Taphonomic biases in the insect fossil record: shifts in articulation over geologic time

Jered A. Karr and Matthew E. Clapham

Abstract.—Insect taphonomy is a topic that has drawn interest because of its potential biases on diversity patterns and the ecological information recorded by ancient insect faunas. Other than the onset of common amber fossilization in the Cretaceous, very little is known about long-term trends in the nature and quality of insect preservation and, as a result, the effects of taphonomic biases are poorly constrained. We assembled a database of nearly 7000 Carboniferous–Pliocene insect adpression (compression and impression) species from the primary literature to assess changes in insect taphonomy over time and test biotic and environmental controls on preservation. We grouped the fossils into 10-Myr bins and scored preservation of holotype specimens as either articulated bodies or isolated wings; articulated specimens with a body implied a generally higher quality of preservation. Paleozoic and Triassic insect holotypes are known overwhelmingly from isolated wings (only 12% articulated bodies), but our database shows a significant increase in the percentage preserved as articulated bodies, to more than 70%, beginning about 160 Myr ago in the Late Jurassic. 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 orders in the database exhibit significant increases in articulation. Instead, a shift to increased preservation in lacustrine paleoenvironments, which contain a greater proportion of articulated body fossils, explains most of the trend. The pronounced Late Jurassic increase in articulation has implications for evolutionary and ecological reconstructions, for example, suggesting that preserved insect diversity may be biased downward in the earlier part of their history when articulation was poor.

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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 preservational biases. Taphonomic processes can change our view of ecologic roles and importance or can obscure taxonomically-important characters and evolutionary relationships among groups (e.g., the case of Protorthoptera [Béthoux 2005, 2007]). Labandeira and Sepkoski (1993) note that their diversity curve is likely biased by exceptional Tertiary deposits such as Baltic amber and Florissant, so understanding insect preservation can also help us elucidate their true past diversity trends.

Although their fossil record is richer than generally assumed (Labandeira and Sepkoski 1993; Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005), insects lack mineralized tissue and their preservation usually requires extraordinary circumstances, commonly in Konservat-Lagerstätten. These insect Konservat-Lagerstätten come from varied environments, particularly lacustrine settings and amber, but also shallow-marine or lagoonal deposits and small ponds (Labandeira 1999), each of which may have been influenced by a variety of biases. Because amber preservation became common only in the Early Cretaceous, has a more ephemeral record than lacustrine deposits (Labandeira 1999), and was influenced by a different set of taphonomic biases (Zherikhin et al. 1999; Martinez-Delclòs et al. 2004), we will focus only on insects preserved as adpressions (compressions and impressions) in sedimentary rocks.

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Smith (2012) divided the factors that control preservation quality into “insect inputs” and “depositional factors.” Factors such as insect size, morphology, and taxonomic group (“insect input” variables), or environment type, bathymetry, and energy levels (“depositional factors”) influence if and how well an insect is preserved in the fossil record, so temporal trends in their importance may cause systematic biases in preservation quality. Maximum insect size has broadly decreased since the late Paleozoic (Clapham and Karr 2012), while taxonomic changes in insect assemblages, such as radiations of groups with high preservation potential like beetles (e.g., Labandeira and Sepkoski 1993) might also have influenced levels of preservation. The dominant depositional environment of insect Konervat-Lagerstätten has also changed, from Carboniferous delta plain Lagerstätten to Early Jurassic shallow marine and Cretaceous–Cenozoic lacustrine deposits (Allison and Briggs 1991; Briggs 2003), but it is unknown how this shift has affected preservation of all animal groups and in particular insects.

