Smith and Moe-Hoffman 2007). Although the Coal Creek Member has produced fossils of 15 different insect orders, it has a dramatically skewed distribution of insect types. Fully two thirds of all the fossil insects belong to either the dipteran family Chironomidae or the hemipteran family Corixidae. Again, such skewed distributions are not uncommon amongst insect Lagerstätte. Solite is dominated by a single family of water bugs (Belostomatidae); Messel is dominated by beetles (63%) with another 24.8% of the fossil insects at Messel either winged ants (Formicidae) or burrowing bugs (Cydnidae) (Lutz 1988). Skewed distributions are also found in extant insect populations. The very high diversity of insects found in tropical environments is accompanied by representation of many species by few

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or single specimens (Archibald et al. 2013 and references cited therein). Interestingly, while a large degree of insect diversity is characteristic of both the Green River and Florissant sites, fossiliferous facies at the former may be derived from shallow water while the latter is thought to originate in a deep water environment (McLeroy and Anderson 1966; Gierlowski-Kordesch and Park 2004). However, the spatially and temporally heterogeneous nature of the lakes of the Green River Formation makes it difficult to accurately characterize this aspect of these lakes (Carroll and Bohacs 2001; Gierlowski-Kordesch and Park 2004) The actual depths of paleolakes can be difficult to determine, as exemplified by the Pitch Pinnacle site in Colorado, which was determined to be either a "caldera lake" or "shallow water" (Gregory and McIntosh 1996). In addition, it should be noted that nearshore does not necessarily mean shallow water; Messel and Lake Shiobara in Japan were maar and caldera lakes respectively with steeply descending margins (Tsujino and Maeda 1999; Schulz et al. 2002). In the Kishenehn Basin, debris flows and paleotalus from the Roosevelt fault scarp are interlayered with oil shale at the east side of the basin and suggest a steep shoreline and deep water there. The topography of the west side of the basin, where this relationship of coarse clastic material juxtaposed with shales is not as predominant, is thought to have been much less steep (Constenius 1981).

The isolated wings characteristic of the Bembridge Marls are thought to have been deposited along the margins of a flood plain lake (Daley 1972, 1973) and, in general, increased disarticulation has been ascribed to shallower waters (Wilson 1980). However, a deep water environment at Solite was thought improbable because "exquisite preservation of these articulated insects ... negates a free-fall through a significant water body, as turbulence and subsequent disarticulation would likely occur" (Liutkus et al. 2010: 661). Although the few larger insects from the Coal Creek Member tend to be represented by isolated wings (e.g., Neuroptera and Odonata) or legs (e.g., Orthoptera), overall, Coal Creek insects exhibit low levels of disarticulation. Table 1 lists a number of taphonomic characteristics that have been proposed as indicators of the depth and/or nearshore/offshore setting of depositional environments. In most instances, these factors characterize the Coal Creek fossils as having been deposited in a shallow/nearshore environment. The intact nature of most Coal Creek insect fossils and the lack of bioturbation in the annual layers of sediment, thought to suggest deposition in anoxic deep water, may be explained by the ameliorative effects of microbial mats (Archibald and Makarkin 2006).

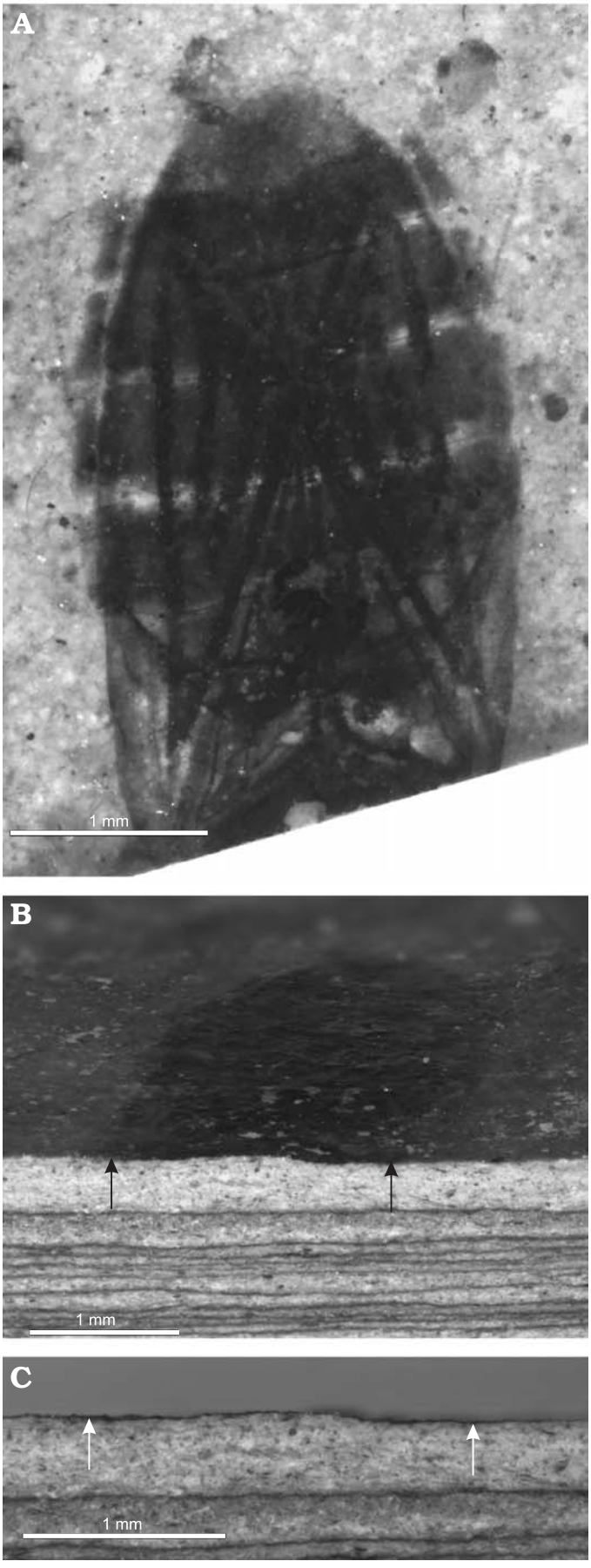


Fig. 12. A varve surface in shale (USNM 560104) from the Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA, in which the fossilized microbial mat contains a water boatman (Hemiptera: Corixidae). **A**. A photograph of the fossil corixid immersed in ethanol. **B**. An oblique view of a cross-section of the dry specimen. Note the varves of widely variable thickness. The corixid (between the arrows) is on the surface of the rhythmite within the microbial mat. **C**. Cross-section showing the only slightly thickened mat at the site of the corixid fossil (arrows).

