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Authors

Karr, Jered A
Clapham, Matthew E

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

Jered A. Karr

Matthew E. Clapham

RRH: TRENDS IN INSECT ARTICULATION

LRH: JERED A. KARR AND MATTHEW E. CLAPHAM

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27

28 *Abstract.*—

29 Insect taphonomy is a topic that has drawn interest because of its potential biases on
30 diversity patterns and the ecological information recorded by ancient insect faunas.

31 Other than the onset of common amber fossilization in the Cretaceous, very little is
32 known about long-term trends in the nature and quality of insect preservation and, as

33 a result, the effects of taphonomic biases are poorly constrained. We assembled a

34 database of nearly 7000 Carboniferous-Pliocene insect adpression (compression and

35 impression) species from the primary literature to assess changes in insect taphonomy

36 over time and test biotic and environmental controls on preservation. We grouped the

37 fossils into 10 Myr bins and scored preservation of holotype specimens as either

38 articulated bodies or isolated wings; articulated specimens with a body implied a

39 generally higher quality of preservation. Paleozoic and Triassic insect holotypes are

40 known overwhelmingly from isolated wings (only 12% articulated bodies), but our

41 database shows a significant increase in the percentage preserved as articulated

42 bodies, to more than 70%, beginning about 160 Myr ago in the Late Jurassic. This

43 transition could reflect variations in the robustness of different insect orders and shifts

44 in the taxonomic composition of insect faunas, but all the major orders in the database

45 exhibit significant increases in articulation. Instead, a shift to increased preservation

46 in lacustrine paleoenvironments, which contain a greater proportion of articulated
47 body fossils, explains most of the trend. The pronounced Late Jurassic increase in
48 articulation has implications for evolutionary and ecological reconstructions; for
49 example, suggesting that preserved insect diversity may be biased downward in the
50 earlier part of their history when articulation was poor.

51 *Jered A. Karr and Matthew E. Clapham. Department of Earth and Planetary*
52 *Sciences, University of California, Santa Cruz, California 95064 U.S.A. E-*
53 *mail: larijer@gmail.com.*

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Introduction

56 Insects are the most diverse and successful animal group today (Gaston 1991)
57 but understanding their past evolutionary patterns, diversity, and ecology may be
58 hindered by preservational biases. Taphonomic processes can change our view of
59 ecologic roles and importance or can obscure taxonomically-important characters and
60 evolutionary relationships among groups (e.g., the case of Protorthoptera; Béthoux
61 2005, 2007). Labandeira and Sepkoski (1993) note that their diversity curve is likely
62 biased by exceptional Tertiary deposits such as Baltic amber and Florissant, so
63 understanding insect preservation can also help us elucidate their true past diversity
64 trends.

65 Although their fossil record is richer than generally assumed (Labandeira and
66 Sepkoski 1993; Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005), insects lack
67 mineralized tissue and their preservation usually requires extraordinary
68 circumstances, commonly in Konservat-Lagerstätten. These insect Konservat-
69 Lagerstätten come from varied environments, particularly lacustrine settings and
70 amber, but also shallow-marine or lagoonal deposits and small ponds (Labandeira
71 1999), each of which may have been influenced by a variety of biases. Because amber
72 preservation only became common in the Early Cretaceous, has a more ephemeral
73 record than lacustrine deposits (Labandeira 1999), and was influenced by a different
74 set of taphonomic biases (Zherikhin et al. 1999; Martínez-Delclòs et al. 2004) we will

75 focus only on insects preserved as adpressions (compressions and impressions) in
76 sedimentary rocks.