Many studies have assessed the factors that influence the quality of insect preservation, but these studies have largely focused on detailed taphonomic investigation of single localities with specific environmental conditions (Wilson 1980, 1988; McCobb et al. 1998; Ansorge 2003; Coram 2003; Wappler 2003; Henning et al. 2012). We examined long-term trends in the articulation of insect fossils, using a large database of specimen data compiled from the primary literature. Although insect preservation quality is multifaceted, we used articulation as a proxy for decay because experiments examining the various stages of insect decomposition found that isolated wings, even with minute details, often represent one of the final stages of decomposition (Duncan et al. 2003). Using a large data set of fossil insect localities allows us to pool multiple sites, removing idiosyncratic, location-specific taphonomic signals to reveal overarching trends. We tested the effects of depositional environment, insect size, morphology/taxonomic group, and geologic age on insect articulation. 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

In order to use insect fossil assemblages for evolutionary, ecological, or diversity studies, it is important to understand the steps from living insect to fossil to published literature. The rate at which an insect passes through these steps influences the quality of preservation by altering the time exposed to predation, decomposition, and disarticulation. An insect must pass through four taphonomic steps, which act as filters, before being preserved as an adpression in the fossil record. First, the body must be transported to an aquatic environment by rafting or aerial deposition (except in the case of aquatic insects, which already inhabit the environment). Most insects are not aquatic so they must next break the surface tension of water. Martínez-Delclós and Martinell (1993) examined insect deaths in aquatic environments of a variety of taxonomic groups and found a large range of outcomes depending on size and weight, described by the SM (wing surface area-to-mass) index (Wagner et al. 1996), and wing type or shape. There tends to be a bias against large-winged or fragile groups such as Lepidoptera and against insects with wingspans smaller than 5 mm, typically leading to enrichment in heavy, medium-sized insects at the sediment interface relative to their life abundance. Archibald and Makarkin (2006) and Wang et al. (2013) showed that insects with larger SM indices 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). After breaking the water surface, the third step requires the insect to sink through the water column. Temperature and chemical composition affect the rate of sinking, and a density change at the thermocline (in deeper lakes or the ocean) or halocline (in some saltwater environments) can prevent sinking,
thus promoting decomposition before carcasses can be deposited on the sediment (Martínez-Delclós et al., 2004). The final step is burial after the insect settles onto the sediment, influenced by the distance from shore, water chemistry, and tectonic setting. In studies of Eocene lakes from British Columbia, Wilson (1980, 1988) noted a trend for more articulated specimens in offshore compared to nearshore 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, which generates a strong bias toward better-preserved material with more diagnostic characters that allow the specimen to be readily identified.

Methods

Using primary literature data from 1560 published papers (see supplementary information), we quantified the articulation, size, taxonomic identity, and depositional environment of Carboniferous-Pliocene insects preserved as adpression fossils. All collections and occurrences, taxonomic names, and size measurements used in this study are housed in the Paleobiology Database (PaleoDB: http://paleobiodb.org); the data used here were downloaded on 12 May 2014. We scored each species on the basis of the holotype specimen and categorized it as either an exoskeleton (“articulated”) or wing element (“disarticulated”). Because holotypes are always more likely to be articulated than the fossil assemblage as a whole, our absolute values of articulation will overestimate the articulation in the entire insect assemblage but the relative shifts will be robust. All wing elements (elytron, tegmen, forewing, hind-wing, or wing) were grouped together, whereas an exoskeleton includes any specimen with both the body and wings. In many cases the wings and/or body are incomplete or fragmentary, but we did not distinguish fragmentation in our analyses. We excluded all species where the holotype body part was unidentified or a nymph/larva and all occurrences of questionably identified genera and species or those in open nomenclature. Because we are also interested in the effect of size on articulation we also excluded all occurrences without a wing measurement.

For each locality, we assessed the depositional environment to test its effect on articulation. The PaleoDB 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. Because we hypothesized that deep lakes have uniquely favorable conditions for insect fossilization, for most analyses we use the term deep lake or non-deep lake (combined marine, delta/lagoon, HE terrestrial, shallow lakes) to categorize the environment. The deep lake category includes large lakes (“lacustrine – large” in the PaleoDB) such as Florissant (Veach and Meyer 2008), the Yixian Formation (Hethke et al. 2013), and Lake Gosiute (Green River Formation; Surdam and Stanley 1980). Because we consider depth to be an important factor, the deep lake category also contains several localities assigned to the PaleoDB “crater lake” environment, with smaller surface area but with significant depth, such as Messel (Harms 2002; Felder and Harms 2004), the Eckfeld Maar (Lutz 2003), Menat (Wappler et al. 2009), and the Randeck Maars (Zeuner 1942). The shallow lake category includes localities referred to as ponds (Engel and Gross 2008) or oxbow lakes like Madygen (Shcherbakov 2008).