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Varve structure and microbial mats.—The classic varve structure, as originally defined for glacial lakes, consists of a light/dark couplet in which the light layer contains coarse silt and fine sand deposited in the spring and summer (e.g., carried by meltwater) and a thinner dark layer of clay and fine silt that accumulated during the during winter season. However, there are many other types of varves and a great deal of variation in their structure exists (Anderson and Dean 1988). Many of the varves of the early Eocene Green River Formation consist of calcite muds with thin dark winter layers of fine sediments and thicker lighter summer layers of sediments (Bradley 1930). Some North American Lagerstätte (e.g., Florissant, Horsefly, and Canyon Ferry) are characterized by alternating light diatomaceous and darker clay laminae (McLeroy and Anderson 1966; O'Brien et al. 2008). The diatomaceous laminae, which contain easily recognized diatom frustules assumed to originate in one or more spring and summer algal blooms, constitute microbial "mats". Varves of the Coal Creek shale do not contain frustules as evidenced by scanning electron microscopy in both this and a previous study (Greenwalt et al. 2013; Figs. 5–7). However, the presence of multiple carbonaceous layers within the uppermost thin dark lamina, and polyaromatic hydrocarbons confined to this same uppermost dark layer, are suggestive of compressed and fossilized mats derived from multiple microbial blooms. Such sequential blooms of plankton have been shown to be preserved as individual microlaminae in varves from other lacustrine environments (Dickman 1985).

The presence of distinct layers of calcite in lacustrine varves is not uncommon in the fossil record (Anderson and Dean 1988) and, in this case, may also be indicative of algal or cyanobacterial blooms. The homogeneous layer of calcite immediately below the mat is assumed to have originated as a "whiting" event (i.e., a massive precipitation of calcite) induced by warming spring temperatures and/or the growth of algae and/or cyanobacteria (Dittrich and Obst 2004; Obst et al. 2009). The precipitation of the calcite appears to have occurred over a short period of time as evidenced by the homogeneity (i.e., lack of other clastic components) of the layer. The presence of the calcite layer itself may indicate a relatively shallow depositional setting. In a deep stratified lake, the calcite would be expected to dissolve in the colder waters of the hypolimnion. Katz and Nishri (2013), however, have found partially dissolved ("pitted") calcite crystals in the hypolimnion of the Dead Sea, an indication that such dissolution is not always complete. Below the calcite layer is a heterogeneous layer of fine-grained, primarily siliceous clasts, which is usually the thickest of the varve's component laminae. This layer is thought to consist of wind-blown siliciclastic grains of either tephra or loess from the higher elevations that surrounded the lake; their angular to subangular structure does not support their deposition by flowing water. The widespread belt of volcanoes in the Challis magmatic belt were coeval with the Coal Creek Member (Janecke and Snee 1993; Dudas et al. 2010).

Scanning electron microscopy of the fossiliferous shale from the Florissant and other sites show fossilized insects enveloped both by frustules and strands of mucilaginous secretions (EPS or extracellular polymeric substance) (Harding and Chant 2000; O'Brien et al. 2002, 2008). O'Brien et al. (2002) postulated a "microbial mucilage mechanism" in which the biofilm created by the diatoms and their EPS are essential to the superior preservation of the insects. Although the possibility that the presence of a biofilm is simply coincidental has been proposed (Thoene-Henning et al. 2012), the taphonomic role(s) of biofilms has gained wide-spread support (Wilby et al. 1996; Dunn et al. 1997; Harding and Chant 2000; Gall 2001; O'Brien et al. 2002, 2008; Peñalver et al. 2002; Archibald and Makarkin 2006; Allison et al. 2008; Iniesto et al. 2013). The fossilized mats form the bedding planes of the Florissant shale, as they do in the Coal Creek Member oil shale and it is within this layer that the fossil insects are found (Harding and Chant 2000; O'Brien et al. 2002, 2008; Figs. 12, 13). The fossilized mats in the oil shale of the Coal Creek Member do not contain diatom frustules and are not the product of diatom blooms. However, blooms of freshwater cyanobacteria also produce mats that secrete large quantities of mucopolysaccharides and it is this "sticky" material that is thought to capture, entrap, and "stabilize" insects that are blown onto or alight on the mat's surface (Seilacher et al. 1985). Such mat-mediated stabilization is also thought to prevent disarticulation during transport of the insect to the lake's bottom (Harding and Chant 2000; Meyer 2003). The microbial mats may protect the entrapped insects from predation and the mucopolysaccharides may have an antibacterial function although there is no experimental data that demonstrates such activity (Gall 1990; Dunn et al. 1997; Martinez-Delclòs et al. 2004).

Table 1. Factors that may define the depositional environment of insects preserved as fossils in lacustrine-derived shale.

