

How Physical Characteristics of Beetles Affect their Fossil Preservation

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Although insect size and robustness often have been hypothesized to be factors that lead to taphonomic bias in the insect fossil record, no studies have examined how these factors directly affect an insect's preservation potential. In this study, laboratory experiments were performed on modern Coleoptera (beetles) to examine the importance of insect morphology on preservation potential. A rotary tumbling barrel was used to determine how insect size and robustness would influence sinking and disarticulation rates. Although size and robustness were not correlated directly, beetles that were larger and more robust were more resistant to disarticulation than smaller, less-robust beetles. Waterlogged specimens gained increased flexibility in their exoskeletons, and were difficult to puncture. Sinking and disarticulation rates were correlated, although it took fewer days for beetles to sink than it took to begin disarticulating. A white-colored film was apparent on all specimens within a few days of their introduction to the tumbling barrel; however, major disarticulation did not occur until the specimens sank to the bottom. An examination of the fossil-beetle literature also suggests the importance of hardness in preservation potential. Although often considered fragile, given the right physical characteristics and environmental conditions, insects can be resistant to disarticulation and decay.

INTRODUCTION

Insects are the most species-rich group today, with estimates of diversity that range from three to fifty million species (Erwin, 1982; Gaston, 1991, 1992; May, 1986). In addition to high levels of modern diversity, insects also have an extensive fossil record, with all extant insect orders found preserved as fossils (Labandeira, 1994). Insects are found preserved in a multitude of depositional environments, including a number of well-known Konservat-Lagerstätten (Rasnitsyn and Quicke, 2002). Over the last decade, there has been an increase in the use of fossil-insect data to understand insect evolution, patterns of diversity, and insect-plant interactions (Labandeira and Sepkoski, 1993; Farrell, 1998; Ronquist et al., 1999; Jarzembowski, 2001). These fossil data also have been used to re-

construct past climates and paleoenvironments (Elias 1994; Poinar et al., 1999; Moe and Smith, 2005).

While the insect fossil record shows great promise in leading to a greater understanding of insect evolution, diversity patterns, and paleoenvironments, researchers only recently have begun to understand preservational biases that may influence some of the apparent patterns within the record. Understanding these biases will be important for determining the limitations of insect fossil data, and for distinguishing between true patterns and artifact.

To date, studies that have attempted to understand preservation bias in the insect fossil record have focused on how insect ecology may have influenced the types of insects found in different depositional environments (Wilson, 1988; Martínez-Délclòs et al., 1991; Henwood, 1993a,b; McCobb et al., 1998; Smith, 2000; Martínez-Délclòs et al., 2004), or on the chemical components of decomposition (Miller, 1991; Briggs et al., 1993; Baas et al., 1995; Bierstedt et al., 1997; Stankiewicz et al., 1997; Briggs et al., 1998; Briggs, 1999). These works have shown that insects' diet and feeding habitats can influence preservation potential, as can the interaction between sedimentary context and the chemical composition of an insect's cuticle.

Insect characteristics, such as size and robustness (hardness of the exoskeleton), often have been hypothesized in the insect-taphonomy literature to be factors that lead to preservation bias in the insect fossil record. For example, biases towards smaller size classes have been noted in a number of depositional environments (Wilson, 1988; Henwood, 1993a, b; Smith, 2000; Martínez-Délclòs et al., 2004), and the relative robustness of different insect groups has been cited as an important character aiding in the level of completeness and the remnant chitin content of insect-fossil remains (Stankiewicz et al., 1997; Briggs, 1999; Smith, 2000). Still, to the authors' knowledge, no studies have directly examined how size and robustness affect an insect's preservation potential.

In this study, an experimental approach is used with modern Coleoptera (beetles) to examine the importance of insect morphology on the preservation of insects in lake environments. The focus is on insects preserved in lake systems because lacustrine conditions are replicated easily in the lab, and because lakes are among the most persistent sedimentary environments that preserve beetles

TABLE 1—Data collected for all beetle species examined. All values are averages for the species.

