Palaeoentomology 009 (2): 160–172
https://www.mapress.com/pe/

Article

ISSN 2624-2826 (print edition)
PALAEOENTOMOLOGY
ISSN 2624-2834 (online edition)

https://doi.org/10.11646/palaeoentomology.9.2.8
http://zoobank.org/urn:lsid:zoobank.org:pub:E7D52AE4-28D1-40DF-962A-E11012DF33A3

A comparison of insect disarticulation during simulated transport and implications for fossil preservation and identification

JOHNATHAN A. SORRENTINO[1, *], PETER R. LIBERTY[1], BRANDT M. GIBSON[2], CORENTIN JOUAULT[3], S. BRUCE ARCHIBALD[4] & MARC LAFLAMME[1]

[1]University of Toronto Mississauga, Department of Chemical and Physical Sciences, 3359 Mississauga Road, Mississauga, ON, L5L 1C6, Canada
[2]University of Tennessee Martin, Department of Agriculture, Geoscience, and Natural Resources, 554 University Street, Martin, TN, 38238, United States of America
[3]Oxford University Museum of Natural History, University of Oxford, Parks Road, Oxford OX1 3PW, UK
[4]University of British Columbia, Beaty Biodiversity Museum, Vancouver Campus, 2212 Main Mall, Vancouver, BC, V6T 1Z4, Canada
johnathan.sorrentino@mail.utoronto.ca; https://orcid.org/0009-0008-5553-1374
p.liberty@mail.utoronto.ca; https://orcid.org/0009-0003-7054-0870
bgibson@utm.edu; https://orcid.org/0000-0001-9620-0063
jouaultc0@gmail.com; https://orcid.org/0000-0002-3680-5172
bruce.archibald@ubc.ca; https://orcid.org/0000-0002-4397-2497
marc.laflamme@utoronto.ca; https://orcid.org/0000-0002-2679-705X
**Corresponding author*

Abstract

The fossil record represents a small fraction of what lived in ancient ecosystems. Transport, the carrying of organisms from their living environment to their burial environment, remains an enigmatic part of the fossilization process. We analyzed the effects of transport on the preservation potential of a wide variety of insects with different morphologies: *Camponotus* spp. (carpenter ants), *Bombus* spp. (bumblebees), *Polyommatus* spp. (butterflies), *Teleogryllus oceanicus* (oceanic house crickets), *Enallagma* spp. (blue damselflies) and Coccinellidae (ladybird beetles). Live specimens were placed in rotary tumblers with water and silt-sized silica sediment for 48 hours. Specimen vitality, buoyancy, and articulation were recorded every two hours to determine the relative preservation potential of these insects. We find that ants, bumblebees, crickets, and ladybird beetles are less likely to disarticulate to unidentifiable degrees—even under long transport times. In contrast, butterflies and damselflies disarticulate relatively rapidly. These results suggest that the more robust group of insects could be overrepresented in environments that would contain many transported specimens, such as fluvial, deltaic, and coastal marine.

Keywords: taphonomy, decay experiments, ants, bees, beetles, butterflies, crickets, damselflies, tumbling

Introduction

Insects are ubiquitous in modern ecosystems and have a vast fossil record stretching back to the Carboniferous approximately 325 million years ago (*e.g.*, Brauckmann & Schneider, 1996; Petrulevičius & Gutierrez, 2016). Given that most modern insects are restricted to specific environments, their distribution through time and space is useful to elucidate the formation and evolution of ancient ecosystems (Archibald *et al.*, 2010, 2014; Jouault *et al.*, 2021; Smith, 2012). However, taphonomic biases that control the mode, rate, and likelihood of insect fossilization can affect taxon representation and preservation quality in fossil assemblages, limiting the usefulness of fossil collections in reconstructing ancient communities (Martínez-Delclòs *et al.*, 2004; Smith, 2012; Álvarez-Parra *et al.*, 2022). Here, we aim to understand how transport processes affect insect preservation potential before fossilization, allowing for better interpretations of ancient ecosystems.

Given the absence of mineralized skeletons, insects are most commonly fossilized as carbonaceous compressions and in amber (Penney & Jepson, 2014); although, they can also be secondarily mineralized (Storari *et al.*, 2024), preserved as cast and molds (Clements *et al.*, 2019), and in tar (Holden *et al.*, 2017). For all soft-tissue fossilization pathways, organisms must be rapidly buried to prevent scavengers and microbial decay from removing them entirely from the fossil record (Briggs, 2003). This principle also applies to insects trapped in resin that later polymerizes into amber. Thus, sinking and rapid burial is important for fossil formation in

Submitted: 16 Oct. 2025; accepted by D.-Y. Huang: 15 Apr. 2026; published: 29 Apr. 2026

sedimentary facies representing a range of depositional environments, including coastal marine and lacustrine. The insects found in these facies are commonly (but not always) terrestrial and allochthonous to the interpreted depositional environment (Smith, 2000, 2012; Henning *et al*., 2012; Penney & Jepson, 2014). Therefore, the taphonomic pressures acting upon transportation from death to burial represent a pivotal control on the diversity and abundance of fossil insects found.

Current research on the effects of transportation on insect fossilization is limited. Smith *et al*. (2006) investigated the level of disarticulation of various beetles using a tumbler, Duncan *et al*. (2003) examined the possible sources of individual fossil cockroach wings using a rotary flume, and Storari *et al.* (2025) examined the disarticulation of larval (aquatic) mayflies and dragonflies using gentle hand vibrations. Laboratory experiments have targeted the disarticulation of other arthropods (*e.g*., shrimp; Allison, 1986), but these lack applicability to fossiliferous sites with a high interspecies diversity of terrestrial insects such as the Green River Formation or Menat Formation. Further, anatomical features that are important for taxonomic identification (*e.g*., wings, hind legs) can be highly specific and require more targeted experiments. Given the various factors that contribute to the eventual transport distance of an organism, it remains unclear what the full extent of the catchment area is for most, if not all, localities, as well as the level of damage experienced during transport (Behrensmeyer *et al*., 2000). Our experiments seek to examine the effects of simulated transport on a large variety of insects representing a broad range of tissue lability and level of anatomical articulation, making it possible to understand how our diverse insect collections are affected by transport prior to burial.

Material and methods

We monitored a diverse assortment of live insects in rotary tumblers partially filled with water and sediment to simulate transport in energetic aquatic environments (detailed below). Both turbulent water and added sediment contribute to the disarticulation of the insect. At each timepoint (every two hours for a total of 48 hours), we removed the insects from the tumblers, visually examined them, and scored their level of disarticulation (see Table 1). During scoring, each specimen spent ~10–20 minutes stationary as it was examined. During the examination we handled all specimens carefully; however, some unintended disarticulation was possibly due to the increasingly fragile state of the specimens. To reduce variation in human-induced disarticulation between trials, and to allow for relative comparisons between species, all insects were handled similarly. For full transparency, we noted when human manipulation may have resulted in additional disarticulation. Preliminary experiments (unpublished) examining the effects of human handling were conducted with both oceanic house crickets and bumblebees prior to the current study. Both experiments found a similar (low) level of disarticulation between specimens that were handled and those that were not handled. One exception was that crickets that had been handled showed ruptured abdomens, while crickets that had not been handled only showed deformed abdomens (see Table 1). Non-invasive imaging was not possible because sediment obscured our view of the insects while they were in the tumbler. Non-invasive photography conducted in our preliminary experiments with and without sediment was ineffective because the detailed anatomy of the insects was obscured by being tucked tightly against the body in response to tumbling. As such, all insects required minimal human disturbance between trials.

The addition of sediment in our tumbling experiments allowed for a closer resemblance to modern aqueous transport processes, and allowed for direct comparisons with Smith *et al*. (2006) whose research identified several trends in the disarticulation of beetles. Our tumbling setup represents a relatively high-energy transportation process such as a turbidite or fast flowing river, and therefore the inclusion of sediment was deemed reasonable despite its hindrance to photographic monitoring without human manipulation.