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

91 Many studies have assessed the factors that influence insect preservation
92 quality, but these studies have largely focused on detailed taphonomic investigation
93 of single localities with specific environmental conditions (Wilson 1980, 1988;
94 McCobb et al. 1998; Ansorge 2003; Coram 2003; Wappler 2003; Henning et al.
95 2012). We examined long-term trends in the articulation of insect fossils using a large

96 database of specimen data compiled from the primary literature. Although insect
97 preservation quality is multifaceted, we used articulation as a proxy for decay because
98 experiments examining the various stages of insect decomposition found that isolated
99 wings, even with minute details, often represent one of the final stages of
100 decomposition (Duncan et al. 2003). Using a large dataset of fossil insect localities
101 allows us to pool multiple sites, removing idiosyncratic, location-specific taphonomic
102 signals to reveal overarching trends. We tested the effects of depositional
103 environment, insect size, morphology/taxonomic group and geologic age on insect
104 articulation. Understanding the overall biases in the fossil record of insects will allow
105 assessment of the ecology and evolution of this group across geologic time and
106 comparison with trends observed in other groups of animals and plants.

107

108 Insect Taphonomy

109 In order to use insect fossil assemblages for evolutionary, ecological, or
110 diversity studies, it is important to understand the steps from living insect to fossil to
111 published literature. The rate at which an insect passes through these steps influences
112 the quality of preservation by altering the time exposed to predation, decomposition,
113 and disarticulation. An insect must pass through four taphonomic steps, which act as
114 filters, before being preserved as an impression in the fossil record. First, the body
115 must be transported to an aquatic environment by rafting or aerial deposition (except
116 in the case of aquatic insects, which already inhabit the environment). Most insects

117 are not aquatic so they must next break the surface tension of water. Martínez-Delclòs
118 and Martinell (1993) examined insect deaths in aquatic environments of a variety of
119 taxonomic groups and found a large range of outcomes depending on size and weight,
120 described by the SM (wing surface area-to-mass) index (Wagner et al. 1996), and
121 wing type or shape. There tends to be a bias against large-winged or fragile groups
122 such as Lepidoptera and against insects with wingspans smaller than 5 mm, typically
123 leading to enrichment in heavy, medium sized insects at the sediment interface
124 relative to their life abundance. Archibald & Makarkin (2006) and Wang et al. (2013)
125 showed that insects with larger SM indices are more prone to disarticulation, likely
126 due to longer floating time at the water surface. Larger wings commonly have
127 microstructures that influence the wettability of the wings and can increase floating
128 time as well (Wagner et al. 1996; Rust 1998; Archibald and Makarkin 2006). After
129 breaking the water surface, the third step requires the insect to sink through the water
130 column. Temperature and chemical composition affect the rate of sinking, and a
131 density change at the thermocline (in deeper lakes or the ocean) or halocline (in some
132 salt water environments) can prevent sinking, which promotes decomposition before
133 carcasses can be deposited on the sediment (Martínez-Delclòs et al., 2004). The final
134 step is burial after the insect settles onto the sediment, influenced by the distance
135 from shore, water chemistry, and tectonic setting. In studies of Eocene lakes from
136 British Columbia, Wilson (1980, 1988) noted a trend for more articulated specimens
137 in offshore compared to nearshore sediment. In another study, Briggs et al. (1998)
138 found that insects from deep-water anoxic zones had 95-98% more chitin preserved

160 forewing, hindwing, or wing) were grouped together, whereas an exoskeleton
161 includes any specimen with both the body and wings. In many cases the wings and/or
162 body are incomplete or fragmentary, but we did not distinguish fragmentation in our
163 analyses. We excluded all species where the holotype body part was unidentified or a
164 nymph/larva and all occurrences of questionably identified genera and species or
165 those in open nomenclature. Because we are also interested in the effect of size on
166 articulation we also excluded all occurrences without a wing measurement.