Taxon	Size (mm ²) n = 10	Hardness (GF) n = 10	Sinking (days) n = 2	Disarticulation (days) n = 2	Fossil Occurrence (No. of specimens)
Carabidae (<i>Cicindella</i> sp.)	17.6	107.3	5.0	12	94
Chrysomelidae (<i>Diabrotica</i> sp.)	10.9	164.1	2.0	11	70
Coccinellidae (<i>Hippodamia convergens</i>)	20.2	124.2	5.0	21	8
Curculionidae (<i>Sitophilus zeamaze</i>)	4.0	207.4	2.0	48	196
Scarabaeidae (large species)	59.4	215.2	39.5	90	137
Scarabaeidae (small species)	13.9	132.0	5.0	13	137
Tenebrionidae (<i>Tenebrus</i> sp.)	68.7	145.1	31.0	51	30
Cerambycidae (<i>Tetraopes</i> sp.)	35.6	220.6	—	—	74
Dermestidae (<i>Dermestes</i> sp.)	18.2	150.0	—	—	7
Melyridae (<i>Collops</i> sp.)	—	111.0	—	—	10

through geologic time (Labandeira, 1999; Smith and Cook, 2001). To determine how insect size and robustness will influence sinking and disarticulation rates, a rotary tumbling barrel was used to simulate agitation of insects along a lake shoreline. The stages of disarticulation that beetle carcasses undergo in the tumbling barrel also are described. A database of fossil beetles is used to conduct a preliminary examination to determine whether beetle size or hardness predict a family's preservation potential.

MATERIALS AND METHODS

Seven species from six beetle families (Table 1) were used to determine the relationship between insect size and robustness and rates of sinking and disarticulation. Two species of Scarabaeidae (scarabs)—one large and one small—were included in the study to capture two common

size classes found within the same family. Prior to their use in the experiment, all specimens were stored in 75% isopropyl alcohol, which is used in entomological collections for the long-term storage of museum-quality specimens because it prevents decay due to microbial activity. Storage in isopropyl alcohol is considered to have minimal effects on beetle exoskeletons, and allowed incorporation of specimens in the study with differing phenologies and from different parts of the country.

To simulate preservational conditions that might exist in a lacustrine environment, two treatments were used—one with dried specimens and another with specimens that were waterlogged. All specimens initially were removed from the alcohol, rinsed with deionized water (diH₂O), and allowed to dry completely for 24 hours under a fume hood. Waterlogged specimens were submerged in diH₂O for a minimum of 24 hours until they were completely saturated. The dry treatment represents insects that died on the shore, thus drying out before being transported into the lake, and the waterlogged treatment represents insects that died in the water or on the water surface.

To determine the size of each species, digital calipers were used to measure the length and width of the dorsal surface of the thorax and elytra of each specimen (Fig. 1). Assuming the dorsal surface was rectangular in shape, the total body length (thorax and elytron length) was multiplied by the width of the thorax to estimate the size of each specimen. The average size was then calculated for each species. Measuring the dorsal surface of specimens, as opposed to obtaining weights, was done to allow for future comparisons of modern beetle size data and size data from fossil specimens.

To determine the robustness of each species, a Wagner Fruit Tester series penetrometer (Model #U0801, with a 0.1-mm tip) was used to measure the grams of force (GF) required to penetrate the insect's thorax and elytron. For each specimen, the insect was placed on a pinning block, and a puncture was made in the center of the thorax as well as in the middle of the proximal region of the right elytron (Fig. 1). An average robustness for each specimen was calculated by taking the average of the GF required to penetrate both the elytron and thorax. An average robustness was calculated for each species by averaging measurements of ten individuals of that species. The GF required to penetrate both the cuticle of beetles that had