Size data were also collected to examine its effect on articulation. The length of the wing, tegmen (Orthoptera and relatives, Blattodea and relatives, some Hemiptera), elytron (Coleoptera), or hemelytron (some Hemiptera)
was recorded. 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 biostratigraphic processes, 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 6915 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-Myr bins, the same as those used in several recent papers (Alroy et al. 2008). Stage-level time intervals were not used because of the paucity of data and uncertain age assignment of many localities.

Model Construction

We performed multiple logistic regression analyses in R (R Development Core Team 2012) to estimate the effect of morphology, depositional environment, and size on the probability of articulation. We log_{10} transformed wing size (measured in mm) to normalize the size distribution. The morphology predictor was coded as a binomial factor (beetle or non-beetle) for simplicity; even though articulation varies within and among orders, beetles have the greatest preservation potential (Smith 2000). It is also difficult, a priori, to predict or assign numerical values to the articulation of each insect order, but if morphology is an important predictor of articulation the comparison of beetles to other insects should show this. We coded the environment predictor as a binomial factor (deep lake or non-deep lake) for simplicity; even though articulation varies within and among orders, deep lakes have the greatest preservation potential (Smith 2000). We then predicted the probability of articulation through geologic time on the basis of the eight possible combinations of the now binomial predictor variables (size, morphology, environment). We compared each combination with the overall shift in articulation. To do that, we created a synthetic data set in which “size” was replaced with values ranging continuously from 1.54 in the oldest bin to 0.83 in the youngest bin. “Environment” was replaced with values ranging from 0.0 to 0.82 (the proportion of insect occurrences occurring in deep lakes in the Carboniferous and Cenozoic, respectively) and “morphology” was replaced with values from 0.0 to 0.26 (the proportion of insect occurrences that are Coleoptera in the Carboniferous and Cenozoic). We also compared actual variations in articulation with predicted articulation proportion, using the relationship derived from overall logistic regression model and the environment (proportion deep lake), morphol-
ogy (proportion beetle), and size (mean size) data for each time bin.

All data files and R scripts for data analysis are available at https://github.com/mclapham/insect_taph.

Results

The proportion of articulated holotypes increased significantly through time. Before the Late Jurassic (Jurassic bin 5, Callovian-Kimmeridgian, ca. 161 Ma), 88.8% of insect holotypes are disarticulated wing elements, whereas 73.4% of holotypes in the Late Jurassic and after are preserved as articulated bodies (Fig. 1). In a comparison of multiple logistic regression models, the model including all three variables (environment, morphology, and size) was the best-supported (Table 1), indicating that morphology, environment, and size all significantly affected insect articulation ($p < 0.001$ for all variables; Table 2).

While holding other parameters constant, beetles were more articulated than insects as a whole, insects in deep lake environments were significantly more likely to be articulated, and specimens with larger wing size were less likely to be articulated (Figs. 2–4).

Morphological Controls

Because higher-level taxonomic groupings typically represent distinctive body plans with

![Figure 1. 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 each 10-Myr bin (maximum 1061). Dashed line represents the beginning of the Callovian (Jurassic bin 5).](image-url)

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<th>Δ AIC</th>
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<td>+ environment</td>
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TABLE 2. Logistic regression model results for all insects and for six common clades. Each row is a unique logistic regression model. Insecta has three predictor variables (size, environment, morphology). Each clade has only two predictor variables (size, environment). Bold values are statistically significant ($p < 0.05$).