167 For each locality, we assessed the depositional environment to test its effect
168 on articulation. The Paleobiology Database (PBDB) allows specification of a wide
169 range of environments for each collection, making analysis unfeasible due to small
170 sample size in some cases, so similar environments were grouped together into the
171 following categories: marine, delta/lagoon, HE (high energy) terrestrial, shallow
172 lakes, and deep lakes. Because we hypothesized that deep lakes have uniquely
173 favorable conditions for insect fossilization, for most analyses we use the term deep
174 lake or non-deep lake (combined marine, delta/lagoon, HE terrestrial, shallow lakes)
175 to categorize the environment. The deep lake category includes large lakes
176 (“lacustrine – large” in the PBDB) such as Florissant (Veach and Meyer 2008), the
177 Yixian Formation (Hethke et al. 2013), and Lake Gosiute (Green River Formation;
178 Surdam and Stanley 1980). Because we consider depth to be an important factor, the
179 deep lake category also contains several localities assigned to the PBDB “crater lake”
180 environment, with smaller surface area but with significant depth, such as Messel
181 (Harms 2002; Felder and Harms 2004), the Eckfeld Maar (Lutz 2003), Menat

182 (Wappler et al. 2009), and the Randeck Maars (Zeuner 1942). The shallow lake
183 category includes localities referred to as ponds (Engel and Gross 2008) or oxbow
184 lakes like Madygen (Shcherbakov 2008).

185 Size data were also collected to examine its impact on articulation. The length
186 of the wing, tegmen (Orthoptera and relatives, Blattodea and relatives, some
187 Hemiptera), elytron (Coleoptera), or hemelytron (some Hemiptera) was recorded. In
188 groups with two pairs of wings (fore and hind wings), the larger of the two pairs was
189 used. Sizes were taken from measurements directly reported in the systematic
190 description or were measured from published illustrations if no size was given in the
191 text. Many fossil wings are incomplete because of biostratigraphic processes,
192 especially in the largest insects, so we used estimates of complete wing size provided
193 in the description. After taxonomic filtering and removing amber specimens we have
194 6915 measured species.

195 We binned the data into 30 time intervals equivalent to geological stages or
196 sets of neighboring stages, starting in the mid Carboniferous. The interval definitions
197 are the PBDB 10-million-year bins, the same as those used in several recent papers
198 (Alroy et al. 2008). Stage level time intervals were not used due to a paucity of data
199 and uncertain age assignment of many localities.

200 Model Construction

201 We performed multiple logistic regression analyses in R (R Development
202 Core Team 2012) to estimate the effect of morphology, depositional environment,

203 and size on the probability of a specimen being articulated. We \log_{10} transformed
204 wing size (measured in mm) to normalize the size distribution. The morphology
205 predictor was coded as a binomial factor (beetle or non-beetle) for simplicity; even
206 though articulation varies within and among orders, beetles have the greatest
207 preservation potential (Smith 2000). It is also difficult, a priori, to predict or assign
208 numerical values to the articulation of each insect order, but if morphology is an
209 important predictor of articulation the comparison of beetles to other insects should
210 show this. We coded the environment predictor as a binomial factor as well, based on
211 whether the specimen came from a “deep lake” or a “non-deep lake” depositional
212 environment. As with morphology, it is not possible to transform the environmental
213 categories into an ordered numerical variable and there are multiple reasons to believe
214 that deep lakes should have superior fossil preservation compared to other
215 depositional environments. Because we wanted to keep the results interpretable, we
216 narrowed our pool of models to only combinations of these three variables and did
217 not include interaction effects. We used Akaike information criterion (AIC) to
218 determine model selection.

219 We also analyzed the effects of environment and size on six common clades:
220 Odonatoptera (dragonflies, damselflies and extinct relatives), Blattodea (cockroaches,
221 excluding termites), Orthoptera (grasshoppers and crickets), Hemiptera (bugs),
222 Diptera (flies), and Coleoptera (beetles) with separate multiple logistic regression
223 models for each group. Finally, we examined the effect of size alone by performing

224 logistic regression models, on all insects and on the same six common groups, with
225 size as the only predictor.

