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**TAPHONOMIC BIASES IN THE INSECT FOSSIL RECORD:
INCONSISTENT PRESERVATION OVER GEOLOGIC TIME**

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF SCIENCE

in

EARTH SCIENCES

by

Jered Karr

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ABSTRACT

Jered Karr

Taphonomic biases in the insect fossil record: Inconsistent preservation over geologic time

Insect taphonomy is a topic that has drawn interest because of its potential biases on diversity and ecological information recorded by ancient insect faunas. To be preserved as a compression fossil, insects must be transported from their original habitat, break water surface tension and sink, and avoid degradation and predation while in the water column and prior to burial. We assembled a database of more than 6400 Carboniferous-Pliocene insect compression fossils from the primary literature to test biotic and environmental controls on preservation quality. We grouped the fossils into 10 Myr bins and scored preservation quality as either articulated bodies or isolated wings; specimens with a body implied higher quality of preservation. Paleozoic and Triassic insect fossils are known overwhelmingly from isolated wings (only 20% articulated bodies), but our database shows a significant increase in the percentage of specimens preserved as articulated bodies beginning in the Late Jurassic, about 160 Myr ago. This transition could reflect variations in the robustness of different insect orders and shifts in the taxonomic composition of insect faunas, but all the major groups in the database exhibit significant increases in articulation. Instead, a shift in the frequency of insects preserved in different paleoenvironments could explain the trend. Lacustrine, especially large lake, sediments contain a greater proportion of articulated bodies. The change in the paleoenvironment of where insects

are preserved is the most important factor in explaining the increase in articulation of insect fossils.

INTRODUCTION

Insects are the most diverse and successful animal group today (Gaston 1991) but understanding their past evolutionary patterns, diversity, and ecology may be hindered by the effects of preservational biases. Studies on other groups of organisms have shown that taphonomic processes can change our view of ecologic roles and importance (Wright et al. 2003; Wilson 2008; Cherns and Wright 2009). Many taxonomically-important characters of insects can be obscured by taphonomic processes, making identification difficult and obscuring evolutionary relationships among groups. Poor identifications can alter apparent diversity (e.g., the case of Protorthoptera (Hughes 1995; Béthoux 2005, 2007)) and bias ecological interpretation about habitats of extinct insects or environmental reconstruction (Béthoux and Nel 2003; Wilson 2008; Cherns and Wright 2009). Labandeira and Sepkoski Jr. (1993) note that their diversity curve is likely biased by exceptional Tertiary deposits such as Baltic amber and Florissant shales. Understanding the factors that influence apparent diversity can also help us elucidate the true past diversity of important groups of animals such as insects.

Although their fossil record is richer than generally assumed (Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005) insects lack mineralized tissue and their preservation usually requires extraordinary circumstances; the presence of insects is considered

indicative of a “Konservat-Lagerstätte” (a fossil locality characterized by exceptional preservation, usually of soft tissues). These Konservat-Lagerstätten come from an array of different environments, such as marine, small ponds, large lakes, or amber, which may have been influenced by a variety of possible biases. Because amber preservation first became common in the earliest Cretaceous and has a different set of taphonomic biases (Zherikhin et al. 1999; Martínez-Delclòs et al. 2004) we will focus only on compression fossil preservation, which was present throughout the insect fossil record.

Factors such as insect size, taxonomic group and depositional environment influence if and how well an insect is preserved in the fossil record. Temporal trends in the importance of those factors may drive systematic biases in preservation quality. Insect size has broadly decreased since the Late Carboniferous/Early Permian (Clapham and Karr 2012). Taxonomic changes in insect assemblages might also have influenced levels of preservation because preservation potential depends on the amount of sclerotization of the exoskeleton and other factors. For example, groups with high preservation potential, such as beetles, have increased and other groups with low preservation potential, such as cockroaches, have decreased since the Carboniferous (Labandeira and Sepkoski Jr. 1993). Smith (2001) showed that during the Cenozoic Diptera and Coleoptera are found in more types of depositional environments and that their quality in terms of preservation is more exceptional. Other researchers have noted a systematic change in the paleoenvironment of Konservat-Lagerstätten but it is unknown how this shift has affected preservation of all animal groups and in

particular insects. The Carboniferous is noted for abundant delta plain Lagerstätten while the Jurassic has many marine Lagerstätten, and more onshore and lacustrine Lagerstätten occur in the Cretaceous and Cenozoic (Allison and Briggs 1991; Briggs 2003).

Many studies have assessed the factors that influence insect preservation quality, but these studies have largely focused on single localities with specific environmental conditions (Wilson 1980, 2008; McCobb et al. 1998; Ansorge 2003; Coram 2003; Wappler 2003). We examined long-term trends in the preservation of insects, which may bias studies of taxonomy, diversity, or paleoecology, using a large database of specimen data from the primary literature. We tested the effects of depositional environment, insect size, taxonomic group and geologic age on the quality of insect preservation. Understanding the overall biases in the fossil record of insects will allow assessment of the ecology and evolution of this group across geologic time and comparison with trends observed in other groups of animals and plants.

Insect Taphonomy

Smith (2012) divides the factors that control preservation quality into “insect inputs” and “depositional factors”. The morphology and ecology of the insect are included in “insect inputs”, including variables such as body size, shape and insect group. Depositional factors include environment type and tectonic setting, including differences in sediment types, sources, bathymetry and energy levels in the system

and various other factors. These factors determine how an insect progresses through various steps on the path to preservation.

To make inferences about paleoenvironment and the biological community, the steps from living insect to fossil to published literature must be understood. The rate at which an insect passes through these steps influences the quality of preservation, affecting the time exposed to predation, decomposition and disarticulation. An insect must pass through four taphonomic steps, which act as filters, before being preserved as a compression in the fossil record. First, the body must be transported to an aquatic environment, by rafting, aerial deposition, or by being aquatic as a lifestyle. Most insects are not aquatic so they have to go through the second step: breaking the surface tension of water. Martínez-Delclòs and Martinell (1993) examined insect deaths in aquatic environments of a variety of taxonomic groups. There was a large range of outcomes depending on size, weight, wing type, SM (Surface area-to-Mass) index and shape, with a bias against large-winged or fragile groups such as Lepidoptera and against insects with wingspans smaller than 5 mm, leading to enrichment in heavy-to-medium sized insects at the sediment interface. The SM index is a ratio of the surface area of the wings (cm^2) to the body mass ($\text{g}^{0.667}$) of the insect (to deal with the allometric relationship between surface and mass, mass is raised to the two thirds power) (Wagner et al. 1996). Archibald & Makarkin (2006) and Wang et al. (2013) show that insects with larger SM indexes are more prone to disarticulation likely due to longer floating time at the water surface. Larger wings commonly have microstructures that influence the wettability of the wings and can

increase floating time as well (Wagner et al. 1996; Rust 1998; Archibald and Makarkin 2006). Another important factor in how long it takes an insect to break the water surface is whether it arrives on the water surface alive or dead. Already dead insects take longer to sink than those that die by asphyxia on the water surface, because the intake of water into the tracheal system of insects struggling at the surface decreases buoyancy. After breaking the water surface, the third step is sinking through the water column. The rate at which an insect sinks is determined by the temperature and chemical composition of the water. The density change at the thermocline or halocline (in salt water environments) prevents sinking and promotes decomposition before carcasses can be deposited on the sediment (Martínez-Delclòs et al., 2004). The final step is burial after the insect settles onto the sediment. The rate at which burial occurs depends on the distance from shore, water chemistry, and tectonic setting. In studies of Eocene-aged lakes from British Columbia, Wilson (1980, 1988) noted a trend for more articulated specimens in offshore compared to near shore sediment. In another study Briggs et al. (1998) found that insects from deep-water anoxic zones had 95-98% more chitin preserved than insects from the shallower oxygenated part in Pliocene lake sediments from Willershausen, Germany.

After being preserved as a fossil the insect must still be collected and described, which may impart a different set of biases. Due to differences in sampling intensity and the emphasis of the collector, widely different ratios of taxonomic groups can be collected at the same locality (Sukacheva and Rasnitsyn 2004). The final step after being collected is description and entering the published literature. There presumably

is a strong bias towards describing better-preserved material, which have more diagnostic characters that allow the specimen to be readily identified.