A morphological scoring system was used to examine the level of disarticulation of the tumbled insects (Table 1). In general, this system identifies the earliest time points when specific appendages become damaged and/or subsequently separated from the rest of the body. We considered the thorax to be the central component of the insect to which most other body parts are connected. Therefore, the disarticulation state of all other body parts is given with reference to the thorax. In addition to changes in morphological features, we noted the hour of death and sinking for each specimen. Although all data was collected directly from samples removed from the tumbler, photographs were also taken using a digital camera to highlight specific disarticulation states.

We selected six different types of terrestrial insects for their varied morphology and ease of collection (Fig. 1): *Camponotus* spp. (carpenter ants), *Bombus* spp. (bumblebees), *Polyommatus* spp. (butterflies), *Teleogryllus oceanicus* (oceanic house crickets), *Enallagma* spp. (blue damselflies) and Coccinellidae (ladybird beetles). We collected adult ladybird beetles at Woodbine Beach, Toronto, Canada, while adult butterflies, bumblebees, blue damselflies, and carpenter ants were collected in proximity to the University of Toronto Mississauga (UTM) campus. We collected worker ants and bees given their relative

TABLE 1. Categorical scoring system of insect disarticulation.

Category	Scoring	Description
Vitality	Alive	Some motion (leg twitching or wing flapping)
	Dead	No indication of movement
Buoyancy	Floating	Specimen remained at the surface
	Sunken	Specimen sank to the bottom
Colour Presence	Vibrant	All bright colours remain
	Fading	Colour from the exoskeleton has started to degrade
	Absent	All colour has left the exoskeleton except black stripes/patches
Abdomen Presence	Intact	The abdomen is fully intact and in life position
	Deformed	The abdomen is bulging or stretching
	Ruptured	There is a tear where the exoskeleton has ruptured
	Partial Loss	Part of the abdomen is missing
	Absent	The abdomen is disarticulated from the thorax
Prothorax Presence	Intact	Prothorax is pristine or in life position
	Damaged	Prothorax is stretched
	Absent	Prothorax has disarticulated from the rest of the thorax
Legs, Wings, Head, Antennae, Cerci, Ovipositor Presence	Intact	Body part is pristine or in life position
	Damaged	Body part is damaged, missing pieces, or frayed
	Absent	Body part is disarticulated from the thorax
Scale Presence	75–100%	Percentage of scales remaining (butterfly only)
	50–75%	
	25–50%	
	0–25%	

abundance, ease of collection, and broader applicability compared to fossil collections. The Biological Core Facilities at UTM bred oceanic house crickets in lab and provided our live adult specimens. Only female crickets were selected so that we could examine the preservation of the ovipositor, a key indicator of sex and useful for species identification.

We tumbled three individuals of each insect type with each individual occupying its own tumbler. We followed previous studies (*e.g*., Allison, 1988; Smith *et al*., 2006; Sansom *et al*., 2010, 2011; Iniesto *et al*., 2018, 2021; Newman *et al*., 2019; Gäb *et al*., 2020; Gibson *et al*., 2023; Mähler *et al.* 2023) by conducting all experiments in triplicate, thus allowing for better comparisons with these pioneering studies. This approach further allowed for a broader range of insect groups to be qualitatively compared. The qualitative and descriptive nature of the dataset allows for effective comparison with similar taphonomic experiments (Allison, 1988; Duncan *et al*., 2003; Butler *et al*., 2015; Bath Enright *et al*., 2017, 2021; Klompmaker *et al*., 2017; Gibson *et al*., 2023; Mähler *et al*., 2023), but the small sample sizes are inappropriate for direct statistical or quantitative comparisons.

We tumbled the insects in a VEVOR Jewelry Polisher Tumbler (Model Number: KD-68081) consisting of a hexagonal prism with a short diameter (*i.e*., from face to face) of 9.5 cm, face length of 6 cm, and prism length of 13 cm, and set to the lowest possible rotational speed. The rotational speed was consistent for individual tumblers across all experiments (±1 RPM) but varied between tumblers from 106±1 RPM to 124±1 RPM due to inherent equipment variability. At this rotational speed, the behaviour of the water-silt slurry is turbulent and corresponds to cataracting to centrifuging motion as described by Mellmann (2001).

We filled each tumbler with 500 mL of tap water that had been left out to degas for at least 24 hours. Additionally, we added 31.5 g of silt-sized silica sediment (99.7% SiO_2 and 97.8% finer than 45 μm; U.S. Silica Company SIL-CO-SIL® 45) to mimic the suspension of sediment in turbulent water. We used a similar sediment-water ratio as the beetle transport experiments conducted by Smith *et al.* (2006) to allow for comparison. While rotating, the sediment/water mixture behaves as a slurry, but when the tumbler is turned off, the silt settles to the bottom of the tumbler. The water-silt mixture is carried up and around

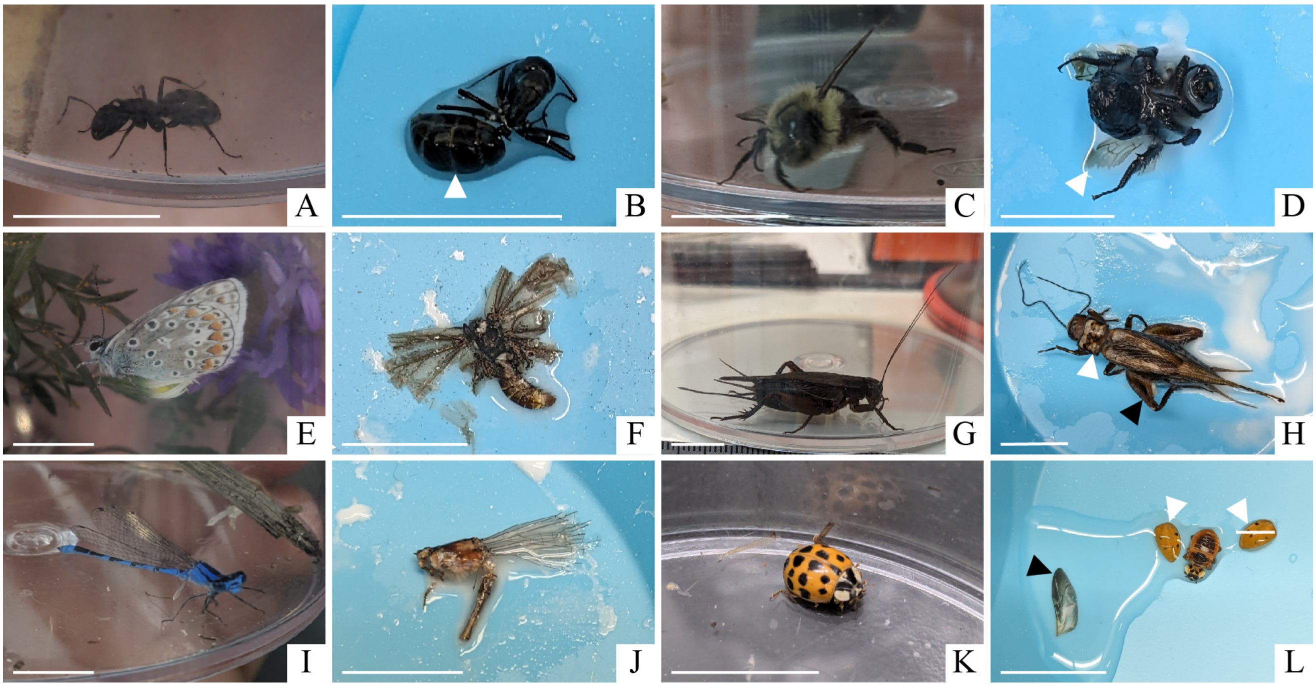

FIGURE 1. Example photographs of the insects before the experiments began (**A**, **C**, **E**, **G**, **I**, **K**) and after 48 hours of tumbling (**B**, **D**, **F**, **H**, **J**, **L**). It is not necessarily the same replicate shown in both photos. **A**, **B**, *Camponotus* sp. White arrowhead points to some stretching on the abdomen. **C**, **D**, *Bombus* sp. White arrowhead points to ruffled edges of the hind wings. **E**, **F**, *Polyommatus* sp. **G**, **H**, *Teleogryllus oceanicus*. White arrowhead points to loss of pigment/exoskeleton in the pronotum. Black arrowhead points to a hindleg which has ruptured on the ventral side. **I**, **J**, *Enallagma* sp. **K**, **L**, Coccinellidae. White arrowhead points to intact forewings (elytra) that remain intact and identifiable but are separated from the body. Black arrowhead points to an intact but separated hindwing. Scale bars: 1 cm.