Taphonomic characteristic	Water depth	References
Terrestrial insects with weak flying ability	shallow/nearshore	Wilson 1980
Low degree of disarticulation	deep/offshore	Wilson 1980, 1982
Lack of bioturbation	deep/offshore	Wilson 1977
Aquatic and immature (autochtonous) insects	shallow/nearshore	Penalver and Gaudant 2010
Presence of coprolites (without fish bones)	shallow/nearshore	Wilson 1980; but see Richter and Wedmann 2005
Presence of small fish	shallow/nearshore	Wilson 1980, 1988
High diversity	shallow/nearshore	Wilson 1980, 1982
Large winged insects/alates	deep/offshore	Rust 2000; Wilson 1982

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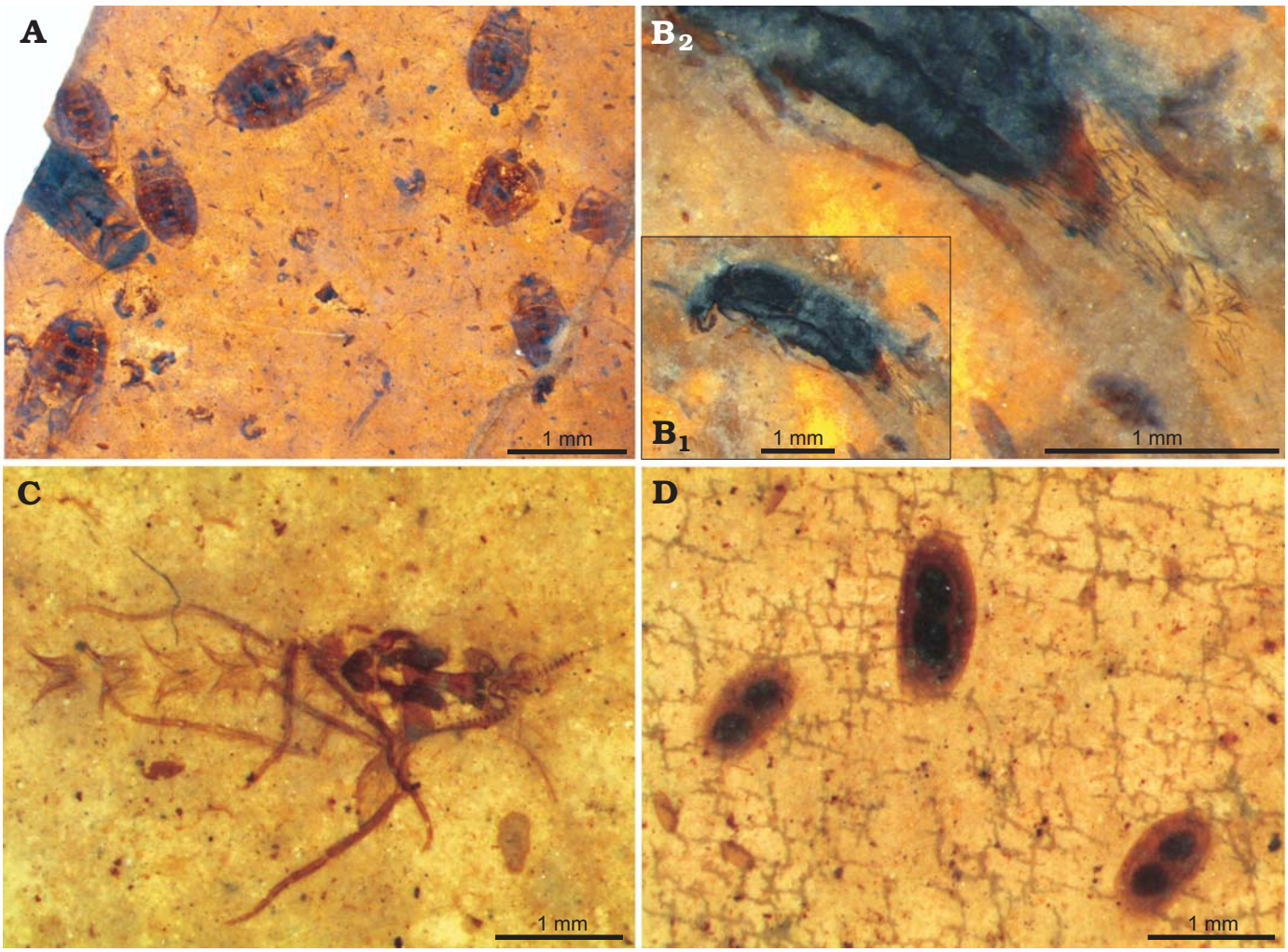


Fig. 13. Examples of preserved insect behavior with taphonomic implications in shales from the Coal Creek member of the Kishenehn Formation, Eocene, Montana, USA. **A**. A micrograph of an adult water boatmen (Hemiptera: Corixidae) (USNM 559597) surrounded by eight corixid nymphal exuviae on the surface of a microbial mat. **B**. A rove beetle (Coleoptera: Staphylinidae) (USNM 559598) within a microbial mat (B_1), enlargement (B_2). The legs of the insect are swept posteriorly and numerous setae have been torn from the posterior portion of the abdomen. **C**. An adult midge (Diptera: Chironomidae?) (USNM 553696) in the process of emerging from its pupal exuvium (from Greenwalt and Labandeira 2013). **D**. Ephippia of *Daphnia* (*Ctenodaphnia*) sp. (USNM 595136).