METHODS

All data used in this study are based on primary literature from 1743 references. We entered all of the occurrences, collections, taxonomy and sizes used in this study into the Paleobiology Database (PaleoDB: <http://paleodb.org>); the data used here were downloaded on 31 May 2013. All Insecta were included in this study. We scored each species based on the holotype specimen and categorized it as either an exoskeleton (“articulated”) or wing element (“disarticulated”); that categorization was applied to all records of the species. All wing elements (elytra, tegmen, forewing, hindwing, wing) were grouped together (Fig. 1). An exoskeleton is composed of any specimen with a substantial portion of the body, with or without wings. We excluded all species where the type body part was unidentified or where the body part was a nymph, cephalon/head, abdomen, appendages, other, carapace, or thorax or limb element(s). The PaleoDB includes occurrences where the fossil has not been identified to the species level, usually due to poor preservation. We excluded these generically or specifically indeterminate occurrences due to our decision to score articulation based on the holotype, and we also excluded questionably identified genera and species. We considered specimens scored as “exoskeleton” to be indicative of better preservation because it indicates a larger proportion of the animal instead of a fragment such as a wing. Experiments examining the various stages of insect decomposition found that

the body of insects decomposes even as the wings remain intact (Duncan et al. 2003), indicating that even well preserved isolated wings are representative of one of the final stages of decomposition.

For each locality, we assessed the depositional environment to test its effect on preservation. The Paleobiology Database allows specification of a wide range of environments for each collection, making analysis unfeasible due to small sample size in some cases, so similar environments were grouped together into the following categories: marine, delta/lagoon, HE (high energy) terrestrial, shallow lakes, and deep lakes. All collections with amber as a lithology were excluded. The paleoenvironment for each collection was either determined from the original paper or was based on other papers discussing the locality. The approximate area of some localities that we classified as large lakes range from 31 km² for Florissant (Veach and Meyer 2008) and 20 km² for the Yixian Formation (Hethke et al. 2013), to 40,000 km² for Lake Gosiute (Green River Formation; Surdam and Stanley 1980). Some localities do not have published estimates of lake area. In these cases, basin size and duration were used to determine the nature of the environment, based on the assumption that a large lake would have thick beds of lacustrine sediment indicating a homogeneous depositional environment for a sustained amount of time, compared to a small lake that is ephemeral with a short record. Because we consider depth to be an important factor, this category contains several lakes with smaller surface area but with significant depth; including most crater lakes such as Messel (depth of 300-400 m) (Harms 2002; Felder and Harms 2004), the Eckfeld Maar (depth of 110-150 m) (Lutz

2003), Menat (mentioned as a deep crater lake) (Wappler et al. 2009), and the Randeck Maars (depth of 150 m) (Zeuner 1942). We used the term “deep lake” to signify all these types of lacustrine environments.

Size data were also collected to examine their impact on articulation. The length of the wing, tegmen (Orthoptera and relatives, Blattodea and relatives, some Hemiptera), elytron (Coleoptera), or hemelytron (some Hemiptera) was recorded, along with the wing width. In groups with two pairs of wings (fore and hind wings), the larger of the two pairs was used. Sizes were taken from measurements directly reported in the systematic description or were measured from published illustrations if no size was given in the text. Many fossil wings are incomplete because of taphonomic degradation following the death of the insect, especially in the largest insects, so we used estimates of complete wing size provided in the description. After taxonomic filtering and removing amber specimens we have 6409 measured species.

We binned the data into 30 time intervals equivalent to geological stages or sets of neighboring stages, starting in the mid Carboniferous. The interval definitions are the PaleoDB 10-million-year bins, the same as those used in several recent papers (Alroy et al. 2008). Stage level time intervals were not used due to a paucity of data and uncertain age assignment of many localities, with many stages having no occurrences at all when applying all the sifting criteria.

Model Construction

We performed regression analysis to estimate the relationship between variables. Our dependant variable (whether a specimen was articulated or not) is binary so we performed logistic regression analysis. We created logistic regression models in R (R Development Core Team 2012) with different combinations of three independent variables; “size”, “morphology”, and “environment”. We \log_{10} transformed wing size to normalize the size distribution. All measurements are in mm. We coded the morphology predictor as a binomial factor; beetle or non-beetle. We did this for simplicity and even though different orders/groups have different preservation potential beetles have the greatest preservation potential (Smith 2000). If morphology is an important predictor of whether or not a specimen is articulated the fact that the specimen was a beetle or not should show this. We coded the environment predictor as a binomial factor as well, whether the specimen came from a “deep lake” or a “non-deep lake” paleoenvironment. Non-deep lake environment includes marine, delta/lagoon, HE (high energy) terrestrial environments, and shallow lakes. We did this principally for simplicity but also because there are multiple reasons to believe that deep lakes should have superior fossil preservation compared to other environments. Because we wanted to keep the results interpretable, we narrowed our pool of models to only combinations of these three variables and did not include interaction effects. We used Bayesian information criterion (BIC) to determine model selection.

To determine which predictor variable has the largest effect on articulation we looked at the odds ratio, which is a measure of effect size. In the case of the “environment” predictor it is simply the odds of an insect being articulated in a deep lake divided by the odds of an insect being articulated in a non-deep lake. An odds ratio of one means there is no relationship between the predictor and the dependent variable. An odds ratio of less than one means indicates a negative relationship.

To look at how different variables affected different orders we analyzed six common orders: Odonata (dragonflies and damselflies), Blattodea (cockroaches), Orthoptera (grasshoppers and crickets), Hemiptera (bugs), Diptera (flies), and Coleoptera (beetles). Separate logistic regression models were run for these six common orders to see how the two variables “environment” and “size” affected articulation.

To examine the effect that size had on articulation alone we ran a logistic regression model with just size as a predictor. We also performed this analysis on the same six orders.

We wanted to be able to look at the relative importance of all three predictor variables on modeled articulation. “Environment” and “morphology” are both binomial predictors while “size” is continuous, making comparison of the relative importance of size more difficult. We used the mean \log_{10} size for the Cenozoic as “small” (0.868) and the mean for the Carboniferous as “large” (1.60), converting size to a binomial predictor comparable to environment and taxon. We then predicted the probability of articulation through geologic time based on the eight possible

combinations of the now binomial predictor variables (size, morphology, environment). We also wanted to see how well the changes observed in the dataset of these three variables could predict the probability of articulation through geologic time. “Size” was then replaced with values ranging continuously from 1.60 in the oldest bin to 0.868 in the youngest bin. “Environment” was replaced with values ranging from 0.06 to 0.9 (the proportion of insect occurrences occurring in deep lakes in the Paleozoic and Cenozoic, respectively) and “morphology” was replaced with values from 0.0 to 0.4 (the proportion of insect occurrences that are Coleoptera in the Paleozoic and Cenozoic). A new predicted probability of articulation was calculated based on these values in the three variables.

All occurrences (open grey circles) in graphs have been “jittered” this adds a small amount of noise to the points. Giving a better sense of the quantity of occurrences in each 10 Myr bin.

RESULTS

Overall Pattern

The percent of articulated insect fossils has increased in through time. Before the Late Jurassic (Jurassic bin 5, Callovian-Kimmeridgian, ~161 Ma), 78.1% of insect holotypes are disarticulated wing elements, whereas 72.2% of holotypes in the Late

Jurassic and after are preserved as articulated bodies (Fig. 2). All orders except Lepidoptera (small sample size and dramatic size decrease) that have occurrences before and after the Late Jurassic show an increase in articulation after the Kimmeridgian (~150 Ma). For a logistic regression model with only age as a determinate variable the predicted probability of articulation changes from ~14% to ~83% over time (Fig. 3).

We created multiple logistic regression models and compared them using BIC. The logistic regression model including all three variables (environment, morphology, and size) was the best-supported (Table 1), suggesting that environment, morphology, and size all significantly affect insect preservation. The odds ratios for all the predictor variables are in the first row of Table 2. They are a measure of effect size each predictor has on articulation. The odds ratio for “size” is significantly less than one, meaning increases in size decrease the odds of a specimen being articulated. The odds ratios of “morphology” and “environment” are both significantly ($P < 0.001$) larger than one indicating that being a beetle or from a deep lake increases the odds of the specimen being articulated.

Morphological Controls.

Testing if orders have changed in abundance we grouped orders into higher-level groups to examine the changes in proportions of groups. The major groups we recognized are Antliophora, Coleoptera, Hymenoptera, Orthopteroid, Paraneoptera, Paleoptera, Neuropterida, Dictyoptera, Amphiesmenoptera and Protelytroptera (Fig.

4). The paleopteroid groups (Paleoptera) lack wing-folding mechanisms and are the earliest winged insects. Orthopteroid taxa, Dictyoptera Paleoptera groups are composed of typically larger and/or less robust taxa with large SM ratios and diagnostic wing elements. Of the eight most common orders in our database, Blattodea (Dictyoptera), Orthoptera (Orthopteroid), and Odonatoptera (Paleoptera) are dominant in the early part of the record whereas Coleoptera, Diptera (Antliophora), and Hymenoptera, which are all smaller and/or more robust taxa commonly requiring body features for identification, become dominant in the late Mesozoic and Cenozoic (Fig. 4). This shift likely contributed to increased articulation in younger collections, but was not the principle factor because all well-sampled taxonomic groups independently increase in articulation through time (Fig. 5).