<table>
<thead>
<tr>
<th>Group</th>
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<th>2.5% Confidence interval</th>
<th>97.5% Confidence interval</th>
<th>p-value</th>
<th>Environment odds ratio</th>
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<td>0.185</td>
<td>0.564</td>
<td>&lt;0.001</td>
<td>13.888</td>
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</table>

different preservation potential, shifts in the abundance of major groups over time (Labandeira and Sepkoski 1993) likely affected articulation. Of the eight most common clades in our database, Blattodea, Orthoptera, and Odonatoptera are dominant in the early part of the record, whereas Coleoptera, Diptera, 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 (Labandeira and Sepkoski 1993). This shift likely contributed to increased articulation in younger collections, but was not the principal factor because all well-sampled taxonomic groups independently increase in articulation through time (Fig. 2).

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). Their wing venation is complex and distinctive for taxonomic identification. Only 26.9% of Odonatoptera species have been described from articulated bodies, but overall articulation increased significantly in younger collections. Articulation did not change significantly within environments (Fig. 2A).

Blattodea.—Blattodea (cockroaches, excluding termites in our analyses) 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. 2B). The high diversity of Paleozoic species influences the mean percent articulation, and only 22.6% of species have been

<table>
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<tr>
<th>2.5% Confidence interval</th>
<th>97.5% Confidence interval</th>
<th>p-value</th>
<th>Morphology odds ratio</th>
<th>2.5% Confidence interval</th>
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<th>p-value</th>
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</table>

Figure 3. Phanerozoic insect holotype occurrences (gray circles) with logistic regression model fits relating articulation as a function of age in all environments (black line), and in only deep lake environments (dotted line), and in only non-deep lake environments (hashed line). Points representing articulated and non-articulated insect specimens have been randomly jittered for visibility.
described from articulated bodies. As in Odonatoptera, articulation did not change significantly over time within 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 (15.8% of species holotypes are articulated) and increased significantly in younger deposits. 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 deep lakes (Fig. 2C).

Hemiptera.—Hemiptera (true bugs) are one the most heterogeneous orders, with some families consisting of small robust species similar to Coleoptera (such as some Heteroptera) and other families consisting of large-winged fragile groups more similar to Odonatoptera. Overall articulation increased considerably, with some contribution from the shift to deep lake preservation, but with a larger contribution from changes in articulation within both deep lakes and non-deep lakes (Fig. 2D).

Diptera.—Diptera (flies) are typically small insects with simple wing venation, making description from isolated wings challenging. They are generally so small that it can be difficult for them to break surface tension (Martínez-Delclòs and Martinell 1993), but they are well articulated (75.5% of species described from complete bodies). Articulation increased 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. 2E).

Coleoptera.—Coleoptera (beetles) are well articulated (77% of species holotypes are complete bodies) and increase in abundance toward the modern (7.1% of occurrences before the Late Jurassic and 22.1% after in our database). Although overall articulation increased significantly, due to the shift toward preservation in deep lakes, within-environment articulation apparently decreased both in deep lakes and, to a greater degree, in non-deep lakes (Fig. 2F).

Environment

The predicted probability of a specimen being articulated increased through time in both non-deep lake localities from ~10% to
~50%, and from ~45% to ~90% in deep lake environments, but preservation in deep lakes significantly increased the likelihood of articulation in all six clades (Table 2, Fig. 3). Deep lake environments also became more common over time: only 6% of pre-Late Jurassic insect occurrences are from deep lakes, compared with 79.4% of younger occurrences. The taxonomic composition of deep lake and non-deep lake assemblages likely also influenced articulation. Orthoptera and Odonatoptera, which have low articulation, are generally strong fliers and are nearly equally common in the three main environments, including marine settings far from their original habitats. In contrast, Coleoptera, which commonly are articulated, are generally poor fliers and are found in much higher percentages (73%) in deep lakes (Table 3).

**Relative Importance of Size, Morphology, and Environment**

The odds of an insect preserved in a deep lake being articulated are 1350% higher than the odds for an insect in a non-deep lake environment. By comparison, the odds of articulation for beetles are nearly 119% higher than the odds for non-beetles, implying that changes in environment have a greater effect on insect articulation than differences in insect morphology. For every tenfold increase in size the odds of articulation decrease by nearly 85%. Deep lake environments (bars in column A of Fig. 6) consistently have greater articulation, regardless of taxonomy or size, implying that although size and taxon group affect articulation, environment is the largest contributor.