the inside of the tumbler for almost the entire rotation. The Froude number (Fr) is a measure of turbulence in a rotating system calculated as $Fr = \omega^2 R/g$, where ω is the angular velocity (rad/s), R is the radius of the cylinder (m), g is the acceleration due to gravity (m/s^2). The Froude number for our setup is high (1.20±0.02 to 1.62±0.03) indicating a centrifugal motion; however, the hexagonal shape of the tumbler disrupts the centrifugal motion causing additional turbulence and resulting in some cataracting behaviour. Approximating the shape of the tumbler as a cylinder and assuming a maximum theoretical speed that would occur near the tumbler wall, the equivalent linear travel speed of an object inside the tumbler is 1.9–2.2 km/h. As such, the total travel distance for each experiment (after 48 hours) is estimated as 91–105 km.

Results

The results are organized first by organism and then by morphological character within each organism. When multiple times are presented for transitional events or loss of characters, each individual replicate (A, B, and C) is indicated separately and may not represent an ascending or descending order. For damage to wings and legs, general trends are described with the timing of events followed in parentheses. When fewer times are presented than number of appendages (*e.g.*, five times for six legs) this indicates that some appendages were not damaged or lost. Any exceptions are noted. Results are summarized in Figs. 1 and 2 and are present in full in Supplemental Data Table 1.

Ants

The ants died at hours 2, 8, and 10, and sank at hours 6, 10, and 14 (note: replicate B floated and sank intermittently from hour 10 to 20 and replicate C "resurfaced" for one measurement at hour 34). No legs or heads disarticulated from any specimen. Replicate A had one antenna damaged between hour 36 and 40. Replicated B had one antenna damaged by hour 36. Ants showed slight damage to their abdomens with initial occurrences at hours 46, 36, and 36. We witnessed abdominal bloating (Fig. 1B), weakened connection to the thorax, and rupturing of the abdomen throughout the tumbling. There was little to no change in pigmentation due to either abrasion or chemical degradation.

Bumblebees

All bumblebees died by the first data collection at hour 2 and sank at hours 24, 42, and 26. No replicate showed any damage to the legs, heads, abdomen, or antennae; however they did display slight damage to their wings: by the termination of the experiment (48 hours), all replicates had sightly ruffled edges with some breakage and chipping (Fig. 1D). Determining wing damage was difficult due to the wings frequently folding over themselves when they were removed from the water, causing them to incorrectly appear broken. Damage was first observed to the wings of replicates A and B after an average of 40 hours (for each wing: A:30, 44, 42, 42; B:14, 44, 40, 40); wing damage was first observed on replicate C much earlier at ~4 hours (C: 4, 2, 4, 8), but the final damage at the end of the experiment was not visibly greater than any of the other replicates. No loss of colour was noted in any replicate.

Butterflies

Butterfly death occurred at hours 8, 4, and 6. Replicates A and B sank at hours 48 and 46 respectively while replicate C never sank. Butterfly legs readily disarticulated with most legs lost between hours 6 and 20 (Note that replicate C started the experiment missing its right midleg; A: 20, 16, 20, 6, 8; B: 48, 10, 10, 10, 10; C: 46, 18, 10, 8, 10). Leg attachments were delicate, and human manipulation was likely the source of damage at hour 10 when four of the legs detached from replicate B, as the specimen grew increasingly fragile. These results highlight the overall delicacy of the connection between the legs and body. The attachment of the head to the specimen weakened over time, with the head of replicate B fully detaching at hour 42. The proboscises were sometimes visible having unraveled from the mouth. Antennae damage was quite variable across replicates: replicate A showed no damage to either of its antennae; replicate B lost both antennae at hours 26 and 36, while replicate C had one antenna damaged at hour 4 and the other antenna broke off entirely at hour 38 with no prior damage.

The first signs of structural damage to the wings were recorded at hours 2–10 (A: 8, 10, 4, 6; B: 8, 6, 4, 4; C: 8, 6, 6, 2). Butterfly wings deteriorated consistently from the outside of the wing inwards so that by the end of the experiment the wings were limited to stubs (Fig. 1F). Broken components of wings were generally very small although one wing broke off as a single piece. The scales on all butterfly specimens began to fall off after two hours of tumbling, and the percentage of scales left on the butterfly wings were reduced to 25% by hours 14, 18, and 20. Despite this, scales were never fully lost from the wings as the scales closest to the body remained until the end of the experiment.

Crickets

All crickets died by hour 2 and sank after an average of 22 hours of decay with some time spent intermittently sinking and floating (28, 16, and 24 hours). The right hind leg of replicate A detached at hour 4. No other legs fully detached; however, the other hindlegs began showing damage at hour 18 (replicate A; left only), hour 20 (replicate C; right and left), and hour 30 (replicate B; right and left). Damage to legs occurred in two distinct modes: 1) stretching and tenuous connections between the femur and coxa and 2) exoskeleton splitting along the ventral side of the femur (Fig. 1H). Heads remained articulated in all specimens; however, the pronotum showed signs of damage by hours 10, 8, and 10. The connective tissue between the head and pronotum, and the pronotum and forewings, began to stretch causing an elongation in the overall cricket body. No body fully detached at the pronotum. Antennae damage occurred throughout the experiment with all antennae damaged by hour 44 (A: 28, 28; B: 8, 44; C: 2, 30); however, no antennae were fully lost. Slight abdominal damage (bloating and rupturing) was recorded starting at hours 34, 32, and 40. There was very little damage to hind wings in their folded position. Damage to forewings was first recorded between hours 28–36 (A: 28, 28; C:30, 36); however, Replicate B showed no damage to any wing. Damage to the forewings showed primarily as holes in the center or tears along the folded sides of the wing (Fig. 1H). The dark brown cuticle of the cricket body faded slowly in patches, sometimes resulting in holes along parts of the head, pronotum, and forewings (Fig. 1H). This damage was first noted at hours 16, 16, and 22. The cerci remained undamaged from their initial condition. No damage to the ovipositor was seen in any replicate.

Damselflies

Damselflies died at hours 2, 2, and 4, and sank at hours 6, 6, and 10. Note that at hour 28, replicate A was mistakenly left out in the fume hood for two hours (*i.e.*, before the next time stamp). These two hours were not considered tumbling time. When put back into the tumbler it began floating again and did not sink again until hour 40. The legs on the damselflies readily disarticulated with replicates losing all or almost all legs continuously from hours 14–48 (A: 26, 20, 38, 40, 30, 22; B: 48, 30, 46, 14, 16; C: 32, 16, 26, 16, 24). The heads of all replicates disarticulated at hours 8, 8, and 12. Antennae damage was not monitored because of their small size and difficulty in identification. Abdominal damage progressed rapidly from hours 24, 10, and 12 and starting from the most distal part of the abdomen; however, a portion of the abdomen remained attached to the thorax in all cases (Fig. 1J). Wing deterioration occurred similarly to butterflies where wings broke from the distal edge first (A: 6, 8, 8, 8; B: 8, 8, 8, 6; C: 8, 8, 8, 12). The bright blue colour of the damselflies slowly faded to pale yellow/beige starting at hours 12, 16, and 16, with complete loss of blue colour by hours 28, 24, and 26. The dark brown/black stripes remained for the entirety of the experiment (Fig. 1J).