226 Direct comparison of the relative importance of all three predictor variables
227 using the magnitude of the odds ratios is not possible because “environment” and
228 “morphology” are both binomial predictors while “size” is continuous. We converted
229 size to a binomial predictor comparable to environment and morphology by using the
230 mean \log_{10} size for the Cenozoic as “small” (0.83) and the mean for the
231 Carboniferous as “large” (1.54). We then predicted the probability of articulation
232 through geologic time based on the eight possible combinations of the now binomial
233 predictor variables (size, morphology, environment). We compared each combination
234 to the overall shift in articulation. To do that, we created a synthetic dataset in which
235 “size” was replaced with values ranging continuously from 1.54 in the oldest bin to
236 0.83 in the youngest bin. “Environment” was replaced with values ranging from 0.0
237 to 0.82 (the proportion of insect occurrences occurring in deep lakes in the
238 Carboniferous and Cenozoic, respectively) and “morphology” was replaced with
239 values from 0.0 to 0.26 (the proportion of insect occurrences that are Coleoptera in
240 the Carboniferous and Cenozoic). We also compared actual variations in articulation
241 to predicted articulation proportion using the relationship derived from overall
242 logistic regression model and the environment (proportion deep lake), morphology
243 (proportion beetle), and size (mean size) data for each time bin.

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

246

247 **Results**

248 The proportion of articulated holotypes increased significantly through time.
249 Before the Late Jurassic (Jurassic bin 5, Callovian-Kimmeridgian, ~161 Ma), 88.8%
250 of insect holotypes are disarticulated wing elements, whereas 73.4% of holotypes in
251 the Late Jurassic and after are preserved as articulated bodies (Fig. 1). In a
252 comparison of multiple logistic regression models, the model including all three
253 variables (environment, morphology, and size) was the best-supported (Table 1),
254 indicating that morphology, environment, and size all significantly affected insect
255 articulation ($p < 0.001$ for all variables; Table 2). While holding other parameters
256 constant, beetles were more articulated than insects as a whole, insects in deep lake
257 environments were significantly more likely to be articulated, and specimens with
258 larger wing size were less likely to be articulated (Figs. 2-4).

259 Morphological Controls

260 Because higher-level taxonomic groupings typically represent distinctive body
261 plans with different preservation potential, shifts in the abundance of major groups
262 over time (Labandeira and Sepkoski 1993) likely affected articulation. Of the eight
263 most common clades in our database, Blattodea, Orthoptera, and Odonatoptera were

264 dominant in the early part of the record whereas Coleoptera, Diptera, and
265 Hymenoptera, which are all smaller and/or more robust taxa commonly requiring
266 body features for identification, become dominant in the late Mesozoic and Cenozoic
267 (Labandeira and Sepkoski 1993). This shift likely contributed to increased
268 articulation in younger collections, but was not the principle factor because all well-
269 sampled taxonomic groups independently increase in articulation through time (Fig.
270 2).

271 *Odonatoptera*.—Odonatoptera (total-group Odonata and extinct relatives like
272 Meganisoptera) includes large insects with high SM index wings that are spread away
273 from the body at rest (except in Zygoptera). Their wing venation is complex and
274 distinctive for taxonomic identification. Only 26.9% of Odonatoptera species have
275 been described from articulated bodies, but overall articulation increased significantly
276 in younger collections. Articulation did not change significantly within environments
277 (Fig. 2A).

278 *Blattodea*.—Blattodea (cockroaches, excluding termites in our analyses) have
279 forewings that are hardened into tegmina, which are more resistant to degradation
280 than bodies or hindwings. Blattodea holotypes are most commonly an isolated tegmen
281 in Paleozoic deposits but in the Mesozoic and Cenozoic they are more commonly
282 articulated bodies (Fig. 2B). The high diversity of Paleozoic species influences the
283 mean percent articulation and only 22.6% of species have been described from

284 articulated bodies. Like in Odonoptera, articulation did not change significantly
285 over time within environments.