Several studies of the organic geochemistry of the rocks, including the oil shales, in the Coal Creek Member of the Kishenehn formation have been performed (Curiale 1987, 1988; Curiale et al. 1988). In these studies biomarkers such as botryococcane, considered to be derived from the freshwater microalgae *Botryococcus braunii* (Moldown et al. 1985; McKirdy et al. 1986), and C28–C30 5α(H)-4-methylsteranes, biomarkers for dinoflagellates (Robinson 1984), were found. While this suggests that algae-based mats existed in the Coal Creek member of the Kishenehn basin, the lack of frustules in the oil shales indicate that they were not diatomaceous in nature; whether they were cyanobacteria or non-diatomaceous green algae has yet to be determined. In addition to algal biomarkers, terrestrial biomarkers such as onocerane were detected in the Coal Creek shale (Curiale 1988). The high total organic content (>6%) and high hydrogen index (>800 mg/g) of the rocks of the Coal Creek Member indicate high productivity and anoxic conditions during deposition of these sediments (Demaison and Moore 1980; Curiale et al. 1988). High productivity combined with anoxia have been shown to be an important factor in the preservation of organic rich rocks (Peters et al. 2005). The rocks of Coal Creek Member of the Kishenehn Formation contain type 1 kerogens which have been classified as thermally immature by vitrine reflectance (VR = 0.33 – 0.44%). The low maturity of the rocks has been further confirmed by terpenoid biomarker ratios (Curiale 1988; Curiale et al. 1988). Low maturity is an important factor in the preservation potential of both fossils and biomolecules (e.g., eumelanin) (McNamara et al. 2012; Glass et al. 2013). The preservation of heme and heme-derived porphyrin fragments in a fossil blood-engorged mosquito from the Coal Creek Member may be related to the low thermal maturity of this oil shale (Greenwalt et al. 2013).

There is no agreement as to whether microbial mats or their precursors first interact with insects at the water's sur-

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face, within the water column or at the bottom of the lake; at different times and in different environments, all three may be involved. Again, there are no published experimental data that address this question. This point is of particular importance as mats that entrap insects at the lake's bottom would extend the temporal window for the preservation of insects. If entrapment occurred only during periods in which surface blooms secreted large amounts of mucopolysaccharides in response to overgrowth-induced stress, the time available for the "sampling" of the native insect population would be greatly restricted (Archibald et al. 2010). This effect decreases, however, with the production of multiple sequential microbial blooms within a single season. Data from the present study can be interpreted as supporting both surface mat-insect and bottom mat-insect interactions. Water boatmen (Corixidae) typically inhabit shallow/nearshore waters and come to the water surface only very briefly to replenish their air supply (Stonedahl and Lattin 1986). The large number of corixid exuviae found in the Coal Creek Member fossilized mats suggests that mats entrapped these specimens at the bottom of the lake. Similarly, *Daphnia* would not be expected to release egg capsules on the surface of a floating mat. On the other hand, the very small rove beetle (Staphylinidae) depicted in Fig. 13B appears to have been alive and attempting to escape a mat's sticky surface, an activity likely to have occurred on the water's surface; experimental studies have demonstrated that insects die on the water's surface prior to sinking (Martinez-Delclòs and Martinell 1993).

Peñalver (2002) and Peñalver et al. (2002) have argued that the mats can't be either surface or subsurface as the mat, in sinking to the bottom, would disintegrate and result in a chaotic array of fossil insect positions not observed in the fossils themselves. In addition, they argue that, if completely enveloped within a surface mat, disarticulation patterns observed in the fossils from the Rubielos de Mora Basin would not be possible. Others, however, contend that photosynthetic mats could not grow on a lake's anoxic bottom (Harding and Chant 2000). The assumed need for an anoxic environment often conflicts with evidence of a shallow depositional environment. This conundrum has often been resolved by proposals that, while shallow, the waters are toxic and/or saline, and exclude life forms that would prey on and/or decompose the insects at a mat's surface. The lack of diversity in the Bicorb Basin and the Solite sites is not thought to be due to deep water but rather shallow saline/brackish water (Liutkus et al. 2010; Peñalver and Gaudant 2010). Such extreme environments may also explain the lack of bioturbation that is seen in other Lagerstätte thought to have been deposited in shallow waters. On the other hand, numerous large (>2 cm) well preserved wings of palaeontinids (Hemiptera: Cicadomorpha) occur amongst fossil clam shrimps (Crustacea: Branchiopoda: Conchostraca) in the Middle Jurassic Daohugou site (Jiulongshan Formation) thought to have been deposited in shallow freshwater (Wang et al. 2013). Extant clam shrimps are filter feeders/scavengers commonly found in ephemeral bodies of fresh water; they can be associated with algal mats or burrowed in mud (Frank 1988). Ostracods, most extant species of which live either on or in the surface sediments, are present in the Coal Creek Member shales. Again, the quandary here is that the anoxia-based lack of bioturbation required for the preservation of these fossils would not be expected to exist in a shallow fresh water environment that contained numerous scavengers.

Although Demaison and Moore (1980) suggested that the middle sequence of the Coal Creek member was deposited in an anoxic environment, the gastropod fauna of the Coal Creek Member is distinctly fresh water in nature (Pierce and Constenius 2001, 2014). A possible explanation for the preservation of insects entrapped in microbial mats at the bottom of a shallow lake is based on observations of the structure of cyanobacterial mats. While photosynthetic bacteria compose the uppermost layers of the mat, the oxygen content decreases to zero at depths within the mat of as little as 2–5 mm (Gerdes et al. 1991; Kühl and Fenchel 2000; Fourcans et al. 2004). This observation, combined with the ability of the cyanobacterial fauna that constitute the mat to move and grow quickly (Castenholz 1969), suggests that entrapped insects can quickly become buried within the mat to a point where oxidative decomposition is not a factor.