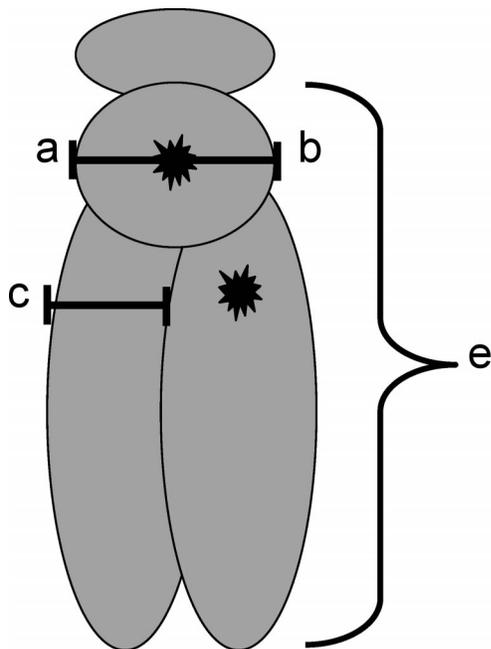


FIGURE 1—Schematic beetle with measurements indicated; the width of the thorax and each elytron was taken from A to B and C to D, respectively. Total length (thorax and elytron) is represented by E. Black stars indicate where punctures were made on the specimens to quantify robustness.

been set out to dry for 24 hours and beetles that had been waterlogged for 24 hours was then calculated.

Sinking and Disarticulation Rates

For each species, the rates of sinking and disarticulation were determined by placing beetle specimens from each family into a small Lortone rotary tumbler (Model 3A) individually. The tumbler has a rotation speed of 50 rotations per minute, and the barrel of the tumbler is smooth sided, with an internal diameter of 95.25 mm. Two specimens that previously had been dried for 24 hours were used to quantify the time it took for sinking and disarticulation for each family. To simulate the level of abrasion typically found in near-shore lacustrine environments, the rotary tumbler contained a mixture of 709.76 ml (three cups) of water (23°C) and 44.36 ml (three tablespoons) of clay/silt sized sediment. The water was not inoculated with microorganisms because the actual time to disarticulation was not a concern; rather, the relative rates of disarticulation between the different beetle species were of interest. The sediment was obtained by pulverizing pieces of shale from the lower shale unit of the Florissant Formation—a site well known for exceptional preservation of fossil insects. Shale first was reduced to pea-sized fragments with a rock hammer, then ground for two minutes in a shatter box with tungsten-carbide containers. A variety of conditions occurs in lakes, and use of a rock tumbler probably simulated a slightly higher-energy environment than most lakes would present.

During this experiment, each specimen was placed into the tumbler for a maximum of 90 days, during which time the tumbling barrel was rotating constantly. The tumbler was stopped briefly every 48 hours to determine the overall pattern and degree of disarticulation (order and timing of body parts separating from the rest of the body) and sinking rates (timed from the beginning of the experiment). Sinking was defined as the point when the specimen was completely waterlogged, and sank to the bottom of the tumbling barrel. Full disarticulation was defined as the point at which the beetle head, thorax, abdomen, and appendages became separated from one another.

Size, Robustness, and Preservation Potential

To determine whether the morphological characteristics of insects influence their preservation potential, a database compiled from the literature (and unpublished data) was used to compare the size and robustness of modern representatives of different beetle families to the occurrences of their respective families in the fossil record. The database used in this study included records for 1,875 fossil beetle specimens from the Permian through the Pleistocene, and included fifty-five lacustrine localities from around the world. It was assumed that the number of specimens from each family preserved in the fossil record was an indication of the preservation potential of that family. For the Scarabaeidae, an average size and robustness were calculated across the two species to represent the value of that family, but the number of fossil occurrences remains the same for the scarabs overall, regardless of size class. Also included in this part of the study are

representatives from three other beetle families, including the Cerambycidae, Dermestidae, and Melyridae (Table 1).

Statistical Analysis

Linear regression analyses were used to determine the relationship between hardness and size and sinking and disarticulation rates. Multiple regression analyses were used to determine whether size, hardness, and the interactive effects of size and hardness explained time to sinking and time to disarticulation, and to determine if size, hardness, or their interactive effects predicted the preservation potential of a given family in the fossil record. Finally, a paired t-test was conducted to determine whether the number of days it took insects to disarticulate was different from the number of days it took insects to sink. All statistical analyses were done with the use of JMP 4.0.2 (SAS Institute, 2000).