Odonatoptera

Odonatoptera (total-group Odonata and extinct relatives like Meganisoptera) includes large insects with high SM index wings that are spread away from the body at rest (except in Zygoptera). Only 30.9% of Odonatoptera species have been described from articulated bodies, but articulation increases significantly in younger collections.

Because articulation does not change significantly within environments (Fig. 5a), the trend appears to be due entirely to the shift from more non-deep lake environments in earlier localities to more deep lake environments in younger strata.

Blattodea

Blattodea (cockroaches) have forewings that are hardened into tegmina, which are more resistant to degradation than bodies or hindwings. Blattodea holotypes are most commonly an isolated tegmen in Paleozoic deposits but in the Mesozoic and Cenozoic they are more commonly articulated bodies (Fig. 5b). The abundance of Paleozoic species influences the mean percent articulation with only 25.1% of species being described from articulated bodies. Like in Odonoptera, articulation did not change significantly over time within environments so the overall trend toward better preservation can be explained by a shift from non-deep lake to deep lake environments.

Orthoptera

Orthoptera (crickets and grasshoppers) can be quite large (the suborder Titanoptera reached wing lengths of 180 mm during the Triassic) and have sclerotized forewings like Blattodea. Overall articulation is even lower than in Blattodea (14.9% of species holotypes are articulated). Within-environment trends are more difficult to reconstruct because there are no deep-lake occurrences of Orthoptera before the Jurassic, but articulation likely increased significantly both in non-deep lakes and in deep lakes (Fig. 5c). The shift in environment contributed to increased articulation but unlike in Blattodea, cannot fully explain the trend. Within-environment increases in articulation are opposite to predictions based on the smaller size of Cenozoic Orthoptera (see size section) but may have been caused by shifts in taxonomic composition within Orthoptera.

Hemiptera

Hemiptera (true bugs) are one of the most heterogeneous orders, with some families consisting of small robust species similar to Coleoptera and other families consisting of large winged fragile groups more similar to Odonatoptera. Overall articulation increases considerably, with some contribution from the shift to deep lake preservation, but with a larger contribution from changes in articulation within deep lakes and non-deep lakes (Fig. 5d).

Diptera

Diptera (flies) are small insects and have simple wing venation, making them difficult to identify in the fossil record without articulated preservation. They are so small that it is normally difficult for them to break surface tension, but are well articulated (70% of species described from complete bodies). Articulation increases slightly in both non-deep lakes and deep lakes. Increased preservation in deep lakes accounts for a greater proportion of the overall trend toward increased articulation in Diptera (Fig. 5e).

Coleoptera

Coleoptera (beetles) are well articulated (71.8% of species holotypes are complete bodies) and increase in abundance towards the modern (11.3% of occurrences before the Late Jurassic and 20.3% after in our database). Although overall articulation

increases significantly, due to the shift towards preservation in deep lakes, within-environment articulation apparently decreases in both deep lakes and, to a greater degree, in non-deep lakes (Fig. 5f). Nearly 70% of beetle species described before 1950 were from Cenozoic localities, compared to less than 25% of species described after 1950. Restricting the analysis to species described after 1950 reduces the effects of taxonomic practice and indicates no significant shift in articulation within environments and confirms the importance of the shift to preservation in deep lakes (Fig. 6).

Size

Size has a negative relationship with articulation in our database (Fig. 7). Insect size decreases towards the modern while articulation increases, suggesting it is possible that this decrease in size could have played a causal role in the increase in articulation. Because other morphological factors vary among orders, it is important to look at the trends within each order to assess the effects of size alone. Of the six best sampled orders only three have a strong negative relationship between size and articulation (Fig. 8). The odds ratios in Orthoptera and Blattodea indicate increases in size are positively correlated with increased articulation while in the other four orders it is negatively correlated with increases in articulation (Table 2). There is a strong trend of orders with large wing size (and likely body size) being less articulated than orders with small wing size, implying that intra-order decreases in size had a smaller effect on articulation than the replacement of larger orders by typically smaller ones.

Environment

The predicted probability of a specimen being articulated increased through time in non-deep lake localities from ~20% to ~40%, and from ~60% to ~85% in deep lake environments (Fig. 3). In all six orders, the odds ratios indicate preservation in deep lake environments significantly increased articulation (Table 2). Changes over time in the abundance of deep lake environments, which have greater articulation because of low water energy and frequent anoxia, exerts a major influence on temporal trends in insect preservation (Fig. 9). Only 5% of pre-Late Jurassic insect occurrences are from deep lakes, compared with 76.3% of younger occurrences. Orthoptera and Odonata are generally strong fliers and are nearly equally common in the three main environments, including marine settings far from their original habitats. Coleoptera and Diptera are generally poor fliers, however, and are found in much higher percentages in deep lakes; 69.3% for Diptera and 58.8% for Coleoptera (Table 3). Because few if any insects are marine, lake environments are closer to their original habitat.

Predictor variables importance

For an insect preserved in a deep lake the odds of being articulated are 918% higher than the odds for an insect in a non-deep lake environment. The odds of articulation for beetles are 107.2% higher than the odds for non-beetles, implying that changes in environment have a greater effect on insect preservation than differences in insect morphology. For every \log_{10} increase in size the odds of articulation decrease by

77.5%. Figure 10 shows the relative importance of all three predictors while holding the others constant (resulting in eight possible combinations). Deep lake environments (filled circles in column A) consistently have greater articulation, regardless of taxonomy or size, implying that although size and taxon group affect articulation, the largest contributor is environment.

We modeled the effects of environment, size, and morphology by creating a simulated dataset and compared the results to the observed trends (black line in Fig. 10, based on articulation over time). Using our logistic regression model on this idealized database we were able to closely simulate the change in articulation over time, indicating that changes in these three predictors are the primary controls on insect articulation in the fossil record.

DISCUSSION

Morphological Controls.

Insects are a very disparate group with major morphological differences among orders, which likely influences overall assemblage articulation due to changes in the relative diversity of insect orders through time (Labandeira and Sepkoski Jr. 1993).

Articulation proportions based on published holotypes depend not only on taphonomic biases during fossilization, but also on conventional taxonomic practices for species description in a particular group. The characters that would help an insect

survive fossilization and be preserved as an articulated specimen include robustness, small size, low SM index (the ratio of wing area to body weight) and an aquatic lifestyle. However, paleoentomologists are less likely to describe new species based on isolated wing elements if the group (such as Coleoptera or Diptera) has relatively nondescript elytra or wings and species discrimination is instead heavily reliant on body features. As a result, Coleoptera or Diptera holotypes are more likely to be articulated than the average specimen, whereas Odonata holotypes (a group where wing venation contains relevant taxonomic characters) will be less biased.

Of the six orders we analyzed there is three general patterns 1) each environment has a steady level of articulation, but overall articulation increases. Odonatoptera and Blattodea show this pattern. 2) Both environments increase in articulation and overall articulation increases. Hemiptera, Orthoptera and Diptera exhibit this pattern. 3) Both environments decrease in articulation and overall articulation increases. Coleoptera is the only order with this pattern. Blattodea and Odonatoptera have had a fairly stable morphology and a robust record in both environments over geologic time. Hemiptera, Orthoptera and Diptera all have had changes in morphology through time which likely influences the increase in each environment. Coleoptera has had a change in taxonomic practices, which due to the nature of the literature unduly decreased articulation in the Cenozoic.

Odonatoptera

Odonoptera wings are highly diagnostic and provide important taxonomic information. This plus the fact that they are a Paleopteroidea and can't fold their large wings decreases their articulation. Odonoptera are the one Paleoptera group that has a steady number of occurrences in our database did not readily decrease in abundance.

Blattodea

It has been hypothesized that abundance of isolated cockroach tegmina in the Paleozoic is due to arachnid predators eating the body and leaving isolated forewings (Duncan et al. 2003). Because poor articulation was not restricted to the Paleozoic, this hypothesis could not explain the consistently low levels of articulation in non-deep lakes. Blattodea found in lacustrine sediments would be subjected to a completely different set of taphonomic filters. Vrřanský (2004) also noted higher levels of disarticulation during warmer periods in the latest Jurassic and earliest Cretaceous, but we cannot distinguish temperature-related trends in our data set. Instead the shift from non-deep lake to deep lake environments explains why cockroaches have increased in articulation (Fig. 5b).

Orthoptera

Some descriptor bias is likely partly responsible for Orthoptera articulation being lower than Blattodea. Orthoptera forewings have less plastic venation than Blattodea, making forewing venation useful for taxonomic identification. Cenozoic Orthoptera are largely composed of Acrididae (short-horned grasshoppers) and Tettigoniidae

(katydids), two orders that been observed to have an unusual response to drowning in actualistic experiments (Martinez-Delclos and Martinell 1993); possibly extinct orders did not have this behavior. There is also a trend of wing reduction in Orthoptera (Sharov 1968), which would decrease their SM index and promote sinking.