Ladybird beetles

Ladybird beetles died at hours 2, 4, and 2, and sank at hours 10, 10, and 4. The pronotum started to show signs of stretching and elongation by hour 22, 24, and 20. At hour 46, the entire head, prothorax, and both forelegs of replicate A detached from the rest of the body in one piece and remained together for the remainder of the experiment. Antennae damage was not monitored because they were difficult to identify across all experiments. Leg damage/loss was uncommon. All forewings (*i.e.*, elytra) detached between hours 22–34 (A: 26, 22; B: 24, 26; C: 24, 34). After detaching, the forewings remained undamaged and recognizable for the remainder of the experiment (Fig. 1L). At the beginning of the experiment, the hindwings were folded underneath the forewings and were not visible; however, within 2–4 hours all hindwings unfolded and were clearly visible. The hindwings similarly remained intact although they were crumpled and not easily examined unless physically manipulated. The hindwings showed slight signs of damage at hours 26–46 (A: 46, 46; B: 32, 40; C: 32, 26), with most of them fulling detaching by hours 38–48 (B: 40, 48; C: 48, 38). The orange colouring on the dorsal part of the abdomen began to fade at hours 34 and 46 for replicates A and C respectively.

Discussion

Mechanisms of disarticulation

In our experiments, three primary pathways are likely to have damaged and disarticulated the insects: 1) turbulence within the silt-water slurry, with the higher density of the slurry (due to suspended silica silt) generating greater torque than pure water; 2) abrasion from the silt particles, in which individual grains are presumed to collide with the cuticle, resulting in broken pieces (*i.e.*, particulate erosion); and 3) repeated physical impacts against the tumbler walls. These factors are not mutually exclusive and are compounded as the structural integrity of the insects is weakened during decay. As the insects are tumbled, their bodies are twisted and pulled apart by the silt-water slurry in response to turbulence. Additionally, the silt is constantly scraping/abrading the insect exoskeleton, sometimes resulting in damage and even the removal of tissues. Finally, when the insects hit the walls of the tumbler, a rapid change in momentum results in a large shock that can damage more resilient tissues, not necessarily that different from insects hitting larger sediment particles or plant debris. In each case, the effect on the insect's articulation is governed by the speed of the tumbler and morphology of the insect. Importantly, in the absence of mechanical stimulation (*i.e.*, decay and sinking in stagnant water), disarticulation is extremely rare (Sorrentino *et al.*, 2026).

Body shape and size were important factors in disarticulation. Relatively long, skinny insects, such as the damselfly, are twisted more strongly than spherical ones, such as the bumblebee, because larger bending moments are generated along the long axis of the abdomen. The larger bending moments can also explain why the wings break from distal sections first and why the abdomen of the damselfly loses distal segments first. This pattern of disarticulation is clearly reflected in the fossil record across both space and time, with many damselfly specimens preserved under such conditions showing either breakage of the distal abdomen or complete separation of the abdomen from the rest of the body, as seen, for example, in the Green River Formation (Eocene, USA) and the Menat Formation (Paleocene, France) (Nel & Jouault, 2022; Ware *et al.*, 2025). Butterfly fossils from the lacustrine Campagne-Calavon Formation (Oligocene, France) also show wing damage along distal sections similar to the results from our experiments (Rajaei *et al.*, 2026).

Body part stiffness was also likely a source of variation. All ladybird beetle wings broke off as complete body parts with little to no further damage. We think this is due to both the increased durability and stiffness of their forewings (elytra) and the reduced stiffness and increased flexibility of their hindwings, which are stored folded underneath the elytra. The hydrophobicity of specimens is less likely to be a source of variance. All tested specimens contain superhydrophobic structures except the bumblebees, whose hairy bodies are considered more wettable (Bello *et al.*, 2023). Despite this, bumblebees took the second longest to sink (Fig. 2) showing that hydrophobicity is not a primary control on disarticulation.

Interspecies comparisons

Ants and bumblebees had little to no observable damage across all measured categories (Fig. 3A, B). Bumblebees were less likely to disarticulate because, when compared to most of the other insects, they are more sphere-shaped, thus reducing the torques generated by turbulence and shock impacts. Their wings are also relatively short and do not protrude far from the body. The ants are entirely wingless, and their bodies curled inwards after death thus additionally reducing the moments exerted on the individual body segments. These specimens were

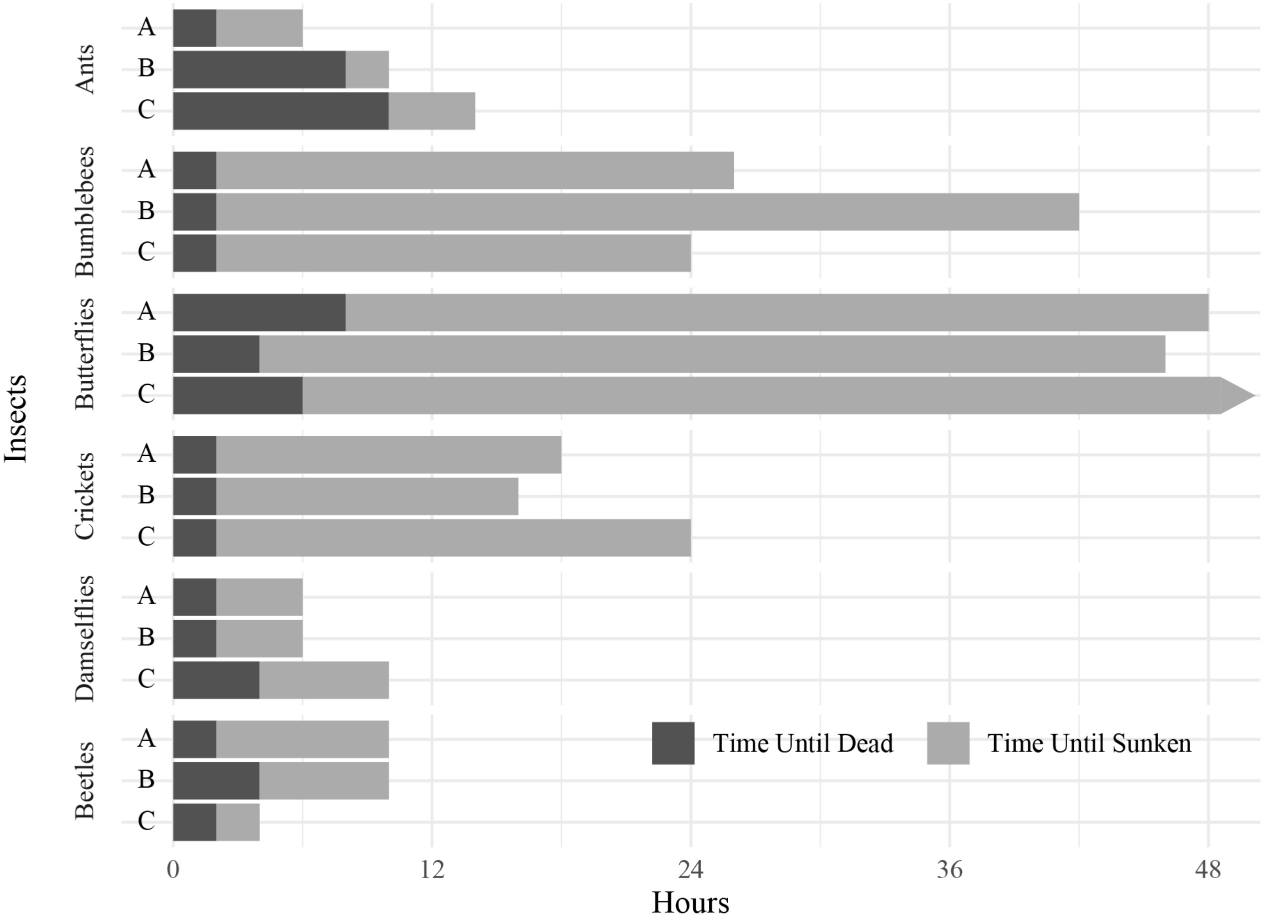

FIGURE 2. The time each replicate spent in the tumbler until it was considered dead (dark grey) and then subsequently sunken (light grey). The first instance of sinking for each insect is presented. Periods of intermittent floating and sinking are not presented. Butterfly C did not sink during the experiment.

exceptionally robust and appeared relatively intact even after 48 hours of tumbling (equivalent to approximately 91–105 km of effective travel distance). For bumblebees, their rounded shape covered in hair likely reduced abrasion from silt and cushioned impacts against the tumbler sides. For ants, curling into a near-sphere with their legs retracted beneath the body likely reduces the surface area in contact with the silt, thereby limiting abrasion, while their thick cuticle provides resistance to impacts against the tumbler walls.