RESULTS

Beetle Size and Robustness

The smallest beetles in the study were the Curculionidae (weevils), while the largest beetles were the Scarabaeidae (Table 1). The hardness of the beetle cuticle was found to be affected by whether or not the insects were waterlogged. Dry specimens were brittle and easily punctured by the penetrometer, while the waterlogged specimens became extremely flexible, which increased their resistance to breakage. Because most waterlogged specimens became relatively impenetrable, the penetrability measures for the dry specimens are used in all further analyses. Of the dry specimens, the most physically robust beetle was the large scarab, and the least robust was the Carabidae (tiger beetles; Table 1). The average size of each beetle species used in this study was not correlated with its robustness ($r^2=0.03$, $n=7$, $p=0.70$).

Sinking and Disarticulation Rates

All of the tested beetles sank within two to thirty-nine and a half days. The fastest-sinking insects were the Curculionidae and the Chrysomelidae, while the large Scarabaeidae took the longest to sink (Table 1). Smaller beetles sank more quickly than larger beetles ($r^2=0.91$, $n=7$, $p=0.0008$). However, the amount of time it took for a beetle species to sink was best explained by the interactive effect of the species' hardness and size (hardness**size*: $F_{1,6}=14.57$, $p=0.032$). This analysis showed that increases in robustness do not influence sinking time positively as much for smaller beetles as they do for larger beetles (Fig. 2).

Of all the taxa in this study, the Chrysomelidae fully disarticulated the fastest (11 days) and the large Scarabaeidae did not show signs of disarticulation after 90 days (Fig. 3A). Disarticulation rates were explained additively by beetle size ($F_{1,6}=14.82$, $p=0.018$) and robustness ($F_{1,6}=19.82$, $p=0.011$). That is, larger, more-robust beetles were more likely to resist disarticulation than smaller, less-robust beetles. No interactive effect was found between beetle hardness and size and disarticulation rates ($F_{1,6}=0.35$, $p=0.59$).

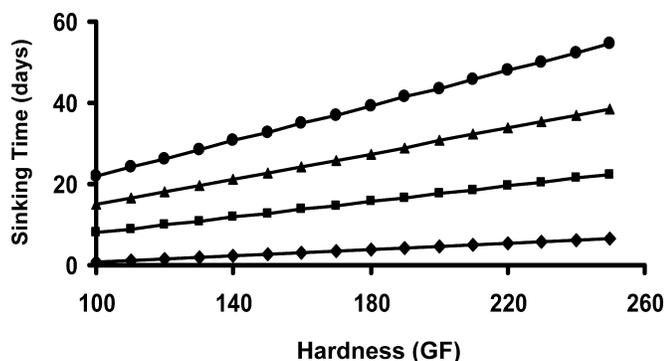


FIGURE 2—The interactive effect of hardness (GF, or grams of force needed to penetrate the elytra and thorax) and beetle size on sinking time is such that an increase in elytra hardness increases sinking rates for larger beetles much more than it does for smaller beetles ($Y = -16.3 + \text{hardness} (0.09) + \text{Size} (0.52) + 0.003 ((\text{size}-27.81) \times (\text{hardness}-156.47))$). This figure illustrates how changes in beetle hardness affect sinking time in beetles that are 10 (◆), 30 (■), 50 (▲), and 70 (●) mm² in size.

Sinking and disarticulation rates were positively correlated ($r^2=0.72$, $n=7$, $p=0.016$). However, on average, it took fewer days for beetles to sink ($12.79 \pm \text{SE } 5.90$ d) than it took to disarticulate (37.19 ± 9.88 d) (paired t -test, $t_{1,15}=2.04$, $p=0.062$; Fig. 4).

Patterns of Disarticulation

The beetles examined in this study had a characteristic pattern of disarticulation. After two to three days in the tumbler, all beetles developed a white, filmy substance that was concentrated along the sutures of the body and in the tracheal openings (Fig. 3A). This film seemed to begin with the breakdown of internal tissues. However, the composition of the film and the source of any associated microorganisms are unknown. During the first few days, limbs began to disarticulate from the body. Some specimens lost all legs within the first two days, while others lost only a few. The white film and limb loss both occurred while specimens were still suspended in water before they sank. After sinking to the bottom of the tumbler, the beetles underwent further disarticulation. For the majority of beetles, the head and thorax first disarticulated from the rest of the body as a unit. Next came full disarticulation, or the point at which the elytra disarticulated from the abdomen (Fig. 3B), and the head separated from the thorax. By this last stage, some beetles had experienced severe damage to body parts, including decayed and barely recognizable thoracic and abdominal segments.