We modeled the effects of environment, size, and morphology by creating a simulated data set and compared the results to the observed trends (Fig. 7). Using our logistic regression model on this idealized database we were able to closely simulate the change in articulation over time in most time bins. Articulation predicted only from the proportion of deep-lake occurrences, the proportion of Coleoptera occurrences, and the average size does not always correspond to actual values, most notably during some time bins dominated by deltaic or lagoonal deposits (e.g., Solnhofen, ca. 150 Ma). Although every locality has a unique set of taphonomic characteristics, the good agreement between actual and predicted articulation implies that changes in depositional environment, beetle abundance, and size can explain much of the

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<th>HE terrestrial</th>
<th>Delta/coastal</th>
<th>Marine</th>
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variation in insect articulation in the fossil record.

**Discussion**

**Morphological Controls**

Insects are a very disparate group with major morphological differences among orders. This structural variability likely influences overall articulation, due to changes in the relative diversity of insect orders through time (Labandeira and Sepkoski 1993). In addition, articulation proportions based on published holotypes depend not only on taphonomic biases during fossilization (related to robustness, size, and SM index), but also on conventional taxonomic practices for species description in a particular group.

Three general patterns of articulation over time are evident among the six suprafamilial groups we analyzed: (1) Each environment had a consistent level of articulation over time, but overall articulation increased (observed in Odonatoptera and to some extent in Blattoidea). (2) Overall articulation increased, as did articulation in both deep lake and non-deep lake environments (observed in Hemiptera, Orthoptera and Diptera). (3) Articulation decreased in both of these environments but overall articulation increased (observed only in Coleoptera).
Consistent within-environment articulation trends in Odonatoptera (and Blattodea) are best explained by the conservative morphology of those groups. Because their overall body plan has changed little over their evolutionary history, taphonomic controls on articulation were similar in the Carboniferous or the Cenozoic. Both groups are more consistently articulated in deep lakes, and the overall increase in articulation resulted from the post-Jurassic increase in the number of deep lake deposits (Fig. 2A,B).

A shift to greater preservation in deep lakes also significantly enhanced articulation in Hemiptera, Orthoptera, and Diptera (Fig. 2C–E), but in addition those three groups exhibited considerable within-environment increases in articulation. Changing articulation in deep lakes and non-deep lakes likely reflects evolutionary trends within the clades that resulted in morphologically distinct families changing in proportional abundances. For example, Heteroptera, a suborder within Hemiptera that often contains smaller, beetle-like species with folded tegmina and lower SM indices, is in general more articulated, and constitutes a larger proportion of occurrences later in the fossil record, than “Homoptera,” a paraphyletic assemblage of generally large-winged and poorly sclerotized Hemiptera. Similarly, Cenozoic Orthoptera are largely composed of Acrididae (short-horned grasshoppers) and Tettigoniidae (katydids), two lineages that been observed in actualistic experiments to have an unusual response to drowning, which might increase sinking rate (Martínez-Delclòs and Martinell 1993). Extinct lineages may not have had this response. There is also a trend of wing reduction in Orthoptera (Sharov 1968), which would decrease their SM index and promote sinking. The patterns in Diptera possibly reflect a shift
from more fragile, gracile dipteran groups such as Tipulomorpha to more stout-bodied, robust groups such as Muscomorpha.