However, robustness does not necessarily translate into higher preservation potential. In ants, fossilization likelihood may depend less on resistance to mechanical damage and more on behavioural factors, specifically their ability to escape from the transport medium (in this case, water), as observed in our experiments. While their thick cuticle may theoretically favour preservation, their frequent escape would limit deposition and fossilization. This aligns with the fossil record, where ants preserved in rock (or as imprints) are often reproductive individuals and not workers. The presence of wings in these reproductive specimens may have increased surface tension, reducing their ability to escape the water column and ultimately promoting sinking. Such patterns are evident in deposits like the Bembridge Marls of the Isle of Wight and the Green River Formation (Archibald *et al.*, 2011; Dlussky & Perfilieva, 2014).

In our experiments preservation potential (*i.e.*, likelihood of fossilization) is governed by three characteristics: 1) ability to escape the turbulent environment (*e.g.*, ants *vs*. bumblebees); 2) time spent in suspension (*i.e.*, not sunken); and 3) level of disarticulation. The ants withstood up to 10 hours of tumbling before death, giving them ample time to possibly escape the water medium, or even attract predators with their struggling. The bumblebees, on the other hand, died and sank quickly, providing an excellent opportunity for fossilization. This is supported by independent sinking experiments where bumblebees sank relatively rapidly in still freshwater before biofilms formed (Sorrentino *et al.*, 2026). The turbulence in our current experiments prevented the growth of biofilms that previously acted to hinder sinking in still environments (Sorrentino *et al.*, 2026); however, the exact role of biofilms on insect

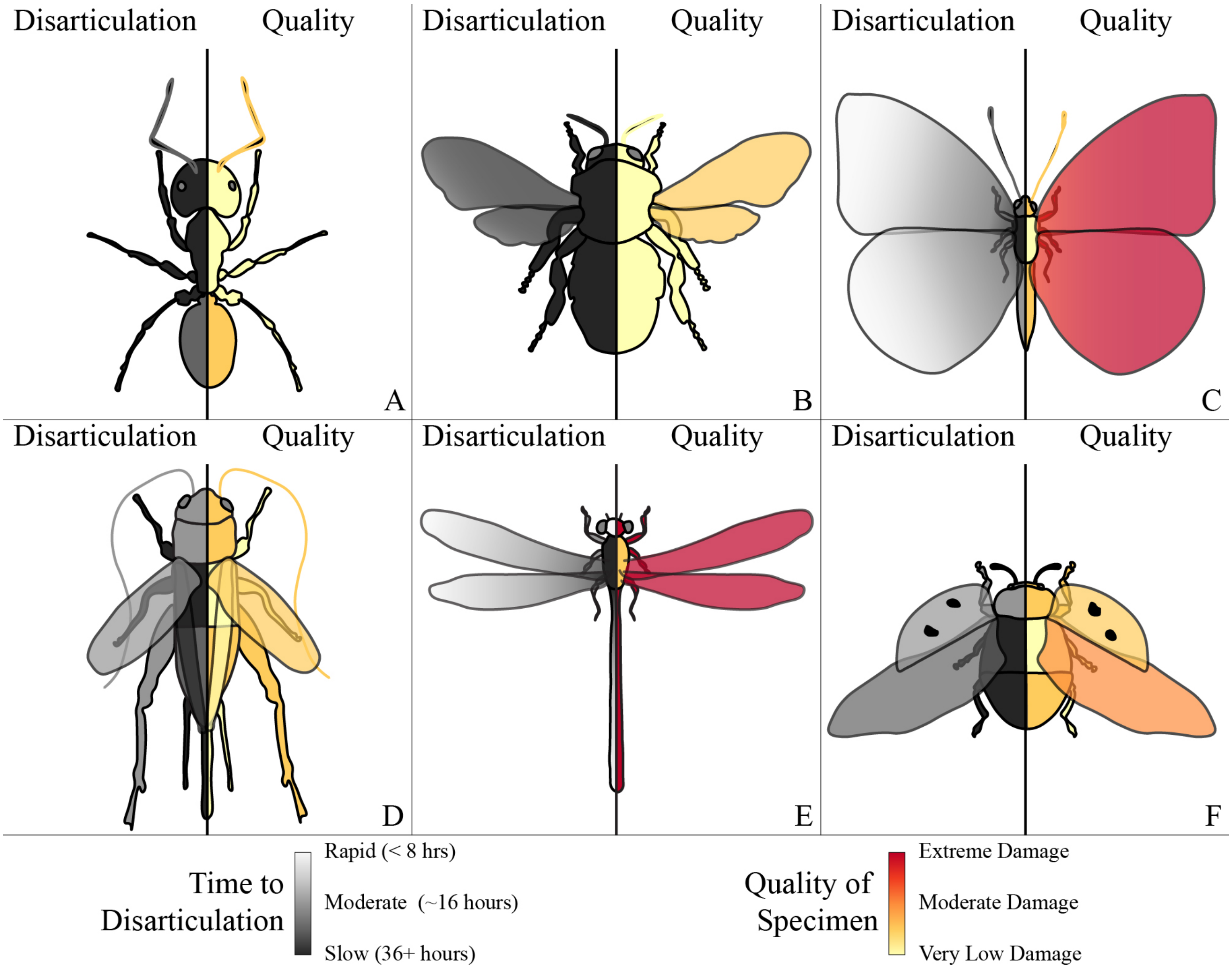

FIGURE 3. General trends of preservation seen with insects used in the experiments. The left side shows how rapidly damage and disarticulation occurs for each specimen. The right side shows the quality of the specimen at the end of the experiment.

fossilization has been debated with some speculation that biofilms might in fact facilitate sinking (O'Brien *et al.*, 2002, 2008). Ants were additionally unique in that they were capable of actively climbing out of the container during the data collection points when the tumblers were paused. Of the flying insects, only the butterflies demonstrated the ability to escape the tumbler during pauses by lifting themselves off the surface of the water. Therefore, we hypothesize that the size of a pond, lake, or stream is likely to influence the fossilization potential of different groups. For instance, ants seem to be relatively good swimmers and would be able to escape even large bodies of water. In contrast, the bumblebees were less capable swimmers, and although they might be able to escape in small ponds, they would struggle to escape in larger bodies of waters. Consequently, in these conditions their fossilization potential is reduced not only by their limited ability to escape but also by external factors such as predators.

Crickets were also robust to tumbling as all specimens retained most morphological features with limited amounts of disarticulation (*i.e.*, legs, forewings, and pronotum), though the exoskeleton lost rigidity and became partially translucent towards the end of the experiment (Figs 1H, 3D). The ovipositors were undamaged, suggesting that these gender-specific appendages are likely to transfer to the fossil record. This might explain some of the excellent preservation of crickets seen at places like the Crato Formation or Jinju Formation (Kim *et al.*, 2021; Storari *et al.*, 2024).

Butterflies showed the lowest preservation potential, consistent with their extremely scarce fossil record (De Jong, 2017). Our experiments suggest that this scarcity is largely due to the rapid degradation of their wings, particularly during transport, which greatly reduces their chances of fossilization. Consequently, only a few complete butterfly specimens are known from the entire Cenozoic (Sohn *et al.*, 2015). Under our experimental conditions, butterflies survived for a long time despite submersion during tumbling, remained afloat until very late in the experiment, and readily disarticulated (Fig. 3C). Wing breakage occurred continuously and rapidly, with extensive damage occurring within 20 hours. Nonetheless, some colourful scales persisted on wing stubs attached to the body even to the very end of the experiment. This can explain why colourful scales are preserved in specimens from Messel (McNamara *et al.*, 2012), even in transported and heavily disarticulated specimens. Therefore, complete specimens, such as those seen at Florissant (lacustrine; Meyer, 2003) and Fur Formation (marine; Rust, 2000), are exceptional fossils, likely preserved after minimal transport. Even partially damaged specimens such as that seen at Campagne-Calavon Formation (lacustrine; Rajaei *et al.*, 2026) likely represent short travel distances. Over geological timescales, such degradation provides a plausible mechanism for the rarity of butterfly fossils, resulting in a poor fossil record that complicates efforts to reconstruct their evolutionary history.