Hemiptera

That large increase within environments is likely due to a change in abundances of different families. Heteroptera, a suborder within Hemiptera that often contains smaller, beetle-like species with folded tegmina, are in general more articulated and constitute larger proportion of occurrences later in the fossil in record as compared to ‘Homoptera’ a paraphyletic assemblage of generally large-winged and less articulated Hemiptera.

Diptera

Articulation increases slightly in both non-deep lakes and deep lakes, possibly reflecting a shift from more fragile dipteran groups such as Tipulomorpha to more robust groups such as Muscomorpha. Diptera does have high percent articulation through out the fossil record. Most of the increase seen in the total articulation reflects a shift in preservation environment.

Coleoptera

Coleoptera have a higher preservation potential than other insect orders in both modern, actualistic studies and lab experiments (Smith 2000; Smith et al. 2006). Coleoptera forewings have been highly modified into hard sheaths called elytra, which are generally not very diagnostic at the species level. Our results support these findings, as Coleoptera is one the most highly articulated group in our study. The predicted the probability of articulation decreases in both deep lake and non-deep lake (Fig. 5). This is due to the fact that earlier paleoentomologists, especially in the 19th century, described many species based on isolated elytra from Cenozoic localities such as Radoboj, Oeningen and Florissant. Mesozoic and Paleozoic isolated elytra typically have little taxonomic value (even at the family or suborder level) and are rarely named by modern paleoentomologists (Arnoldi et al. 1977; Ponomarenko 2002). Several recent studies of Mesozoic localities have instead of describing isolated elytra, listed them in a series of morphotypes with no taxonomic assessments (Papier et al. 2005; Martin 2010). Figure 6 illustrates the effect of this change in philosophy of what specimens should be described. With this difference removed articulation is stable in deep lake and non-deep lake and that total increases in percent articulation over time are due to a shift from non-deep lake to deep lake. The fact that even Coleoptera; the order with the highest preservation potential, follow this trend indicates that depositional environment is an overriding factor.

If morphology changes in insects was the most important factor an order that should show this change would be Coleoptera, but overall insect percent articulation did not

increase until the Late Jurassic even though Coleoptera had been an important group since the Early Triassic (~240 Ma).

Size

It is thought that size (wing length) can affect articulation for several reasons. Large winged insects have better flying capabilities and can be found in a wider range of habitats, including marine environments that are less ideal for articulation. Larger winged insects are also likely to have a higher SM index, which increases floating time on the surface of the water (Wagner et al. 1996). SM index accounts for allometric scaling therefore a dragonfly with a wing length of 20 mm will have a very similar SM index to a dragonfly with a wing length of 100 mm, due to their similar body-to-wing proportion. There are however large differences in the SM index among orders due to the great disparity in insect body plans. For example a dragonfly with the same wing size as a wasp will have a very different SM index because the wing size-to-body ratio is low in Hymenoptera and high in Odonata. Larger insects also require more sediment accumulation before being buried and thus are likely to be at least partially exposed on the sediment surface longer and hence more prone to disarticulation. Larger insects are subjected to more intense predation (Blanckenhorn 2000; Chown and Gaston 2010) disarticulating them or removing them from the death assemblage. Smaller insects are more common in modern ecosystems (and have always been), increasing the odds of having at least one specimen with more favorable preservation. Henning et al. (2012) and Smith and Moe-Hoffman (2007)

found that there was a bias towards larger insects in deep water facies at Florissant, and that they also had higher articulation. They concluded this was caused by a wider size range of insects being deposited in the deep lake because sediment accumulation was slower and the death assemblages had longer to accumulate. Flight capabilities influencing burial environment, water surface floating time, predation, and burial time are likely the four most important size-related factors that affect articulation.

Changes in the median size of insects through time could influence articulation and it is known that the size of insects has changed over time (Dudley 1998; Okajima 2008; Clapham and Karr 2012). The median wing size of insects in our database during the Carboniferous is more than 30 mm but decreases to only 7 mm during the Cenozoic. The difference in median wing size before the Late Jurassic (12 mm) and after (7.9 mm) is less dramatic. This trend towards a decrease in size towards the modern is not uniform across all orders. Odonoptera wing length changed from a median of 140 mm in the Carboniferous to a median of 35 mm during the Cenozoic, whereas Coleoptera median size remained astonishingly stable at around 5 mm. The overall trend of decreasing median size seen in insects is influenced by two factors. The first is the replacement of large winged Paleopteran orders such as Palaeodictyoptera and Megasecoptera with small winged orders such as Diptera and Hymenoptera. The second is a decrease in median size of both Orthoptera and Odonoptera, two large winged groups, which are found abundantly throughout the insect fossil record. And our results indicate that size is an important factor on whether an insect is preserved as articulated or disarticulated specimen.

Environmental Controls

Our results indicate that insects have consistently been more articulated when buried in deep lakes over their entire evolutionary history, in agreement with detailed studies of specific localities (Wilson 1980; Smith and Moe-hoffman 2007; Henning et al. 2012). Deep lakes favor better preservation through a variety of physical and chemical mechanisms.

Deep lake floors are calm, low-energy environments, which are unlikely to physically break up dead insects, whereas carcasses in smaller lakes are subjected to higher energy due to mixing of the water column. Insect carcasses in near shore marine and marginal marine environments are subject to greater wave action than found in lakes. Even insects preserved in offshore marine sediments must still pass through the wave-influenced mixed layer, which is thicker in the ocean than in lakes because of the longer fetch of wind-generated ocean waves. Physical destruction or disarticulation during transport also reduces preservation probability or quality. Because nearly all insects are terrestrial, transport distance to the ocean is usually farther than to lacustrine environments, leading to better preservation in lakes.

Anoxia is known to be important in increasing the quality and likelihood of preservation by preventing scavengers and bioturbators from disturbing insect carcasses on or in the sediment. Anoxia is also known to promote microbial mats that may enhance mineral precipitation around a soft bodied organism such as an insect

(Allison 1988; Behrensmeyer et al. 2000). Anoxic bottom waters are frequently developed (at least seasonally) in large deep lakes. It is uncommon for shallower lakes to have anoxic bottom waters because mixing of the water column prevents the depletion of oxygen in the bottom waters (Olsen 1990; Scheffer 2004). Ocean basins are also prone to anoxic bottom waters and several famous Konservat-Lagerstätten are from anoxic environments (e.g. Solnhofen). Water chemistry is also important, with high solute concentration having been noted to help with preservation of soft bodied organisms by facilitating the precipitation of authigenic minerals (Briggs 2003). Whereas the ocean's solute concentration is relatively stable and smaller water bodies usually don't have time to accumulate large amounts of solutes, endorheic lakes such as Lake Gosiute (Green River Formation), which often formed in interior rift basins (Surdam and Wolfbauer 1975; Smith et al. 2008), can have extremely high levels of minerals that lead to unusual water chemistry that can be beneficial for preservation (Allison and Pye 1994).

Variations in taxonomic composition among depositional environments likely influences articulation, specifically differences in the abundance of groups with different intrinsic preservation potential (Table 3), but this is a secondary factor.

The dramatic shift in preservation environment can explain a large amount of the major increase in articulation over time due to the fact that deep lakes have higher levels of articulation than all other environments. This holds true across different groups (Fig. 5), sizes and through time.

Our results indicate that insect morphology, size, and depositional environment all significantly affect articulation, but what is the relative importance of each factor? The odds ratios (Table 2) and Figure 10 clearly suggest that the environment that an insect was preserved in has the largest influence on whether or not a specimen was articulated.

CONCLUSION

Insect preservation in the fossil record has changed over geological time to become dominated by articulated specimens with well-preserved bodies and wings. Insects after the Late Jurassic have higher chances of being articulated. This shift is due to three factors. The first is a decrease in the average size of insect specimens. Larger insects are less articulated than smaller insects but this variable is not very strong or consistent when subjected to deeper analysis. The second factor is change in taxonomic groups. Earlier paleopteroid groups, which lack wing folding mechanisms, and orthopteroid groups were much more common in the Carboniferous and Permian whereas a more modern fauna dominated by Coleoptera, Diptera and Hymenoptera did not become established until the Jurassic. Coleoptera, Hymenoptera and Diptera (especially Coleoptera) all have characteristics that should lead to better preservation and their fossils are on average much more articulated. In contrast to paleopteroids, which have all the characteristics that are hypothesized to lead to disarticulation. However, even paleopteroids increase in articulation over time, implying that taxonomic shifts also cannot completely explain the observed increase in articulation.

Our analysis suggests that the depositional environment in which an insect is preserved is the most important control on preservation quality. Insect fossils from deep lakes have higher rates of articulation compared to the other paleoenvironments and there is a dramatic shift in the Late Jurassic from delta/coastal, marine and smaller lakes to deep and/or large lakes. This shift in preservation could affect the patterns in insect diversity, evolution, and ecology that are preserved in the fossil record, for example by biasing diversity in older parts of the insect record where preservation quality is poorer. Accounting for differences in depositional setting is essential to truly understanding the fossil record of insects and likely other groups including birds and plants that are also found largely in Konservat-Lagerstätten.