Coleoptera have a higher preservation potential than other insect orders in both modern, actualistic studies and lab experiments (Smith 2000; Smith et al. 2006), primarily because their forewings have been highly modified into hard sheaths called elytra. Our results support these findings, as Coleoptera is one of the most highly articulated groups in our data. In contrast to the other five well-sampled clades, Coleoptera exhibit a highly unusual pattern where the probability of articulation actually decreased both in deep lakes and, especially, in non-deep lakes (Fig. 2F). This trend does not reflect changes in beetle body plans, which have remained stable over most of their evolutionary history, or size, which also has not changed substantially. Instead, decreased articulation is most likely an artifact of taxonomic practices. Earlier paleoentomologists, especially in the nineteenth century, described many species based on isolated elytra from Cenozoic localities. 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), often being placed in morphotypes instead (Papier et al. 2005; Martin 2010). More than 81% of beetle species described before 1950 were from Cenozoic localities, compared to fewer than 12.5% of species described after 1950. Restricting the analysis to species described after 1950 reduces the effects of outdated taxonomic practices and indicates no significant shift in articulation within environments (Fig. 8). Articulation of holotypes does not change significantly with year of publication in other taxonomic groups (Fig. 9), indicating that shifting taxonomic practices only affect Coleoptera (supplementary figure 1). When outdated species are excluded, Coleoptera have a pattern of articulation similar to that of other morphologically stable groups (Odonatoptera and Blattodea), in which the shift to greater deep lake preservation primarily caused the increase in articulated holotypes.
Wing Size

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). Large insects have greater wing area relative to body mass on average (high SM index value) and will float on the water surface longer than smaller-winged, heavier-bodied insects (low SM index value) (Archibald and Makarkin 2006). Larger insects may also be subjected to more intense predation (Blanckenhorn 2000; Chown and Gaston 2010), which might favor their disarticulation and/or removal from the death assemblage.

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, although this trend is not uniform across all orders. Odonatoptera wing length decreased from a median of 140 mm in the Carboniferous to a median of 35 mm during the Cenozoic, whereas Coleoptera median size remained remarkably stable at around 5 mm. The overall trend of decreasing median wing size seen in insects is influenced by two factors. The first is a shift from large-winged groups such as Palaeodictyoptera and Megasecoptera to small-winged orders such as Diptera and Hymenoptera. Because the degree of articulation varies widely among groups, with smaller fossils typically being more articulated, this taxonomic replacement is the major mechanism by which size has affected articulation. The second cause is a decrease in median size of both Orthoptera and Odonatoptera, two large winged groups that are found abundantly throughout the insect fossil record. It is less clear whether this size decrease also drives the size-articulation relationship, because the logistic regression results are inconsistent when orders are tested individually. Although small specimens were significantly more articulated in Odonatoptera, Hemiptera, and Diptera, the reverse was true in Orthoptera and Blattodea, even after accounting for environment (Table 2).

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 disarticulate dead insects, whereas carcasses in smaller lakes are subjected to higher energy due to mixing of the water column. Insect carcasses in marine environments are
subject to greater wave action than those 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 (Zherikhin 2002).

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; Behrensmeier 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). Restricted ocean basins can also be prone to anoxic bottom waters and several famous, insect-bearing Konservat-Lagerstätten are from such 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). Endorheic lakes, such as Lake Gosiute of the 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 and thus an unusual water chemistry that promotes preservation (Allison and Pye 1994).

Our results further imply that variations in taxonomic composition among depositional environments influence articulation, although this is likely a secondary factor. In particular, small-bodied, weak fliers like Coleoptera and Diptera, which have high intrinsic articulation (Smith 2001), are overrepresented in deep lake environments relative to other settings (Table 3). It is difficult to assess causality and it is possible that Diptera are dominantly found in deep lakes because they require the exceptional preservation of those settings. It does

![Figure 9. Articulation of insect (solid line) and only Coleoptera (dashed line) holotypes as a function of publication year. Beetles described in older papers are much more likely to be based on isolated elytron holotypes, but there is no trend in holotype articulation among insects as a whole.](image-url)
Our analysis suggests that the depositional environment in which an insect is preserved is the most important control on articulation. Insect fossils from deep lakes have higher rates of articulation than those from the other paleoenvironments and there was a dramatic shift in the Late Jurassic from deltaic, marine, and smaller lake localities to deep and/or large lakes. That shift was the primary reason for the substantial increase in articulation, also in the Late Jurassic. It could affect 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.

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Literature Cited