Damselflies showed rapid and extensive damage (Fig. 3E), but their bodies (and disarticulated body parts) sank rapidly. These results suggest a higher likelihood of fossilization even after transport; however, proper identification of these specimens may be difficult due to damage or loss of taxonomically important features. For example, damselfly wings are essential for species-level identification (Archibald *et al*., 2023), but the wings disarticulated into many tiny fragments rather than separating as complete wings, therefore losing the ability to easily identify the specimen on wings alone.

Ladybird beetles showed overall moderate damage in our experiments (Fig. 3F). This was surprising considering the reputation beetles have as sturdy and robust insects (Anderson & Smith, 2017); however, our results are corroborated by Smith *et al.* (2006) who demonstrated that ladybird beetles were among the least robust beetle specimens. The elytra were the first part of the ladybird beetle to disarticulate, which contrasts with Smith *et al.* (2006) where legs were reported to disarticulate first. It is possible that the discrepancy lies in a difference in preparation methods: Smith *et al.* (2006) used museum specimens that had been stored in alcohol, rinsed, dried, and then submerged in water. The alcohol and drying could have made the legs very brittle and readily disarticulated. Our specimens were placed in the tumbler alive where they were able to tightly curl their legs into their bodies before dying, protecting them from abrasion. Additionally, the tumblers in our experiments rotate much more quickly than the tumblers in Smith *et al.* (2006): their tumblers rotated at 50 RPM, while ours rotated at 106–124 RPM. The increased energy could have forced the elytra to open sooner. Similar to Smith *et al.* (2006), the elytra were not themselves further damaged after disarticulation and sank readily, leaving them likely to be preserved and identifiable. The early loss of elytra but not complete destruction of the body has additional considerations for fossil identification. Elytra are one of the defining features of Coleoptera, meaning the identification of the remaining body might be confused with other insect orders such as Hemiptera (Borror & White, 1970). Given the early disarticulation of the elytra in this study, it is likely that similar groups in the fossil record have been incorrectly identified.

It is likely that our results are generalizable to insect groups not tested here but that have similar morphologies and traits to one of the tested insects. For example, dragonflies may exhibit patterns similar to damselflies due to their comparable body structure, wing shape, and only slightly more robust thorax. Similarly, although slightly different, Ephemeroptera, are extremely fragile insects and are likely to show patterns akin to those of damselflies. For Polyneoptera, generalization is more difficult because this group encompasses a wide diversity of body shapes, strength, and sclerotization (*e.g*., cockroaches versus angel insects). The pattern observed in Lepidoptera may be generalizable to their sister group, the Trichoptera, although Trichoptera have adaptations for life near aquatic environments. Their thin, fragile, scale-covered wings are still somewhat similar to those of butterflies, suggesting potentially similar degradation processes, although this remains to be empirically tested. Generalizing observations for Coleoptera is challenging, as our data are based on only one beetle group, and beetles are known for their highly diverse ecology, morphology, and lifestyles. If the presence of elytra is considered the main defining characteristic, other groups such as Dermaptera (earwigs) might exhibit similar patterns, with rapid disarticulation of their elytra during tumbling or transport. However, empirical evidence for this is currently lacking.

Intraspecies variation

Intraspecies variation may be due to several factors that are not fully controlled for in this experiment such as age and sex. Insect integrity is usually used as a proxy for age: older insects are more damaged than younger insects (Wehmann *et al*., 2022). Therefore, we partially controlled for age by selecting intact adult specimens; however, we were not always successful (*e.g*., butterfly replicate C was missing a midleg). We only analyzed female bumblebees, crickets, and ants; however, we did not record the sex of our butterfly, damselfly, and ladybird beetle specimens. Another confounding variable is an individual specimen's vitality: many specimens were captured in the wild and thus we could not control for the last time they fed, for example. It is likely that some of our specimens were slightly healthier or weaker than others of the same species, however we do not believe it played a significant role in our results.

Comparison to the fossil record

There are many factors that impact insect fossil communities including ecology, depositional environment, and insect morphology (Smith, 2012). Insect fossils from Paleoburn and Anvil Points in the Green River Formation rarely have antennae and many were missing heads and legs (Anderson & Smith, 2017). Conversely, very few of our specimens were missing antennae and only damselflies and butterflies were missing legs and heads. This is surprising considering that our tumbling setup was relatively turbulent. The complete loss of these body parts in the fossil record is possibly due to increased decay before, during, and/or after transport. Decay increases disarticulation during transport (Allison, 1986), and relatively little decay occurred in our experiments. Another possibility is that the insects preserved in the fossil record were transported through particularly turbulent water that would result in more damage than captured in our experiments.

Across several fossil localities, most insect specimens are reported as fully articulated despite the fact that these assemblages are dominated by terrestrial taxa that would have required extensive transport prior to burial, including at Florissant Fossil Beds (Harding & Chant, 2000; Smith & Moe-Hoffman, 2007; Henning *et al*., 2012), Anvil Point and Paleoburn in the Green River Formation (Anderson & Smith, 2017), and the Nova Olinda Member in the Crato Formation (Bezerra & Mendes, 2024). In our experiments, ants, bumblebees, and crickets showed high levels of articulation after 48 hours of tumbling, roughly equivalent to 91–105 km of travel. Most of our ladybird beetles and butterflies would also have been classified as "fully articulated" by these researchers as most studies emphasized only the presence of the head, thorax, and abdomen to be considered articulated (*e.g.*, Anderson & Smith, 2017; Bezerra & Mendes, 2024). Our experiments show that even relatively long and turbulent travel times and distances are insufficient to disarticulate insects, thus supporting the high levels of articulation reported at fossil localities.

Our experiments suggest that the more robust specimens (*e.g.*, ants, bumblebees, crickets, and ladybird beetles) could be overrepresented in transported fossil assemblages; however, the taphonomic signal of transport is likely small compared to competing factors such as ecology and depositional environment. The composition of specimens at Florissant, Green River, and Crato formations varies significantly: most specimens in the Nova Olinda Member are orthopterans or blattodeans (Bezerra & Mendes, 2024), most specimens at Anvil Points and Paleoburn are coleopterans and dipterans (Anderson & Smith, 2017), and most specimens at Florissant are hymenopterans and dipterans (Henning *et al.*, 2012). Our experiments do not discriminate against any of these orders and transport does not explain the differences in composition between these sites. It is noteworthy that the least robust specimens (butterflies and damselflies) are exceedingly rare at all of these localities (Anderson & Smith, 2017; Bezerra & Mendes, 2024; Henning *et al.*, 2012).

Conclusion

Our findings underscore the impact of turbulent transport on insect fossilization, disproportionately removing taxa with elongated, delicate, or easily isolated body parts—structures often critical for taxonomic identification. The effects of tumbling on insect preservation potential were variable across the tested specimens. Butterflies showed the least preservation potential as they disarticulated rapidly, lived for up to 8 hours in the tumbling environment, and then only sank at 46 hours at the earliest. Damselflies died and sank rapidly, but also disarticulated rapidly, including their wings which are often a diagnostic feature. Ants were extremely robust to disarticulation and sank quickly once dead; however, they lived up to 12 hours in the tumbler and demonstrated excellent physical capabilities to escape the tumbling environment, reducing their preservation potential. Ladybird beetles, crickets, and bumblebees showed relatively good preservation potential as they all died and sank relatively rapidly and did not disarticulate. The wings of the ladybird beetle did disarticulate but they broke off as entire wings and remained useful for taxonomic identification. Overall, our results highlight the durability of insects to transport and surmise that the high percentage of articulated specimens in the fossil record is partially due to their resistance to transport-induced disarticulation. These results provide valuable insights into biases in the insect fossil record and the differential preservation of insect lineages.