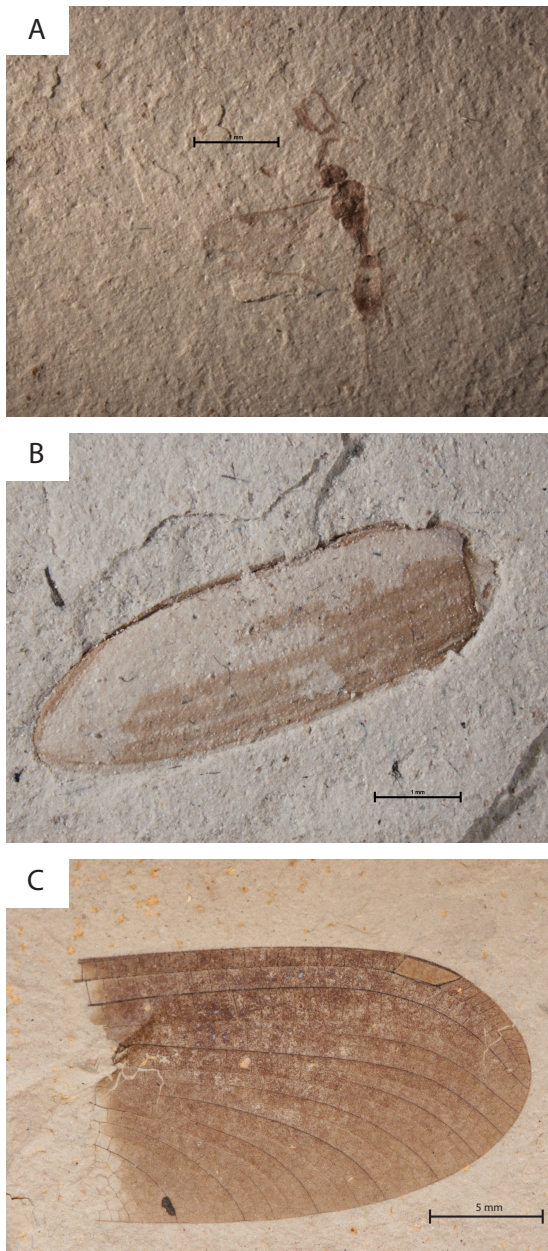


Fig.1. Examples of articulation in fossil insects. (A) Articulated insect fossil; unnamed wasp. UCMP 167601; Stewart Valley paper shales; scale bar=1 mm. (B) Disarticulated insect fossil; unnamed beetle elytron. Author's personal collection; Stewart Valley paper shales; scale bar=1 mm. (C) Disarticulated insect fossil; unnamed damselfly wing fragment. UCM 5836ab; Green River Formation; scale bar=5 mm.

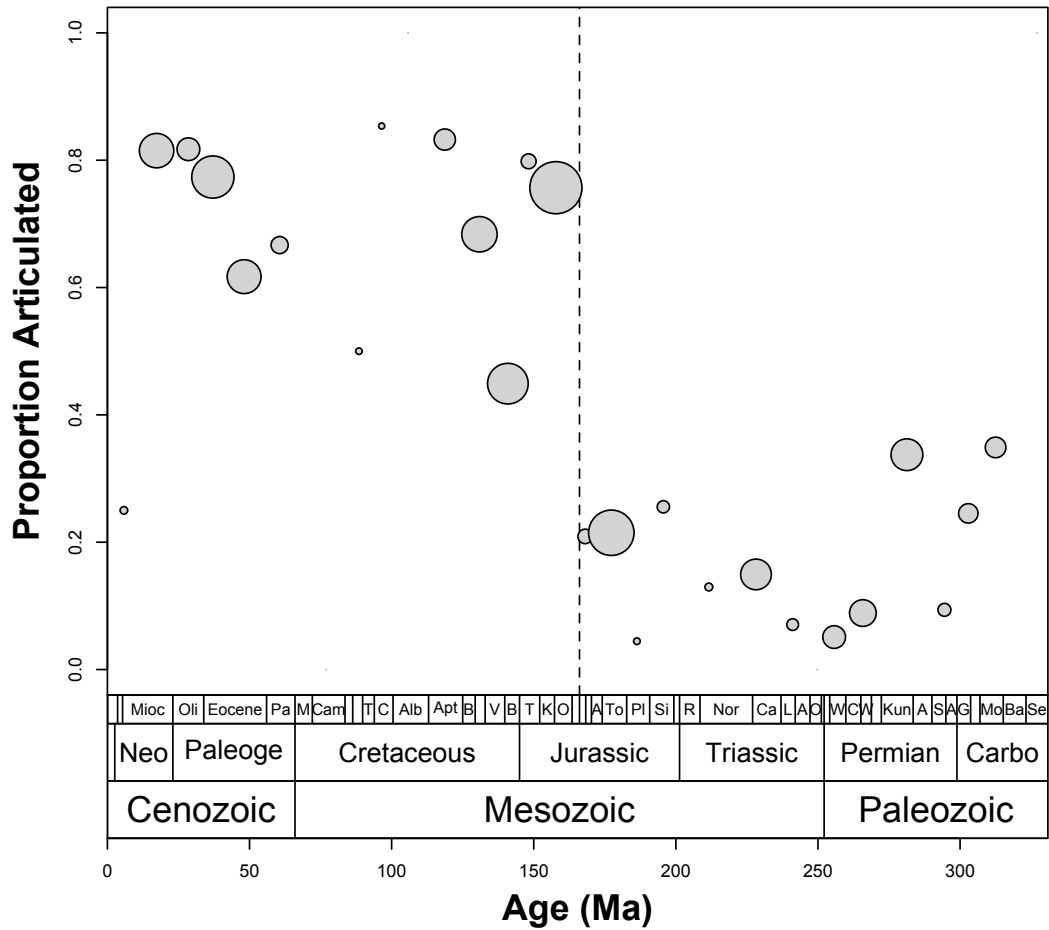


Fig. 2. Phanerozoic trend in insect articulation, based on the proportion of occurrences of species with articulated holotypes in each 10 Myr bin. Bubble size scales with the number of occurrences in 10-Myr bins with the largest bin containing 917 occurrences. Dashed line represents beginning of the Callovian (Beginning of Jurassic Bin 5).

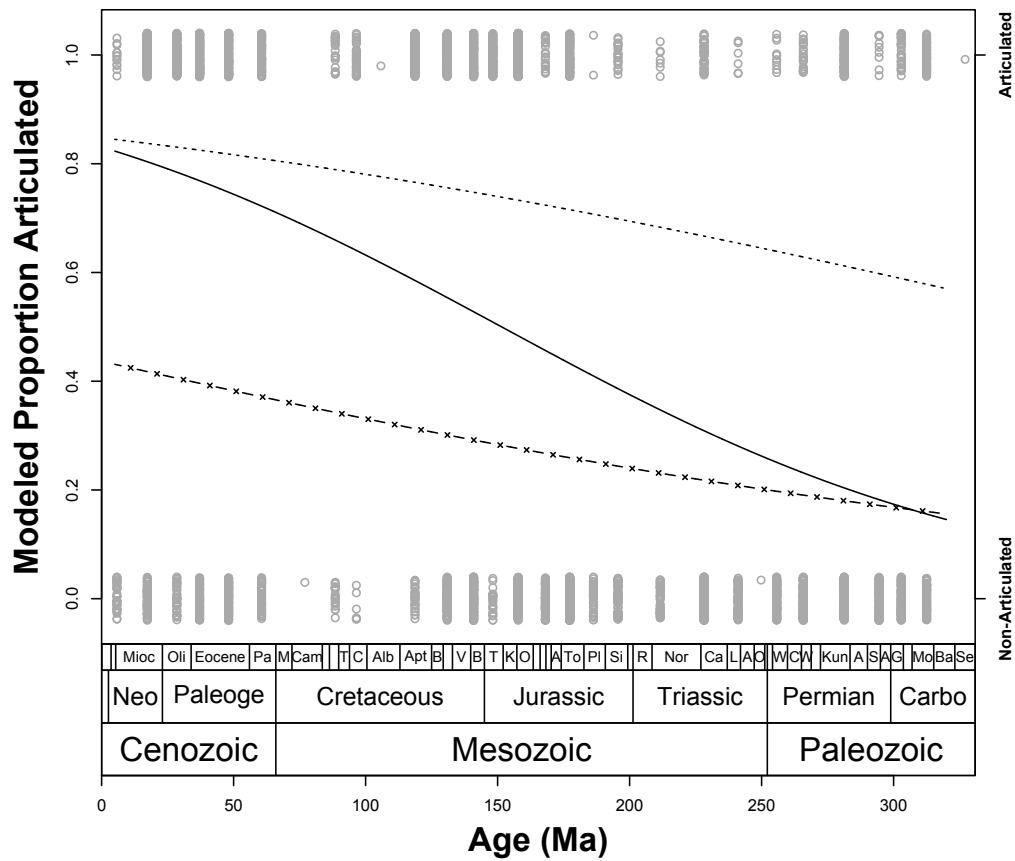


Fig. 3. Jittered occurrences of insects (grey circles) in the Phanerozoic with logistic regression model fit as a function of age in all environments (black line) and fit to only deep lake environments (dotted line) or non-deep lake environments (hashed line).