286 *Orthoptera*.—Orthoptera (crickets and grasshoppers) can be quite large (the
287 suborder Titanoptera reached wing lengths of 180 mm during the Triassic) and have
288 sclerotized forewings like Blattodea. Overall articulation is even lower than in
289 Blattodea (15.8% of species holotypes are articulated) and increased significantly in
290 younger deposits. Within-environment trends are more difficult to reconstruct
291 because there are no deep-lake occurrences of Orthoptera before the Jurassic, but
292 articulation likely increased significantly both in non-deep lakes and in deep lakes
293 (Fig. 2C).

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

300 *Diptera*.—Diptera (flies) are typically small insects with simple wing
301 venation, making description from isolated wings challenging. They are generally so
302 small that it can be difficult for them to break surface tension (Martínez-Delclòs and
303 Martinell 1993), but are well articulated (75.5% of species described from complete
304 bodies). Articulation increased slightly in both non-deep lakes and deep lakes.

305 Increased preservation in deep lakes accounts for a greater proportion of the overall
306 trend toward increased articulation in Diptera (Fig. 2E).

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

313 Environment

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

326 Wing Size

327 Articulation has a clear negative relationship with wing length in our database
328 (Fig. 4). Maximum insect size has decreased over time (Clapham and Karr 2012) but,
329 because other morphological factors also vary among orders, it is important to look at
330 the trends within each clade to assess the effects of size alone. Of the six best sampled
331 clades only Hemiptera and Coleoptera have a strong negative relationship between
332 size and articulation (Fig. 5, Table 2). Larger Diptera are significantly less likely to be
333 articulated after accounting for environment of preservation (Table 2). Odds ratios in
334 Orthoptera and Blattodea indicate that increases in size are positively (although not
335 significantly) associated with increased articulation, whereas Odonatoptera exhibit no
336 significant relationship (Table 2). There is a strong trend of clades with large wing
337 size (and likely body size) being less articulated than clades with small wing size,
338 implying that intra-clades decreases in size had a smaller effect on articulation than
339 the replacement of larger-bodied clades by typically smaller ones.

340 Relative Importance of Size, Morphology, and Environment

341 The odds of an insect preserved in a deep lake being articulated are 1350%
342 higher than the odds for an insect in a non-deep lake environment. By comparison,
343 the odds of articulation for beetles are nearly 119% higher than the odds for non-
344 beetles, implying that changes in environment have a greater effect on insect
345 articulation than differences in insect morphology. For every tenfold increase in size
346 the odds of articulation decrease by nearly 85%. Deep lake environments (bars in

347 column A of Fig. 6) consistently have greater articulation, regardless of taxonomy or
348 size, implying that although size and taxon group affect articulation, environment is
349 the largest contributor.

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

361

362 **Discussion**

363 **Morphological Controls**

364 Insects are a very disparate group with major morphological differences
365 among orders. This structural variability likely influences overall articulation due to
366 changes in the relative diversity of insect orders through time (Labandeira and

367 Sepkoski 1993). In addition, articulation proportions based on published holotypes
368 depend not only on taphonomic biases during fossilization (related to robustness, size,
369 and SM index), but also on conventional taxonomic practices for species description
370 in a particular group.

371 The six suprafamilial groups we analyzed display three general patterns of
372 articulation over time. (1) Each environment had a consistent level of articulation
373 over time, but overall articulation increased (observed in Odonatoptera and to some
374 extent in Blattodea). (2) Overall articulation increased, as did articulation in both deep
375 lake and non-deep lake environments (observed in Hemiptera, Orthoptera and
376 Diptera). (3) Articulation decreased in both of these environments but overall
377 articulation increased (observed only in Coleoptera).

378 Consistent within-environment articulation trends in Odonatoptera (and
379 Blattodea) are best explained by the conservative morphology of those groups.
380 Because their overall body plan has changed little over their evolutionary history,
381 taphonomic controls on articulation were similar in the Carboniferous or the
382 Cenozoic. Both groups are more consistently articulated in deep lakes and the overall
383 increase in articulation resulted from the post-Jurassic increase in the number of deep
384 lake deposits (Fig. 2A,B).