Acknowledgements

JAS thanks the Government of Ontario, the Geologic Society of America, and the Paleontological Society for project funding. ML was supported by NSERC RGPIN-2019-05405. JAS thanks the invaluable assistance of the Biology Core Facilities at the University of Toronto Mississauga, particularly Raani Sarkar. The authors thank two anonymous reviewers for their excellent comments that have improved the quality of our manuscript. JAS also thanks Seshu Iyengar for their helpful comments and edits on earlier drafts.

References

Allison, P.A. (1986) Soft-bodied animals in the fossil record: The role of decay in fragmentation during transport. *Geology*, 14 (12), 979–981. https://doi.org/10.1130/0091-7613(1986)14<979:SAITFR>2.0.CO;2

Allison, P.A. (1988) The role of anoxia in the decay and mineralization of proteinaceous macro-fossils. *Paleobiology*, 2 (2), 139–154. https://doi.org/10.1017/S009483730001188X

Álvarez-Parra, S., Peñalver, E., Nel, A. & Delclòs, X. (2022) New barklice (Psocodea, Trogiomorpha) from Lower Cretaceous Spanish amber. *Papers in Palaeontology*, 8 (3), e1436. https://doi.org/10.1002/spp2.1436

Anderson, E.P. & Smith, D.M. (2017) The same picture through different lenses: Quantifying the effects of two preservation pathways on Green River Formation insects. *Paleobiology*, 43 (2), 224–247. https://doi.org/10.1017/pab.2016.29

Archibald, S.B., Bossert, W.H., Greenwood, D.R. & Farrell, B.D. (2010) Seasonality, the latitudinal gradient of diversity, and Eocene insects. *Paleobiology*, 36 (3), 374–398. https://doi.org/10.1666/09021.1

Archibald, S.B., Johnson, K.R., Mathewes, R.W. & Greenwood, D.R. (2011) Intercontinental dispersal of giant thermophilic ants across the Arctic during early Eocene hyperthermals. *Proceedings of the Royal Society B: Biological Sciences*, 278 (1725), 3679–3686. https://doi.org/10.1098/rspb.2011.0729

Archibald, S.B., Morse, G.E., Greenwood, D.R. & Mathewes, R.W. (2014) Fossil palm beetles refine upland winter temperatures in the Early Eocene Climatic Optimum. *Proceedings of the National Academy of Sciences of the United States of America*, 111 (22), 8095–8100. https://doi.org/10.1073/pnas.1323269111

Archibald, S.B., Ware, J.L., Rasmussen, J.A., Sylvestersen, R.L., Olsen, K. & Simonsen, T.J. (2023) The damselfly genus *Furagrion* Petrulevičius *et al*. (Odonata, Zygoptera) from the early Eocene Fur Formation of Denmark and the dysagrionoid grade. *Zootaxa*, 5278 (2), 289–317. https://doi.org/10.11646/zootaxa.5278.2.4

Bath Enright, O.G., Minter, N.J. & Sumner, E.J. (2017) Palaeoecological implications of the preservation potential of soft-bodied organisms in sediment-density flows: testing turbulent waters. *Royal Society Open Science*, 4 (6), 170212. https://doi.org/10.1098/rsos.170212

Bath Enright, O.G., Minter, N.J., Sumner, E.J., Mángano, M.G. & Buatois, L.A. (2021) Flume experiments reveal flows in the Burgess Shale can sample and transport organisms across substantial distances. *Communications Earth & Environment*, 2 (1), 104. https://doi.org/10.1038/s43247-021-00176-w

Behrensmeyer, A.K., Kidwell, S.M. & Gastaldo, R.A. (2000) Taphonomy and paleobiology. *Paleobiology*, 26 (S4), 103–147. https://doi.org/10.1017/S0094837300026907

Bello, E., Chen, Y. & Alleyne, M. (2023) Staying dry and clean: An insect's guide to hydrophobicity. *Insects*, 14 (1), 42. https://doi.org/10.3390/insects14010042

Bezerra, F.I. & Mendes, M. (2024) A palaeoecological analysis of the Cretaceous (Aptian) insect fauna of the Crato Formation, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 641, 112134. https://doi.org/10.1016/j.palaeo.2024.112134

Borror, D.J. & White, R.E. (1970) *A field guide to the insects of America north of Mexico*. Houghton Mifflin, Boston, 404 pp.

Brauckmann, C. & Schneider, J. (1996) Ein unter-karbonisches Insekt aus dem Raum Bitterfeld/Delitzsch (Pterygota, Arnsbergium, Deutschland). *Neues Jahrbuch für Geologie und Paläontologie-Monatshefte*, 1996 (1), 17–30. https://doi.org/10.1127/njgpm/1996/1996/17

Briggs, D.E.G. (2003) The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Review of Earth and Planetary Sciences*, 31, 275–301. https://doi.org/10.1146/annurev.earth.31.100901.144746

Butler, A.D., Cunningham, J.A., Budd, G.E. & Donoghue, P.C.J. (2015) Experimental taphonomy of *Artemia* reveals the role of endogenous microbes in mediating decay and fossilization. *Proceedings of the Royal Society B: Biological Sciences*, 282 (1808), 20150476, 1–10. https://doi.org/10.1098/rspb.2015.0476

Clements, T., Purnell, M. & Gabbott, S. (2019) The Mazon Creek Lagerstätte: A diverse late Paleozoic ecosystem entombed within siderite concretions. *Journal of the Geological Society*, 176 (1), 1–11. https://doi.org/10.1144/jgs2018-088

De Jong, R. (2017) Fossil butterflies, calibration points and the molecular clock (Lepidoptera: Papilionoidea). *Zootaxa*, 4270 (1), 1–63. https://doi.org/10.11646/zootaxa.4270.1.1

Dlussky, G. & Perfilieva, K. (2014) Superfamily Formicoidea Latreille, 1802. *In*: Antropov, A.V., Belokobylskij, S.A., Compton, S.G., Dlussky, G.M., Khalaim, A.I., Kolyada, V.A., Kozlov, M.A., Perfilieva, K.S. & Rasnitsyn, A.P. (Eds), The wasps, bees and ants (Insecta: Vespida=Hymenoptera) from the Insect Limestone (Late Eocene) of the Isle of Wight, UK. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 104 (3-4), 335–446. https://doi.org/10.1017/S1755691014000103

Duncan, I.J., Titchener, F. & Briggs, D.E.G. (2003) Decay and disarticulation of the cockroach: Implications for preservation of the blattoids of Writhlington (Upper Carboniferous), UK. *Palaios*, 18 (3), 256–265. https://doi.org/10.1669/0883-1351(2003)018<0256:DADOTC>2.0.CO;2

Gäb, F., Ballhaus, C., Stinnesbeck, E., Kral, A.G., Janssen, K. & Bierbaum, G. (2020) Experimental taphonomy of fish – role of elevated pressure, salinity and pH. *Scientific Reports*, 10 (1), 7839.
https://doi.org/10.1038/s41598-020-64651-8

Gibson, B.M., Schiffbauer, J.D., Wallace, A.F. & Darroch, S.A.F. (2023) The role of iron in the formation of Ediacaran 'death masks'. *Geobiology*, 21 (4), 421–434.
https://doi.org/10.1111/gbi.12551

Harding, I.C. & 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 (3), 195–198.
https://doi.org/10.1130/0091-7613(2000)028<0195:SSDMAA>2.3.CO;2

Henning, J.T., Smith, D.M., Nufio, C.R. & Meyer, H.W. (2012) Depositional setting and fossil insect preservation: A study of the late Eocene Florissant Formation, Colorado. *Palaios*, 27 (7), 481–488.
https://doi.org/10.2110/palo.2011.p11-084r

Holden, A.R., Southon, J.R., Will, K., Kirby, M.E., Aalbu, R.L. & Markey, M.J. (2017) A 50,000 year insect record from Rancho La Brea, Southern California: insights into past climate and fossil deposition. *Quaternary Science Reviews*, 168, 123–136.
https://doi.org/10.1016/j.quascirev.2017.05.001