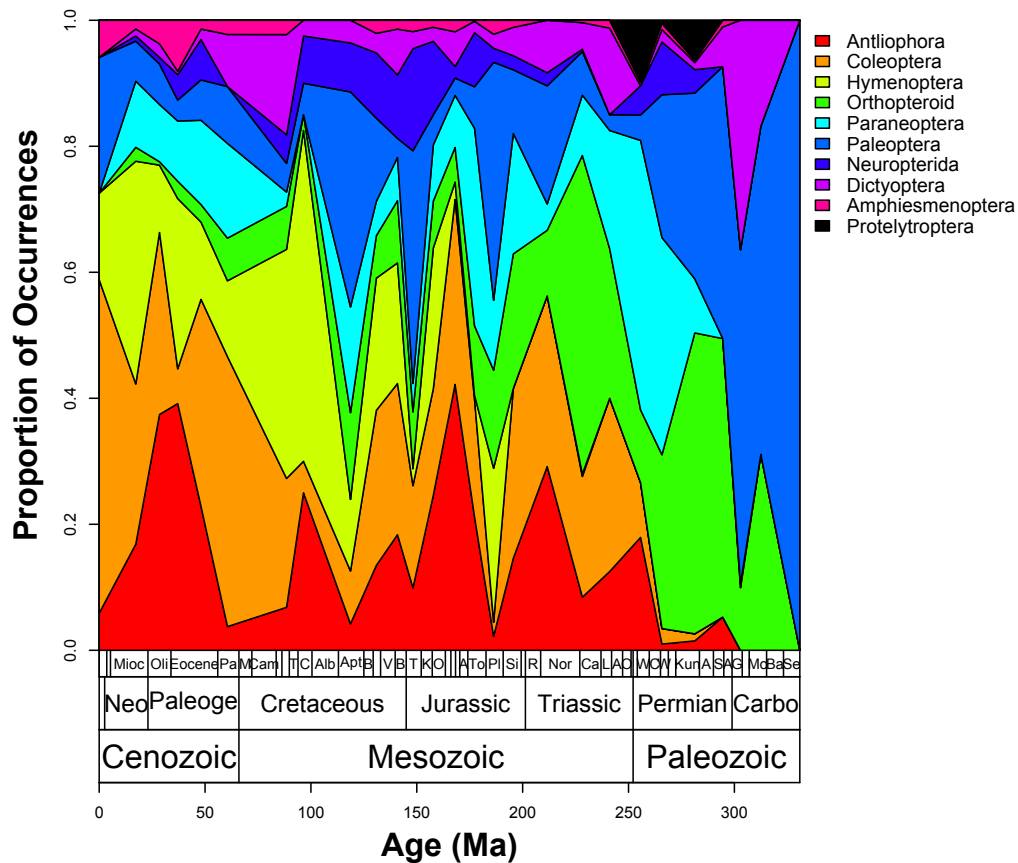


Fig. 4. Temporal changes in the relative abundance of higher-level insect groups. Antliophora consists of two orders: Diptera (flies) and Mecoptera (scorpionflies and hangingflies). Coleoptera (beetles) and Hymenoptera (wasps, ants and bees) are single orders. We use the term Orthopteroid to include many orders of paurometabolous insects included in the Infraclass Polyneoptera, including Orthoptera (grasshoppers and crickets), Notoptera (grylloblattids), Phasmida (stick insects) and Plecoptera (stoneflies), as well as several other rare and/or extinct orders. Paraneoptera includes Hemiptera (bugs), Psocodea (booklice) and Thysanoptera (thrips). Paleoptera includes the extant orders Odonata (dragonflies and damselflies) and Ephemera (mayflies) as well as numerous extinct Paleozoic orders like the Palaeodictyoptera. Neuropterida consists of Neuroptera (lacewings and antlions), Raphidioptera (snakeflies) and Megaloptera (alderflies), and Dictyoptera consists of the orders Blattodea (cockroaches), Isoptera (termites) and Mantodea (mantids). Amphiesmenoptera includes Lepidoptera (moths and butterflies) and Trichoptera (caddisflies). Protelytroptera is an extinct order that has convergently evolved to resemble beetles but is thought to be related to the orthopteroids.

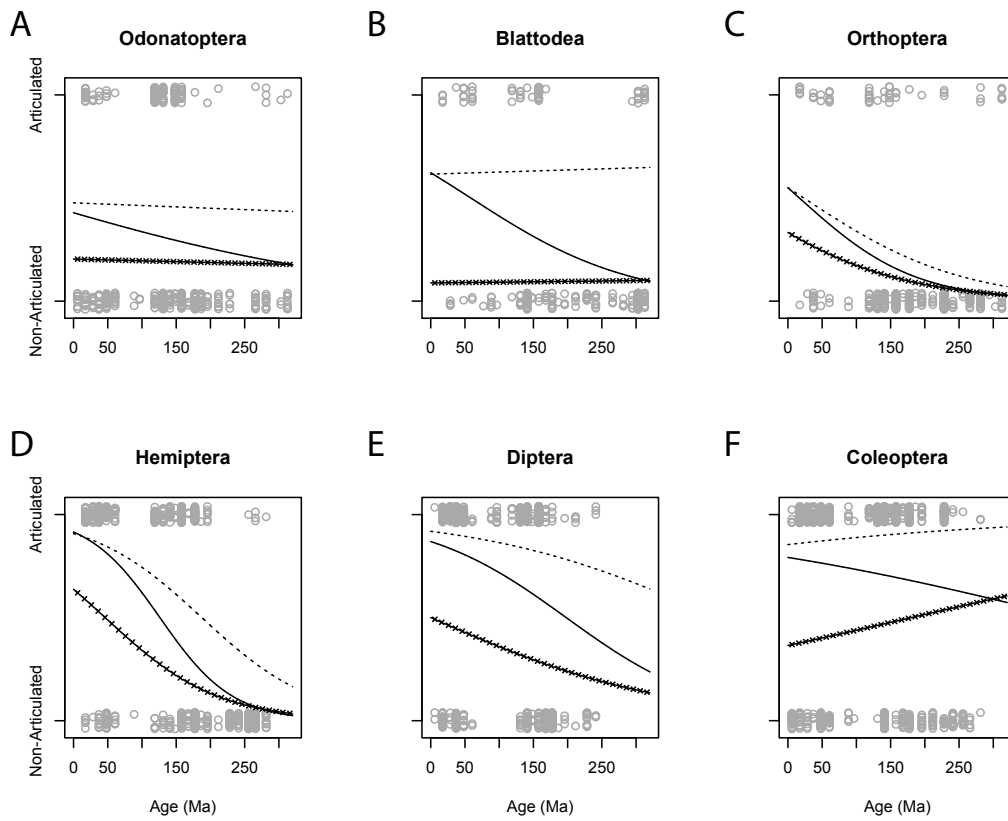


Fig. 5. Jittered occurrences of insects (grey circles) in the Phanerozoic for six common orders with logistic regression models fit as a function of age in all environments (black line), fit to only deep lake environments (dotted line) and fit to only non-deep lake environments (hashed line).