Size, Robustness and Preservation Potential

The size data from this study were found to be unrelated to a family's preservation potential ($r^2=0.03$, $n=8$, $p=0.70$). While not significant, beetle hardness tended to predict the number of specimens occurring in the fossil record for each family ($r^2=0.42$, $n=9$, $p=0.06$). The interactive effects of beetle size and hardness did not explain a family's preservation potential ($F_{1,8}=0.006$, $p=0.95$).

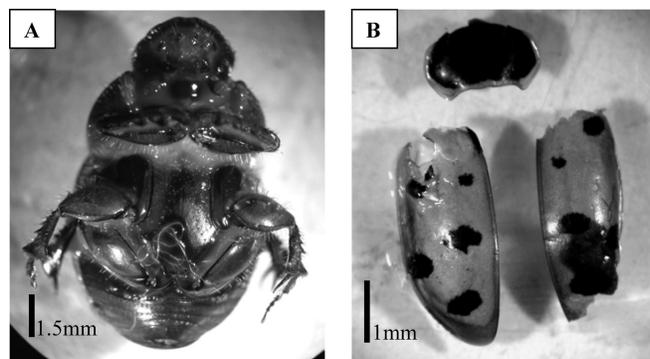


FIGURE 3—Results from tumbling experiments. (A) Scarabaeidae (large species) after 90 days of tumbling. Note the lack of disarticulation and the presence of a white-colored film between the first and second thoracic sternites. (B) Remains of a Coccinellidae after 15 days of tumbling. The specimen has undergone full disarticulation, with only the thorax and elytra present. Despite disarticulation, the elytra retain enough information to make them identifiable.

DISCUSSION

Both insect size and robustness have been hypothesized to influence the preservation of fossil insects in lacustrine environments by influencing the rate at which these insects sink and disarticulate (Martínez-Déclòs and Martínel, 1993; Smith, 2000; Martínez-Déclòs et al., 2004). This study provides evidence to support the hypothesis that these insect characteristics influence sinking and disarticulation rates. For example, the number of days it took beetles to sink was explained by the interactive effects of size and robustness. This latter finding suggests sinking time for smaller beetles depends less on how robust these beetles are than for larger beetles, which sink more rapidly when they are more robust. However, it is not evident whether robustness simply adds proportionally more weight to larger beetles, or whether it affects some other attribute that increases sinking rates in larger insects.

When it comes to rates of disarticulation, it appears both insect size and robustness have an additive affect, with larger, more-robust beetles taking longer to disarticulate than smaller, less-robust beetles. As such, large and robust beetles sink faster (see above) and take longer to

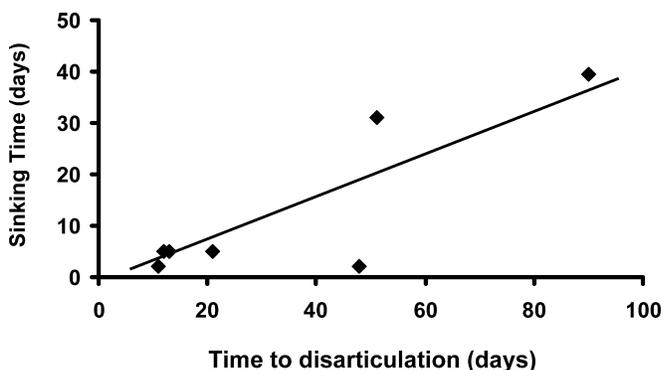


FIGURE 4—The time it took beetles to sink was positively correlated with the time it took a beetle to disarticulate ($r^2=0.72$, $n=7$, $p=0.016$). However, on average, it took fewer days for beetles to sink ($12.79 \pm \text{SE } 5.90$ days) than it took to disarticulate (37.19 ± 9.88 days); paired t -test, $t_{1,15}=2.04$, $p=0.062$.

disarticulate than their large, less-robust counterparts. Although this should be apparent in the fossil record, no such pattern has been documented in the literature previously. On the contrary, when larger beetles are found, they often are represented by isolated, disarticulated parts.