385 A shift to greater preservation in deep lakes also significantly enhanced
386 articulation in Hemiptera, Orthoptera, and Diptera (Fig. 2C-E), but those three groups
387 exhibited considerable within-environment increases in articulation in addition.

388 Changing articulation in deep lakes and non-deep lakes likely reflects evolutionary
389 trends within the clades that resulted in morphologically distinct families changing in
390 proportional abundances. For example, Heteroptera, a suborder within Hemiptera that
391 often contains smaller, beetle-like species with folded tegmina and lower SM indices,
392 is in general more articulated and constitutes a larger proportion of occurrences later
393 in the fossil record as compared to “Homoptera,” a paraphyletic assemblage of
394 generally large-winged, poorly sclerotized and less articulated Hemiptera. Similarly,
395 Cenozoic Orthoptera are largely composed of Acrididae (short-horned grasshoppers)
396 and Tettigoniidae (katydids), two lineages that been observed in actualistic
397 experiments to have an unusual response to drowning, which might increase sinking
398 rate (Martínez-Delclòs and Martinell 1993). Extinct lineages may not have had this
399 response. There is also a trend of wing reduction in Orthoptera (Sharov 1968), which
400 would decrease their SM index and promote sinking. The patterns in Diptera possibly
401 reflect a shift from more fragile, gracile dipteran groups such as Tipulomorpha to
402 more stout-bodied, robust groups such as Muscomorpha.

403 Coleoptera have a higher preservation potential than other insect orders in
404 both modern, actualistic studies and lab experiments (Smith 2000; Smith et al. 2006),
405 primarily because their forewings have been highly modified into hard sheaths called
406 elytra. Our results support these findings, as Coleoptera is one of the most highly
407 articulated groups in our data. In contrast to the other five well-sampled clades,
408 Coleoptera exhibit a highly unusual pattern where the probability of articulation
409 actually decreased in both deep lakes and especially in non-deep lakes (Fig. 2F). This

410 trend does not reflect changes in beetle body plans, which have remained stable over
411 most of their evolutionary history, or size, which also has not changed substantially.
412 Instead, decreased articulation is most likely an artifact of taxonomic practices.
413 Earlier paleoentomologists, especially in the 19th century, described many species
414 based on isolated elytra from Cenozoic localities. Mesozoic and Paleozoic isolated
415 elytra typically have little taxonomic value (even at the family or suborder level) and
416 are rarely named by modern paleoentomologists (Arnoldi et al. 1977; Ponomarenko
417 2002), often being placed in morphotypes instead (Papier et al. 2005; Martin 2010).
418 More than 81% of beetle species described before 1950 were from Cenozoic
419 localities, compared to fewer than 12.5% of species described after 1950. Restricting
420 the analysis to species described after 1950 reduces the effects of outdated taxonomic
421 practices and indicates no significant shift in articulation within environments (Fig.
422 8). Articulation of holotypes does not change significantly with year of publication in
423 other taxonomic groups (Fig. 9), indicating that shifting taxonomic practices only
424 affect Coleoptera (supplementary figure 1). After excluding outdated species,
425 Coleoptera have a similar pattern of articulation to other morphologically-stable
426 groups (Odonatoptera and Blattodea), in which the shift to greater deep lake
427 preservation primarily caused the increase in articulated holotypes.

428 Wing Size

429 Changes in the median size of insects through time could influence
430 articulation and it is known that the size of insects has changed over time (Dudley

431 1998; Okajima 2008; Clapham and Karr 2012). Large insects have greater wing area
432 relative to body mass on average (high SM index value) and will float on the water
433 surface on longer than smaller winged, heavier-bodied insects (low SM index value)
434 (Archibald and Makarkin 2006). Larger insects may also be subjected to more intense
435 predation (Blanckenhorn 2000; Chown and Gaston 2010) favoring disarticulation
436 and/or removal them from the death assemblage.