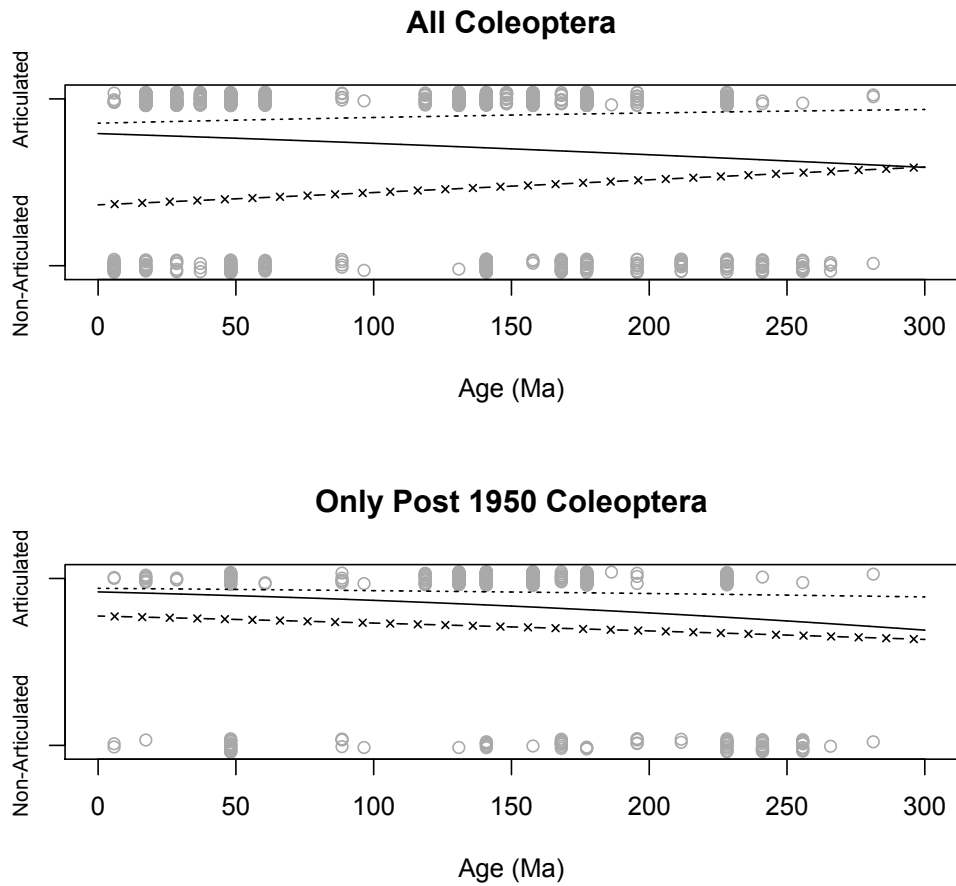


Fig. 6. Jittered occurrences of Coleoptera (grey circles) in the Phanerozoic for all Coleoptera or only those described in the literature after 1950 with logistic regression models fit as a function of age in all environments (black line), fit to only deep lake environments (dotted line) and fit to only non-deep lake environments (hashed line).

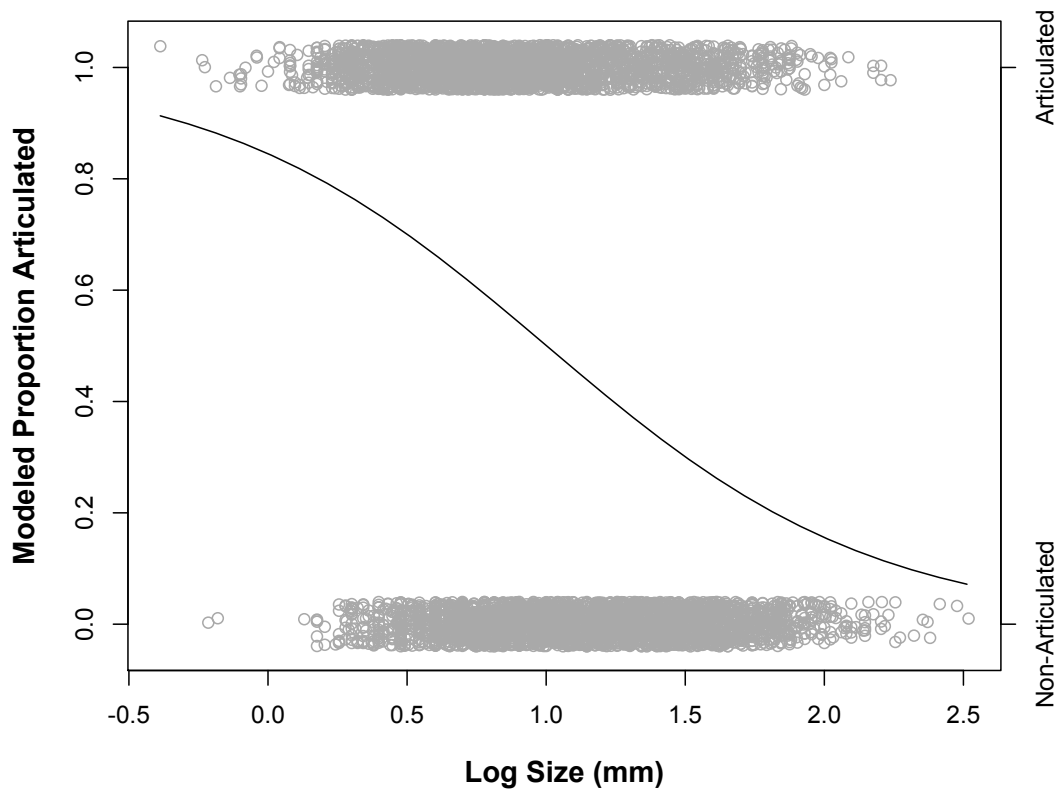


Fig. 7. Jittered occurrences of insects for all sizes (grey circles) with a logistic regression model fit as a function of \log_{10} wing length.

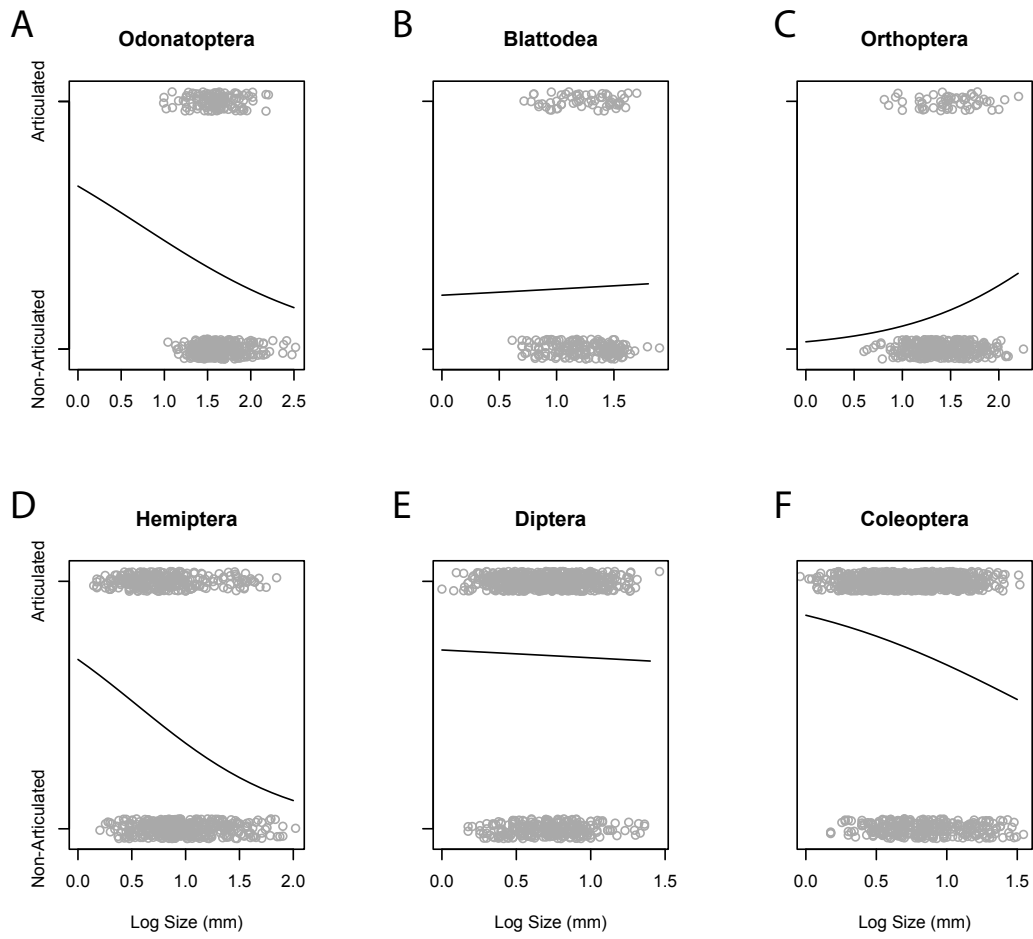


Fig. 8. Jittered occurrences of insects for all sizes (grey circles) for six common orders with a logistic regression model fit as a function of \log_{10} wing length.