Smaller beetles tend to sink and disarticulate faster than larger beetles. Fast sinking times are thought to be very important to insect preservation because insects that remain floating or in the water column are more susceptible to biotic degradation via microbial and fungal decay and scavenging (Norlin, 1967; Briggs and Wilby, 1996; Duncan et al., 2003). Based on the lacustrine beetle record, it appears that sinking rates may be more important than disarticulation rates for beetle preservation. Because smaller beetles sink faster than larger beetles, smaller taxa may be removed from environments that lead to further disarticulation. Previous studies have documented the importance of sinking rates and less exposure to destructive processes in the preservation potential of other organisms, such as marine mollusks (Kidwell and Bosence, 1991) or evergreen leaves (Spicer, 1991). Previous studies also have noted a tendency for smaller beetles to be overrepresented in lacustrine settings (Wilson, 1988; Smith, 2000; Martínez-Délclòs et al., 2004).

Interestingly, it appears that, in lacustrine environments, beetle sinking and disarticulation rates may be correlated, although beetles may sink much more quickly than they disarticulate. In addition, once a beetle enters an aquatic environment, it may become protected from physical breakage. In this study, waterlogged specimens gained flexibility in their exoskeleton, and as a result, their cuticle was difficult to penetrate. This flexibility may make waterlogged beetles less susceptible to mechanical degradation, thereby decreasing their disarticulation rates and increasing their likelihood of being preserved. Actualistic experiments on recent Xiphosurans also have shown that waterlogging increased flexibility of exoskeletons, and that desiccated specimens became more brittle and prone to breakage (Babcock et al., 2000). Increases in mechanical degradation and disarticulation rates also have been shown to increase the amount of microbial decomposition that a specimen experiences (Briggs, 1995) and, in turn, decreases preservation potential (Kidwell and Flessa, 1995; Behrensmeyer et al., 2000).

All beetle specimens studied displayed a similar pattern of disarticulation, and further demonstrate the importance of rapid sinking and levels of water agitation on insect preservation. A white film that could have been caused by decaying soft tissues, microbial or fungal activity, or a combination of these factors, was apparent on all specimens within a few days of their introduction to the rock tumbler. This shows that biotic degradation can occur within a few days after an insect enters a lake environment, a pattern that has been shown in other organisms (Borkow and Babcock, 2003). However, full disarticulation did not occur until the specimens sank to the bottom of the tumbling barrel and were further agitated.

Although size and robustness have been mentioned previously as important components of preservation (see Briggs et al., 1998; Smith, 2000), a preliminary comparison of beetle family characteristics and fossil occurrence showed that beetle hardness may be important in predict-

ing a family's preservation potential, while size may not be. It is cautioned that this is only a preliminary examination, as the emphasis of this study was to understand taphonomic processes. Future studies examining how family morphology determines beetle preservation potential should increase the number of families that are compared, and should address issues surrounding which taxa may represent the fullest range of morphologies within a family. While this study emphasized morphology in determining the preservation potential of beetles, future studies also could examine how variables such as the relative abundance and diversity of families affect their preservation potential.

CONCLUSIONS

This study has shown that preservation potential of beetles appears to be correlated with both the size and robustness of a beetle's exoskeleton because these physical characteristics are strongly correlated with both sinking and disarticulation rates. In addition, waterlogging increases the flexibility of the exoskeleton, potentially decreasing the negative effects of transport and disarticulation of beetle remains. In general, biotic decay sets in rapidly (within 2–3 days), and beetles appear to sink faster and then experience full disarticulation. Because the lacustrine beetle-fossil record suggests that smaller beetles are overrepresented relative to larger beetles, sinking rates may play a more important role in beetle preservation in lake systems than disarticulation rates because smaller beetles sink faster than larger beetles, which are more disarticulation resistant. While larger beetles inherently may be more resistant to disarticulation, remaining in the water column may make them more susceptible to scavenging and microbial and fungal decay (Norlin, 1967; Briggs and Wilby, 1996; Duncan et al., 2003). A preliminary examination of fossil-beetle literature shows that a beetle's hardness may be related to a family's preservation potential.

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