437 The median wing size of insects in our database during the Carboniferous is
438 more than 30 mm but decreases to only 7 mm during the Cenozoic, although this
439 trend is not uniform across all orders. Odonoptera wing length decreased from a
440 median of 140 mm in the Carboniferous to a median of 35 mm during the Cenozoic,
441 whereas Coleoptera median size remained remarkably stable at around 5 mm. The
442 overall trend of decreasing median size seen in insects is influenced by two factors.
443 The first is a shift from large-winged groups such as Palaeodictyoptera and
444 Megasecoptera to small-winged orders such as Diptera and Hymenoptera. Because
445 the degree of articulation varies widely among groups, with smaller fossils typically
446 being more articulated, this taxonomic replacement is the major mechanism by which
447 size has affected articulation. The second cause is a decrease in median size of both
448 Orthoptera and Odonoptera, two large winged groups, which are found abundantly
449 throughout the insect fossil record. It is less clear whether this size decrease also
450 drives the size-articulation relationship because of the inconsistent logistic regression
451 results when testing orders individually. Although small specimens were significantly

452 more articulated in Odonatoptera, Hemiptera, and Diptera, the reverse was true in
453 Orthoptera and Blattodea, even after accounting for environment (Table 2).

454 Environmental Controls

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

460 Deep lake floors are calm, low-energy environments, which are unlikely to
461 physically disarticulate dead insects, whereas carcasses in smaller lakes are subjected
462 to higher energy due to mixing of the water column. Insect carcasses in marine
463 environments are subject to greater wave action than those found in lakes. Even
464 insects preserved in offshore marine sediments must still pass through the wave-
465 influenced mixed layer, which is thicker in the ocean than in lakes because of the
466 longer fetch of wind-generated ocean waves. Physical destruction or disarticulation
467 during transport also reduces preservation probability or quality. Because nearly all
468 insects are terrestrial, transport distance to the ocean is usually farther than to
469 lacustrine environments, leading to better preservation in lakes (Zherikhin 2002).

470 Anoxia is known to be important in increasing the quality and likelihood of
471 preservation by preventing scavengers and bioturbators from disturbing insect
472 carcasses on or in the sediment. Anoxia is also known to promote microbial mats that

473 may enhance mineral precipitation around a soft bodied organism such as an insect
474 (Allison 1988; Behrensmeyer et al. 2000). Anoxic bottom waters are frequently
475 developed (at least seasonally) in large deep lakes. It is uncommon for shallower
476 lakes to have anoxic bottom waters because mixing of the water column prevents the
477 depletion of oxygen in the bottom waters (Olsen 1990; Scheffer 2004). Restricted
478 ocean basins can also be prone to anoxic bottom waters and several famous, insect-
479 bearing Konservat-Lagerstätten are from anoxic environments (e.g. Solnhofen).
480 Water chemistry is also important, with high solute concentration having been noted
481 to help with preservation of soft bodied organisms by facilitating the precipitation of
482 authigenic minerals (Briggs 2003). Endorheic lakes such as Lake Gosiute (Green
483 River Formation), which often formed in interior rift basins (Surdam and Wolfbauer
484 1975; Smith et al. 2008), can have extremely high levels of minerals that lead to
485 unusual water chemistry that can be beneficial for preservation (Allison and Pye
486 1994).

487 Our results further imply that variations in taxonomic composition among
488 depositional environments influence articulation, although this is likely a secondary
489 factor. In particular, small-bodied, weak fliers like Coleoptera and Diptera, which
490 have high intrinsic articulation (Smith 2001), are over-represented in deep lake
491 environments relative to other settings (Table 3). It is difficult to assess causality and
492 it is possible that Diptera are dominantly found in deep lakes because they require the
493 exceptional preservation in those settings. It does seem plausible, however, that
494 marine settings may have fewer weakly-flying taxa because of the greater distance

495 from the original continental habitat, reducing articulation because of the lack of
496 those intrinsically well-preserved taxa.