Conclusions

The fossil insect fauna of the Coal Creek Member of the Kishenehn Formation exhibit exceptional preservation and contain numerous very small insects that are not found in most existing Lagersättten. Their preservation appears to have occurred in a shallow nearshore lacustrine depositional environment as evidenced by a preponderance of small autochthonous aquatic insects, both adult and immature, low levels of insect disarticulation, the presence of small fish and their coprolites, high diversity (15 different insect orders) and preservation of the egg cases of *Daphnia*. Coal Creek Member oil shale varve structures consist of windblown siliciclastic deposits and seasonal accumulations of non-diatomaceous, possibly cyanobacterial, microbial mats which are preserved, in part, as polyaromatic hydrocarbon-containing carbonaceous laminae. These microbial mats are characterized by an absence of perturbation and appear to have been integral to the taphonomic processes involved in preservation of the insects. Evidence suggests that cyanobacterial mats were present, and functioned to envelop insects, both on the surface of the water and at the bottom sediment's surface. Unresolved is the seemingly conflicting existence of a shallow freshwater depositional setting and the near total absence of bioturbation. The presence of discrete layers of calcite in some of the shale, the presumed product of seasonal warming-induced precipitation of calcium carbonate, and numerous *Ctenodaphnia* egg cases provides evidence of both

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a shallow depositional environment and photoperiod seasonality. Further studies of the chemical constituents of the mat layers as well as experimental in vitro and in vivo studies of insect entrapment by such mats is required.

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References

Allison, P.A., Maeda, H., Tuzino, T., and Maeda, Y. 2008. Exceptional preservation within Pleistocene lacustrine sediments of Shiobara, Japan. *Palaios* 23: 260–266.

Anderson, R.Y. and Dean, W.E. 1988. Lacustrine varve structure through time. *Palaeogeography, Palaeoclimatology, Palaeoecology* 62: 215–235.

Archibald, S.B. and Makarkin, V.N. 2006. Tertiary giant lacewings (Neuroptera: Polystoechotidae): Revision and description of new taxa from western north America and Denmark. *Journal of Systematic Palaeontology* 4: 119–155.

Archibald, S.B., Bossert, W.H., Greenwood, D.R., and Farrell, B.D. 2010. Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology* 36: 374–398.

Archibald, S.B., Greenwood, D.R., and Mathewes, R.W. 2013. Seasonality, montane beta diversity, and Eocene insects: Testing Janzen's dispersal hypothesis in an equable world. *Palaeogeography, Palaeoclimatology, Palaeoecology* 371: 1–8.

Benzie, J.A.H. 2005. *The Genus* Daphnia *(including* Daphniopsis*) (Anomopoda: Daphniidae)*. 376 pp. Backhuys Publishers, Leiden.

Bradley, W.H. 1930. The varves and climate of the Green River Epoch. *U.S. Geological Survey Professional Paper* 158: 87–110.

Carroll, A.R. and Bohacs, K.M. 2001. Lake-type controls on petroleum source rock potential in nonmarine basins. *American Association of Petroleum Geologists Bulletin* 85: 1033–1054.

Castenholz, R.W. 1969. The thermophilic cyanophytes of Iceland and their upper temperature limit. *Journal of Phycology* 5: 360–368.

Clapham, M.E. 2013. Taxonomic occurrences recorded in the Paleobiology Database. *Fossilworks*. http://fossilworks.org (accessed 5 November 2013).

Colbourne, J.K., Hebert, P.D.N., and Taylor, D.J. 1997. Evolutionary origins of phenotypic diversity in *Daphnia. In*: T.J. Givnish and K.J. Sytsma (eds.), *Molecular Evolution and Adaptive Radiation*, 163–188. Cambridge University Press, Cambridge.

Constenius, K.N. 1981. *Stratigraphy, Sedimentation, and Tectonic History of the Kishenehn Basin, Northwestern Montana*. 116 pp. Unpublished M.Sc. Thesis, University of Wyoming, Laramie.

Constenius, K.N. 1996. Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. *Geological Society of America Bulletin* 108: 20–39.

Constenius, K.N., Dawson, M.R., Pierce, H.G., Walter, R.C., and Wilson, M.V.H. 1989. Reconnaissance paleontologic study of the Kishenehn Formation, northwestern Montana and southeastern British Columbia. *In:* D.E. French and R.F. Grabb (eds.), *1989 Field Conference Guidebook: Montana Centennial Edition, Vol. 1,* 189–203. Geological Resources of Montana, Billings.

Curiale, J.A. 1987. Steroidal hydrocarbons of the Kishenehn Formation, northwestern Montana. *Organic Geochemistry* 11: 233–244.

Curiale, J.A. 1988. Molecular genetic markers and maturity indices in intermontane lacustrine facies: Kishenehn Formation, Montana. *Organic Geochemistry* 13: 633–638.

Curiale, J.A., Sperry, S.W., and Senftle, J.T. 1988. Regional source rock potential of Oligocene Kishenehn Formation, northwestern Montana. *American Association of Petroleum Geologists Bulletin* 72: 1437–1449.

Daley, B. 1972. Some problems concerning the early Tertiary climate of southern England. *Palaeogeography, Palaeoclimatology, Palaeoecology* 11: 177–190.

Daley, B. 1973. The palaeoenvironment of the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire. *Proceedings of the Geologists' Association* 84: 83–93.

Demaison, G.J., and Moore, G.T. 1980. Anoxic environments and oil source bed genesis. *Organic Geochemistry* 2: 9–31.

Dickman, M. 1985. Seasonal succession and microlaminae formation in a meromictic lake displaying varved sediments. *Sedimentology* 32: 109–118.

Dittrich, M. and Obst, M. 2004. Are picoplankton responsible for calcite precipitation in lakes? *Ambio* 33: 559–564.

Dudas, F.O., Isolatov, V.O., Harlan, S.S., and Snee, L.W. 2010. $^{40}Ar/^{39}Ar$ geochronology and geochemical reconnaissance of the Eocene Lowland Creek volcanic field, west-central Montana. *Journal of Geology* 118: 295–304.

Dunn, K.A., McLean, R.J.C., Upchurch, G.R., Jr., and Folk, R.L. 1997. Enhancement of leaf fossilization potential by bacterial biofilms. *Geology* 25: 1119–1122.