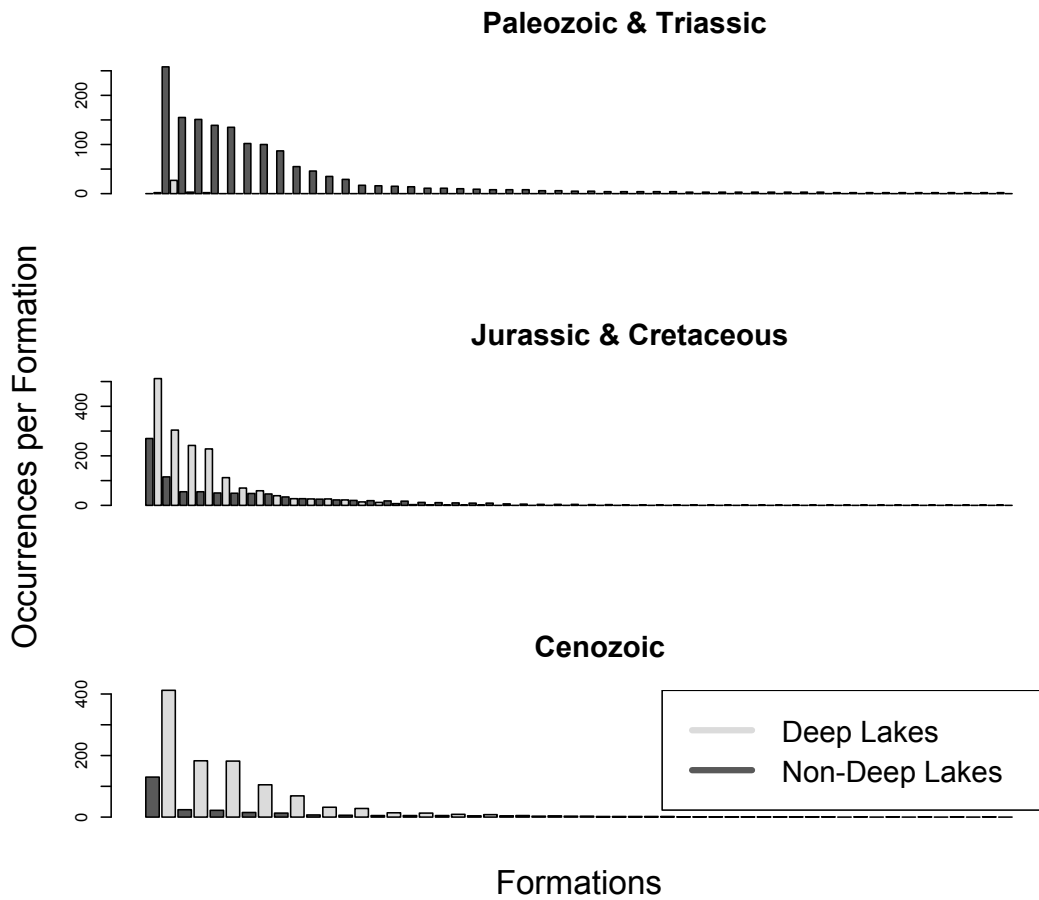


Fig. 9. Change in paleoenvironments of fossil insect-bearing formations in three geologic time intervals. The number of occurrences in most prolific formations has been relatively stable since the Jurassic. The number of actual fossil insect-bearing formations does not increase through time but instead shifts from non-deep lake environments towards deep lake environments.

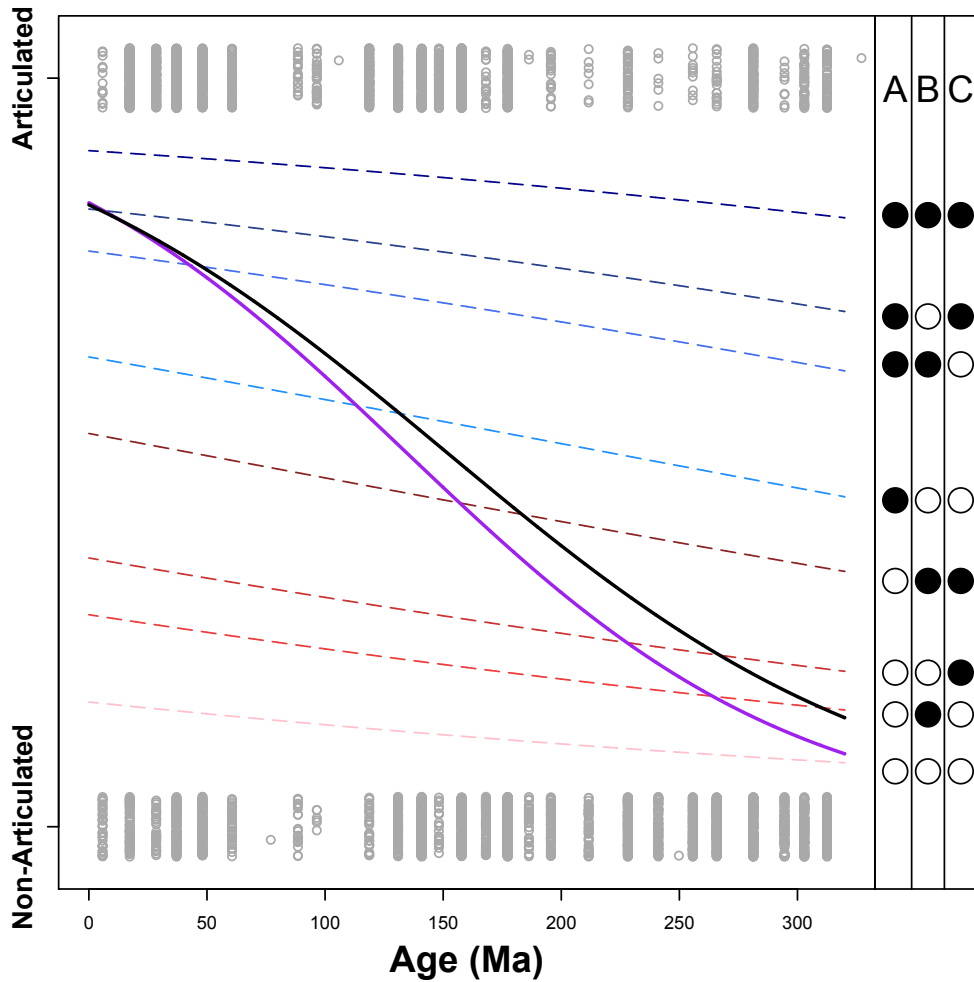


Fig. 10. Jittered occurrences of insects in the Phanerozoic with logistic regression model fit as a function of age in all environments (black line). Dashed colored lines represent different regression models holding different combinations of the three predictors (environment, morphology, size) constant. Filled circles in column A indicate deep lake environments, filled circles in column B indicate beetles, and filled circles in column C indicate small size (0.868). The purple line represents the predicted articulation where all values of the three predictors are simulated to represent the actual fossil record as they change through time. Size changes from 1.60 to 0.868, morphology (proportion beetle) changes from 0.0 to 0.4, and environment (proportion of deep lakes) changes from 0.06 to 0.9. Using these three predictors nearly simulates actual change in proportion of articulated insects through time.

Table 1. Support for models explaining change in articulation ordered from best supported to least supported by Bayesian information criterion.

Models	BIC	Δ BIC
morphology+size+environment	6467.58	0
size+environment	6530.00	62.42
morphology+environment	6824.06	356.48
environment	7003.44	535.86
morphology+size	8116.16	1648.58
size	8196.24	1728.66
morphology	8651.93	2184.35

Table 2. Logistic Regression Models odd ratios for all three predictors for all Insects and six common orders.

Group	Size odds ratio	2.5% Confidence Interval	97.5% Confidence Interval	P-Value	Environment odds Ratio	2.5% Confidence Interval	97.5% Confidence Interval	P-Value	Morpholog y odds ratio	2.5% Confidence Interval	97.5% Confidence Interval	P-Value
Insecta	0.225	0.192	0.264	4.60E-75	10.418	9.215	11.778	8.77E-307	2.072	1.744	2.462	1.16E-16
Coleoptera	0.278	0.166	0.466	4.59E-01	8.698	6.346	11.923	4.24E-08				
Blattodea	5.348	1.209	23.651	2.71E-02	20.428	9.430	44.250	2.01E-14				
Orthoptera	3.140	1.084	9.095	3.50E-02	4.386	2.419	7.952	1.11E-06				
Diptera	0.292	0.143	0.597	7.53E-16	15.237	10.657	21.786	2.14E-48				
Odonatoptera	0.692	0.260	1.837	7.41E-04	3.534	2.250	5.550	2.08E-50				
Hemiptera	0.081	0.044	0.149	1.21E-06	25.123	16.306	38.706	3.37E-41				

Each row is a unique Logistic regression model. Insecta has three predictor variables (Size, Environment, Morphology). Each order only has two predictor variables (Size, Environment).

Table 3. Percent of fossil specimens found in five major paleoenvironments for six common insect orders.

Environment	Odonatoptera	Blattodea	Orthoptera	Hemiptera	Diptera	Coleoptera
Deep lake	43.4%	28.6%	29.3%	40.4%	69.3%	58.8%
Delta/coastal	21.6%	36.0%	25.3%	13.0%	3.8%	11.5%
HE terrestrial	3.4%	2.0%	2.4%	1.9%	7.5%	2.3%
Marine	15.4%	8.6%	16.0%	29.0%	9.1%	14.6%
Shallow lake	16.2%	24.9%	27.1%	15.8%	10.3%	12.8%

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