Iniesto, M., Blanco-Moreno, C., Villalba, A., Buscalioni, Á.D., Guerrero, M.C. & López-Archilla, A.I. (2018) Plant tissue decay in long-term experiments with microbial mats. *Geosciences*, 8 (11), 387.
https://doi.org/10.3390/geosciences8110387

Iniesto, M., Gutiérrez-Silva, P., Dias, J.J., Carvalho, I.S., Buscalioni, A.D. & López-Archilla, A.I. (2021) Soft tissue histology of insect larvae decayed in laboratory experiments using microbial mats: Taphonomic comparison with Cretaceous fossil insects from the exceptionally preserved biota of Araripe, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 564, 110156.
https://doi.org/10.1016/j.palaeo.2020.110156

Jouault, C., Aase, A. & Nel, A. (2021) Past ecosystems drive the evolution of the early diverged Symphyta (Hymenoptera: Xyelidae) since the earliest Eocene. *Fossil Record*, 24 (2), 379–393.
https://doi.org/10.5194/fr-24-379-2021

Kim, D.-Y., Lee, M., Nam, G.-S. & Park, T.-Y.S. (2021) The first orthopteran fossils from the Lower Cretaceous (Albian) Jinju Formation of Korea: Ethological implications for elcanids. *Cretaceous Research*, 125, 104843.
https://doi.org/10.1016/j.cretres.2021.104843

Klompmaker, A.A., Portell, R.W. & Frick, M.G. (2017) Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. *Palaeontology*, 60 (6), 773–794.
https://doi.org/10.1111/pala.12314

Mähler, B., Janssen, K., Lönartz, M.I., Lagos, M., Geisler, T., Rust, J. & Bierbaum, G. (2023) Time-dependent microbial shifts during crayfish decomposition in freshwater and sediment under different environmental conditions. *Scientific Reports*, 13 (1), 1539.
https://doi.org/10.1038/s41598-023-28713-x

Martínez-Delclòs, X., Briggs, D.E.G. & Peñalver, E. (2004) Taphonomy of insects in carbonates and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 203 (1-2), 19–64.
https://doi.org/10.1016/S0031-0182(03)00643-6

McNamara, M.E., Briggs, D.E.G. & Orr, P.J. (2012) The controls on the preservation of structural color in fossil insects. *Palaios*, 27 (7), 443–454.
https://doi.org/10.2110/palo.2012.p12-027r

Mellmann, J. (2001) The transverse motion of solids in rotating cylinders—forms of motion and transition behavior. *Powder Technology*, 118 (3), 251–270.
https://doi.org/10.1016/S0032-5910(00)00402-2

Meyer, H.W. (2003) *The fossils of Florissant*. Smithsonian Institution Press, Washington, D.C., 258 pp.

Nel, A. & Jouault, C. (2022) The odonatan insects from the Paleocene of Menat, central France. *Acta Palaeontologica Polonica*, 67 (3), 631–648.
https://doi.org/10.4202/app.00960.2021

Newman, S.A., Daye, M., Fakra, S.C., Marcus, M.A., Pajusalu, M., Pruss, S.B., Smith, E.F. & Bosak, T. (2019) Experimental preservation of muscle tissue in quartz sand and kaolinite. *Palaios*, 34 (9), 437–451.
https://doi.org/10.2110/palo.2019.030

O'Brien, N.R., Meyer, H.W. & Harding, I.C. (2008) The role of biofilms in fossil preservation, Florissant Formation, Colorado. *In*: *Special paper of the Geological Society of America*. Vol. 435. Geological Society of America, Boulder, pp. 19–31.

O'Brien, N.R., Meyer, H.W., Reilly, K., Ross, A.M. & 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), 1–11.
https://doi.org/10.2113/gsrocky.37.1.1

Penney, D. & Jepson, J.E. (2014) *Fossil insects: an introduction to palaeoentomology*. Siri Scientific Press, Manchester, UK, 222 pp.

Petrulevičius, J.F. & Gutierrez, P.R. (2016) New basal Odonatoptera (Insecta) from the lower Carboniferous (Serpukhovian) of Argentina. *Arquivos Entomolóxicos*, 16, 341–358.
https://doi.org/10.5281/zenodo.12765386

Rajaei, H., Wappler, T., De Jong, R., Wahlberg, N. & Engel, M.S. (2026) Exceptionally preserved Oligocene emperor butterfly from France provides a new calibration point for Apaturinae evolution. *Acta Palaeontologica Polonica*, 71 (1), 185–191.
https://doi.org/10.4202/app.01332.2026

Rust, J. (2000) Fossil record of mass moth migration. *Nature*, 405 (6786), 530–531.
https://doi.org/10.1038/35014733

Sansom, R.S., Gabbott, S.E. & Purnell, M.A. (2010) Non-random decay of chordate characters causes bias in fossil interpretation. *Nature*, 463 (7282), 797–800. https://doi.org/10.1038/nature08745

Sansom, R.S., Gabbott, S.E. & Purnell, M.A. (2011) Decay of vertebrate characters in hagfish and lamprey (Cyclostomata) and the implications for the vertebrate fossil record. *Proceedings of the Royal Society B: Biological Sciences*, 278 (1709), 1150–1157. https://doi.org/10.1098/rspb.2010.1641

Smith, D.M. (2000) Beetle taphonomy in a recent ephemeral lake, southeastern Arizona. *Palaios*, 15 (2), 152–160. https://doi.org/10.2307/3515501

Smith, D.M. (2012) Exceptional preservation of insects in lacustrine environments. *Palaios*, 27 (5), 346–353. https://doi.org/10.2110/palo.2011.p11-107r

Smith, D.M. & Moe-Hoffman, A.P. (2007) Taphonomy of Diptera in lacustrine environments: A case study from Florissant Fossil Beds, Colorado. *Palaios*, 22 (6), 623–629. https://doi.org/10.2110/palo.2006.p06-119r

Smith, D.M., Cook, A. & Nufio, C.R. (2006) How physical characteristics of beetles affect their fossil preservation. *Palaios*, 21 (3), 305–310. https://doi.org/10.2110/palo.2004.p04-91

Sohn, J.-C., Labandeira, C.C. & Davis, D.R. (2015) The fossil record and taphonomy of butterflies and moths (Insecta, Lepidoptera): implications for evolutionary diversity and divergence-time estimates. *BMC Evolutionary Biology*, 15 (1), 12. https://doi.org/10.1186/s12862-015-0290-8

Sorrentino, J.A., Gibson, B.M., Jouault, C., Archibald, S.B., Piunno, P.A.E. & Laflamme, M. (2026) Controls on the sinking of hymenopterans and orthopterans in water of varying salinity: a taphonomic study. *Lethaia*, 59 (3), 1–17. https://doi.org/10.18261/let.59.3.1

Storari, A.P., Osés, G.L., de Almeida-Lima, D.S., Rizzutto, M.A., Bantim, R.A.M., de Lima, F.J., Rodrigues, T. & Sayão, J.M. (2024) Exceptionally well-preserved orthopteran proventriculi from the Cretaceous Crato Formation of Brazil. *Journal of South American Earth Sciences*, 133, 104737. https://doi.org/10.1016/j.jsames.2023.104737

Storari, A.P., Salles, F.F., Guedes da Fonseca, J.L., Saraiva, A.Á.F. & Rodrigues, T. (2025) Taphonomy of aquatic insects from the Crato Formation Lagerstätte (Aptian, Lower Cretaceous) under an actualistic look. *PLoS ONE*, 20 (9), e0331656. https://doi.org/10.1371/journal.pone.0331656

Ware, J.L., Simonsen, T.J., Rasmussen, J.A. & Archibald, S.B. (2025) Systematics of the extinct suborder Cephalozygoptera (Odonata): a wing-based analysis comparing its genera with those of extant Zygoptera. *American Museum Novitates*, 4043, 1–20. https://doi.org/10.1206/4043.1

Wehmann, H.-N., Engels, T. & Lehmann, F.-O. (2022) Flight activity and age cause wing damage in house flies. *Journal of Experimental Biology*, 225 (1), jeb242872, 1–13. https://doi.org/10.1242/jeb.242872