Fourcans, A., de Oteyza, T.G., Wieland, A., Solé, A., Diestra, E., van Bleijswijk, J., Grimalt, J. O., Kühl, M., Esteve, I., Muyzer, G., Caumette, P., and Duran, R. 2004. Characterization of functional bacterial groups in a hypersaline microbial mat community (Salins-de-Giraud, Camargue, France). *Federation of European Microbiological Societies, Microbiology Ecology* 51: 55–70.

Frank, P.W. 1988. Conchostraca. *Palaeogeography, Palaeoclimatolgy and Palaeoecology* 62: 399–403.

Gall, J.-C. 1990. Les voiles microbiens, Leur contribution à la fossilisation des organismes de corp mou. *Lethaia* 23: 21–28.

Gall, J.-C. 2001. Role of microbial mats. *In*: D.E.G. Briggs and P.R. Crowther (eds.), *Palaeobiology 2*, 280–284. Blackwell Scientific, Oxford.

Gerdes, G., Krumbein, W.E., and Reineck, H.-E. 1991. Biolaminations—ecological versus depositional dynamics. *In*: G. Einsele, W. Ricken, and A. Seilacher (eds.), *Cycles and Events in Stratigraphy*, 592–607. Springer-Verlag, Heidelberg.

Gierlowski-Kordesch, E.H. and Park, L.E. 2004. Comparing species diversity in the modern and fossil record of lakes. *Journal of Geology* 112: 703–717.

Glass, K., Ito, S., Wilby, P.R., Sota, T., Nakamura, A., Bowers, C.R., Miller, K.E., Dutta, S., Summons, R.E., Briggs, D.E.G., Wakamatsu, K., and Simon, J.D. 2013. Impact of diagenesis and maturation on the survival of eumelanin in the fossil record. *Organic Geochemistry* 64: 29–37.

Greenwalt, D. and Labandeira, C. 2013. The Amazing Fossil Insects of the Eocene Kishenehn Formation in NW Montana. *Rocks and Minerals* 88: 434–441.

Greenwalt, D. and Rust, J. 2014. A new species of *Pseudotettigonia* Zeuner 1937 (Orthoptera: Tettigoniidae) with an intact stridulatory field and a revision of the subfamily Pseudotettigoniinae. *Systematic Entomology* 39: 256–263.

Greenwalt, D.E., Goreva, Y., Siljeström, S., Rose, T., and Harbach, R.E.

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2013. Hemoglobin-derived porphyrins preserved in a Middle Eocene blood-engorged mosquito. *Proceedings of the National Academy of Sciences* 110: 18496–18500.

Gregory, K.M. and McIntosh, W.C. 1996. Paleoclimate and paleoelevation of the Oligocene Pitch-Pinnacle flora, Sawatch Range, Colorado. *Geological Society of America Bulletin* 108: 545–561.

Grimaldi, D. and Engel, M.S. 2005. *Evolution of the Insects*. 755 pp. Cambridge University Press, New York.

Grimaldi, D.A., Engel, M.S., and Nascimbene, P.C. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361: 1–71.

Grimaldi, D.A., Shedrinsky, A., and Wampler, T.P. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. *In*: D. Grimaldi (ed.), *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*, 1–76. Backhuys, Leiden.

Groves, C. and Shekelle, M. 2010. The genera and species of Tarsiidae. *International Journal of Primatology* 31: 1071–1082.

Harbach, R.E. and Greenwalt, D.E. 2012. Two Eocene species of *Culiseta* (Diptera: Culicidae) from the Kishenehn Formation in Montana. *Zootaxa* 3530: 25–34.

Harding, I.C. and Chant, L.S. 2000. Self-sedimented diatom mats as agents of exceptional fossil preservation in the Oligocene Florissant lake beds, Colorado, United States. *Geology* 28: 195–198.

Huber, M. and Caballero, R. 2011. The early Eocene equable climate problem revisited. *Climate of the Past Discussions* 7: 603–633.

Huber, J.T. and Greenwalt, D.E. 2011. Compression fossil Mymaridae (Hymenoptera) from Kishenehn oil shales, with description of two new genera and review of Tertiary amber genera. *ZooKeys* 130: 473–494.

Huggert, L. 1979. Cryptoserphus and Belytinae wasps (Hymenoptera, Proctotrupoidea) parasitizing fungus- and soil-inhabiting Diptera. *Notulae Entomologicae* 59: 139–144.

Iniesto, M., Lopez-Archilla, A.I., Fregenal-Martínez, M., Buscalioni, A.D., and Guerrero, M.C. 2013. Involvement of microbial mats in delayed decay: an experimental essay on fish preservation. *Palaios* 28: 56–66.

Ivarsson, M., Broman, C., Sturkell, E., Ormö, J., Siljeström, S., van Zuilen, M., and Bengtson, S. 2013. Fungal colonization of an Ordovician impact-induced hydrothermal system. *Scientific Reports* 3: 3487–3492.

Janecke, S.U. and Snee, L.W. 1993. Timing and episodicity of middle Eocene volcanism and onset of conglomerate deposition, Idaho. *Journal of Geology* 101: 603–621.

Katz, A. and Nishri, A. 2013. Calcium, magnesium and strontium cycling in stratified, hardwater lakes: Lake Kinneret (Sea of Galilee), Israel. *Geochimica et Cosmochimica Acta* 105: 372–394.

Kleiven, O.T., Larsson, P., and Hobaek, A. 1992. Sexual reproduction in *Daphnia magna* requires three stimuli. *Oikos* 65: 197–206.

Kühl, M. and Fenchel, T. 2000. Bio-optical characteristics and the vertical distribution of photosynthetic pigments and photosynthesis in an artificial cyanobacterial mat. *Microbial Ecology* 40: 94–103.

Liutkus, C.M., Beard, J.S., Fraser, N.C., and Ragland, P.C. 2010. Use of fine-scale stratigraphy and chemostratigraphy to evaluate conditions of deposition and preservation of a Triassic Lagerstatte, south-central Virginia. *Journal of Paleolimnology* 44: 645–666.

Lutz, H. 1988. Riesenameisen und andere Raritaten–die Insektenfauna. *In*: S. Schaal and W. Ziegler (eds.), *Messel–Ein Schaufenster in die Geschichte der Erde und des Lebens*, 55–67. Verlag Waldemar Kramer, Frankfurt.

Lutz, H. 1997. Taphozönosen terrestrischer Insekten in aquatischen Sedimenten—ein Beitrag zur Rekonstruktion des Paläoenvironments. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 203: 173–210.

Martinez-Delclòs, X. and Martinell, J. 1993. Insect taphonomy experiments: their application to the Cretaceous outcrops of lithographic limestones from Spain. *Kaupia* 2: 133–144.

Martinez-Delclòs, X., Briggs, D.E.G, and Peñalver, E. 2004. Taphonomy of insects in carbonates and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203: 19–64.

McKenna, M.C. 1990. Plagiomenids (Mammalia: ?Dermoptera) from the Oligocene of Oregon, Montana and South Dakota, and Middle Eocene of northwestern Wyoming. *In*: T.M. Brown and K.D. Rose (eds.), Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior, North America. *Geological Society of America, Special Paper* 243: 211–234.

McKirdy, D.M., Cox, R.E., Volkman, J.K., and Howell, V.J. 1986. Botryococcane in a new class of Australian non-marine crude oils. *Nature* 320: 57–59.

McLeroy, C.A. and Anderson, R.Y. 1966. Laminations of the Oligocene Florissant lake deposits, Colorado. *Geological Society of America Bulletin* 77: 605–618.

McNamara M.E., Briggs, D.E.G., and Orr, P.J. 2012. The controls on the preservation of structural color in fossil insects. *Palaios* 27: 443–454.

Meyer, H.W. 2003. *The Fossils of the Florissant*. 258 pp. Smithsonian Books, Washington, D.C.

Mitchell, A.A. 2013. *EDNA, The Fossil Insect Database.* http//edna.palasshosting.org (accessed 5 November 2013).

Moldowan, J.M., Seifert, W.K., and Gallegos, E.J. 1985. Relationship between petroleum composition and depositional environment of petroleum source rocks. *American Association of Petroleum Geologists Bulletin* 69: 1255–1268.

Ni, X., Meng, J., Beard, K.C., Gebo, D.L., Wang, Y., and Li, C. 2010. A new tarkadectine primate from the Eocene of Inner Mongolia, China: phylogenetic and biogeographic implications. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 277: 247–256.

O'Brien, N.R., Meyer, H.W., and Harding, I.C. 2008. The role of biofilms in fossil preservation, Florissant Formation, Colorado. *In:* H.W. Meyer and D.M. Smith (eds.), Paleontology of the Upper Eocene Florissant Formation, Colorado. *Geological Society of America Special Paper* 435: 19–31.

O'Brien, N.R., Meyer, H.W., Reilly, K., Ross, A.M., and Maguire, S. 2002. Microbial taphonomic processes in the fossilization of insects and plants in the late Eocene Florissant Formation, Colorado. *Rocky Mountain Geology* 37: 1–11.

Obst, M., Wehrli, B., and Dittrich, M. 2009. $CaCO_3$ nucleation by cyanobacteria: laboratory evidence for a passive, surface-induced mechanism. *Geobiology* 7: 324–347.

Peñalver, E. 2002. *Los insectos dípteros del Mioceno del Este de la Península Ibérica; Rubielos de Mora, Ribesalbes y Bicorp. Tafonomía y sistemática*. 550 pp. Ph.D. Thesis, Universitat de València, Valencia.

Peñalver, E. and Engel, M. 2006. Two wasp families rare in the fossil record (Hymenoptera): Perilampidae and Megaspilidae from the Miocene of Spain. *American Museum Novitates* 3540: 1–12.

Peñalver, E. and Gaudant, J. 2010. Limnic food web and salinity of the Upper Miocene Bicorb palaeolake (eastern Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 297: 683–696.

Peñalver, E., Martínez-Delclòs, X., and De Renzi, M. 2002. Evidence of continental microbial mats based on the study of fossil insects—examples from two Spanish Konservat Fossil-Lagerstätten. *In*: M. De Renzi, M. Pardo, M. Belinchón, E. Peñalver, P. Montoya, and A. Márquez-Aliaga (eds.), *Current Topics on Taphonomy and Fossilization*, 281–287. Ayuntamiento de Valencia, Valencia.

Penney, D. 2010. *Biodiversity of Fossils in Amber from the Major World Deposits*. 305 pp. Siri Scientific Press, Manchester.

Peters, K., Walters, C., and Moldowan, M. 2005. *The Biomarker Guide. 2nd ed*. 471 pp. Cambridge University Press, Cambridge.

Petrulevicius, J.F. 2005. A plant hopper (Nogodinidae) from the Upper Palaeocene of Argentina: systematics and taphonomy. *Palaeontology* 48: 299–308.

Pierce, H.G. and Constenius, K.N. 2001. Late Eocene–Oligocene nonmarine mollusks of the northern Kishenehn Basin, Montana and British Columbia. *Annals of the Carnegie Museum* 70: 1–112.

Pierce, H.G. and Constenius, K.N. 2014. Terrestrial and aquatic mollusks of the Eocene Kishenehn Formation, Middle Fork Flathead River, Montana. *Annals of the Carnegie Museum* 82: 305–329.

Poinar, G., Jr., Archibald, B., and Brown, A. 1999. New amber deposit pro-

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vides evidence of early Paleogene extinctions, paeloclimates and past distributions. *The Canadian Entomologist* 131: 171–177.
Richter, G. and Wedmann, S. 2005. Ecology of the Eocene Lake Messel revealed by analysis of small fish coprolites and sediments from a drilling core. *Palaeogeography, Palaeoclimatology, Palaeoecology* 223: 147–161.
Robinson, N., Eglinton, G., Brassell, S.C., and Cranwell, P.A. 1984. Dinoflagellate origin for sedimentary 4α-methylsteroids and 5α (H)-stanols. *Nature* 308: 439–442.
Rust, J. 2000. Fossil record of mass moth migration. *Nature* 405: 530–531.
Schulz, R., Harms, F.-J., and Felder, M. 2002. Die Forschungsbohrung Messel 2001: Ein Beitrag zur Entschlüsselung der Genese einer Ölschieferlagerstätte. *Zeitschrift für Angewandte Geologie* 4: 9–17.
Scudder, S.H. 1890a. The fossil insect localities in the Rocky Mountain region. *Psyche* 5: 363.
Scudder, S.H. 1890b. *The Tertiary Insects of North America. United States Geological Survey of the Territories*. 734 pp. United States Geological Survey, Washington, D.C.
Seilacher, A., Reif, W.-E., Westphal, F., Riding, R., Clarkson, E.N.K., and Whittington, H.B. 1985. Sedimentological, ecological and temporal patterns of Fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London B* 311: 5–24.
Shockley, F.W. and Greenwalt, D.E. 2013. *Ptenidium kishenehnsis*, a new fossil described from the Kishenehn oil shales (Coleoptera: Ptiliidae), with a checklist of previously known fossil ptiliids. *Proceedings of the Entomological Society of Washington* 115: 173–181.
Siljeström, S., Hode, T., Lausmaa, J., Sjövall, P., Toporski, J., and Thiel, V. 2009. Detection of organic biomarkers in crude oils using ToF-SIMS. *Organic Geochemistry* 40: 135–143.
Siljeström, S., Volk, H., George, S.C., Lausmaa, J., Sjövall, P., Dutkiewicz, A., and Hode, T. 2013. Analysis of single oil-bearing fluid inclusions in mid-Proterozoic sandstones (Roper Group, Australia). *Geochimica et Cosmochimica Acta* 122: 448–463.
Smith, D. 2000. Beetle taphonomy in a recent ephemeral lake, southeastern Arizona. *Palaios* 15: 152–160.
Smith, D. 2006. How physical characteristics of beetles affect their fossil preservation. *Palaios* 21: 305–310.
Smith, D. 2012. Exceptional preservation of insects in lacustrine environments. *Palaios* 27: 346–353.
Smith, D. and Moe-Hoffman, A.P. 2007. Taphonomy of Diptera in lacustrine environments: a case study from Florissant fossil beds, Colrado. *Palaios* 22: 623–629.
Stephan, T., Jessberger, E.K., Heiss, C.H., and Rost, D. 2003. TOF-SIMS analysis of polycyclic aromatic hydrocarbons in Allan Hills 84001. *Meteoritics and Planetary Science* 38: 109–116.
Stonedahl, G.M. and Lattin, J.D. 1986. The Corixidae of Oregon and Washington (Hemiptera: Heteroptera). *Oregon State University Agricultural Experiment Station Technical Bulletin* 150: 1–83.
Stross, R.G. and Hill, J.C. 1965. Diapause induction in *Daphnia* requires two stimuli. *Science* 150: 1463–1464.
Thoene Henning, J., Smith, D.M., Nufio, C.R., and Meyer, H.W. 2012. Depositional setting and fossil insect preservation: A study of the late Eocene Florissant Formation, Colorado. *Palaios* 27: 481–488.
Tsujino, T. and Maeda, H. 1999. Stratigraphic and taphonomic features of diatomaceous shale of the Pleistocene Shiobara Group in Tochigi, Japan. *Bulletin of the National Science Museum, Tokyo, Series C* 25: 73–104.
Wagner, T., Neinhuis, C., and Barthlott, W. 1996. Wettability and contaminability of insect wings as a function of their surface sculptures. *Acta Zoologica* 77: 213–225.
Wang, B., Zhang, H., Jarzembowski, A.E., Fang, Y., and Zheng, D. 2013. Taphonomic variability of fossil insects: A biostratinomic study of Palaeontinidae and Tettigarctidae (Insecta: Hemiptera) from the Jurassic Daohugou Lagerstätte. *Palaios* 28: 233–242.
Wappler, T. 2003. Systematik, Phylogenie, Taphonomie und Paläoökologie der Insekten aus dem Mittle-Eozän des Eckfelder Maares Vulkaneifel. *Clausthaler Geowissenschaften* 2: 1–241.
Wilby, P.R., Briggs, D.E.G., Bernier, P., and Gaillard, C. 1996. Role of microbial mats in the fossilization of soft tissues. *Geology* 24: 787–790.
Wilson, M.V.H. 1977. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. *Canadian Journal of Earth Sciences* 14: 953–962.
Wilson, M.V.H. 1978. Paleogene insect faunas of western North America. *Quaestiones Entomologicae* 14: 13–34.
Wilson, M.V.H. 1980. Eocene lake environments: depth and distance from shore variation in fish, insect and plant assemblages. *Palaeogeography, Palaeoclimatolgy, Palaeoecology* 32: 21–44.
Wilson, M.V.H. 1982. Early Cenozoic insects: paleoenvironmental biases and evolution of the North American insect fauna. *Proceedings of the Third North American Paleontological Convention* 2: 585–588.
Wilson, M.V.H. 1988. Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. *Palaeogeography, Palaeoclimatolgy, Palaeoecology* 62: 609–623.
Wilson, M.V.H. 1996. Insects near Eocene lakes of the interior. *In*: R. Ludvigsen (ed.), *Life in Stone, a Natural History of British Columbia's Fossils*, 225–233. The University of British Columbia Press, Vancouver.
Wolfe, J.A. 1995. Paleoclimatic estimates from Tertiary leaf assemblages. *Annual Review of Earth and Planetary Sciences* 23: 119–142.
Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.

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