497 **Conclusion**

498 The fossil record of insects has changed over geological time to become
499 dominated by articulated holotype specimens, with a notable shift in the Late Jurassic.
500 Although holotypes are more articulated than an average specimen, the timing and
501 direction of the shift in articulation is a robust signal. This shift can be explained by
502 three factors. The first is a decrease in the average size of insect specimens. Overall,
503 larger insects are less articulated than smaller insects, even after accounting for
504 environment and taxonomic position. This trend probably reflects taxonomic shifts
505 from larger to smaller groups and is related to shape, especially the ratio of wing to
506 body size, rather than size itself. The second factor involves shifts in dominant
507 taxonomic groups. Archaic groups, which lack wing-folding mechanisms and have
508 large wings relative to their body size, were much more common in the Carboniferous
509 and Permian, whereas a more modern fauna dominated by Coleoptera, Diptera and
510 Hymenoptera did not become established until the Jurassic. Coleoptera, Hymenoptera
511 and Diptera (especially Coleoptera) all have characteristics that should lead to better
512 preservation and their fossils are on average much more articulated. Increased
513 articulation, even within single environments, occurs in clades like Hemiptera,
514 Orthoptera, and Diptera also because of changes in taxonomic composition. In
515 contrast, morphologically conservative groups like Odonatoptera, Blattodea, and

516 Coleoptera do not exhibit increased articulation over time within environments.
517 Although these results confirm the importance of insect morphology, especially
518 factors such as the SM index relating wing size to body mass, all groups display
519 overall increases in articulation with time, implying that taxonomic shifts cannot
520 completely explain trends in insect articulation.

521 Our analysis suggests that the depositional environment in which an insect is
522 preserved is the most important control on articulation. Insect fossils from deep lakes
523 have higher rates of articulation compared to the other paleoenvironments and there
524 was a dramatic shift in the Late Jurassic from deltaic, marine, and smaller lake
525 localities to deep and/or large lakes. That shift was the primary reason for the
526 substantial increase in articulation, also in the Late Jurassic. It could affect patterns in
527 insect diversity, evolution, and ecology that are preserved in the fossil record, for
528 example by biasing diversity in older parts of the insect record where preservation
529 quality is poorer. Accounting for differences in depositional setting is essential to
530 truly understanding the fossil record of insects and likely other groups including birds
531 and plants that are also found largely in Konservat-Lagerstätten.

532

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701 contemporaneous fossil insect sites in North and West Transbaikalia.
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704

705 **Figure Captions**

706 **Fig. 1.** Phanerozoic trend in insect articulation, based on the proportion of
707 occurrences of species with articulated holotypes in each 10 Myr bin. Bubble size

708 scales with the number of occurrences in each 10-Myr bins (maximum 1061). Dashed
709 line represents the beginning of the Callovian (Jurassic bin 5). (one column)

710 **Fig. 2.** Phanerozoic occurrences of insect holotypes (grey circles) for six common
711 suprafamilial groups with logistic regression models fit relating articulation as a
712 function of age in all environments (black line), fit to only deep lake environments
713 (dotted line) and fit to only non-deep lake environments (hashed line).(two Column)

714 **Fig. 3.** Phanerozoic insect holotype occurrences (grey circles) with logistic regression
715 model fit relating articulation as a function of age in all environments (black line) and
716 fit to only deep lake environments (dotted line) or non-deep lake environments
717 (hashed line). Points representing articulated and non-articulated insect specimens
718 have been randomly jittered for visibility.(one column)

719 **Fig. 4.** Occurrences of insect holotypes for all sizes (grey circles) with a logistic
720 regression model fit relating articulation as a function of \log_{10} wing length. (One
721 Column)

722 **Fig. 5.** Occurrences of insect holotypes for all sizes (grey circles) for six common
723 suprafamilial groups with a logistic regression model fit relating articulation as a
724 function of \log_{10} wing length in all environments (black line), fit to only deep lake
725 environments (dotted line) and fit to only non-deep lake environments (hashed line).
726 (two Column)

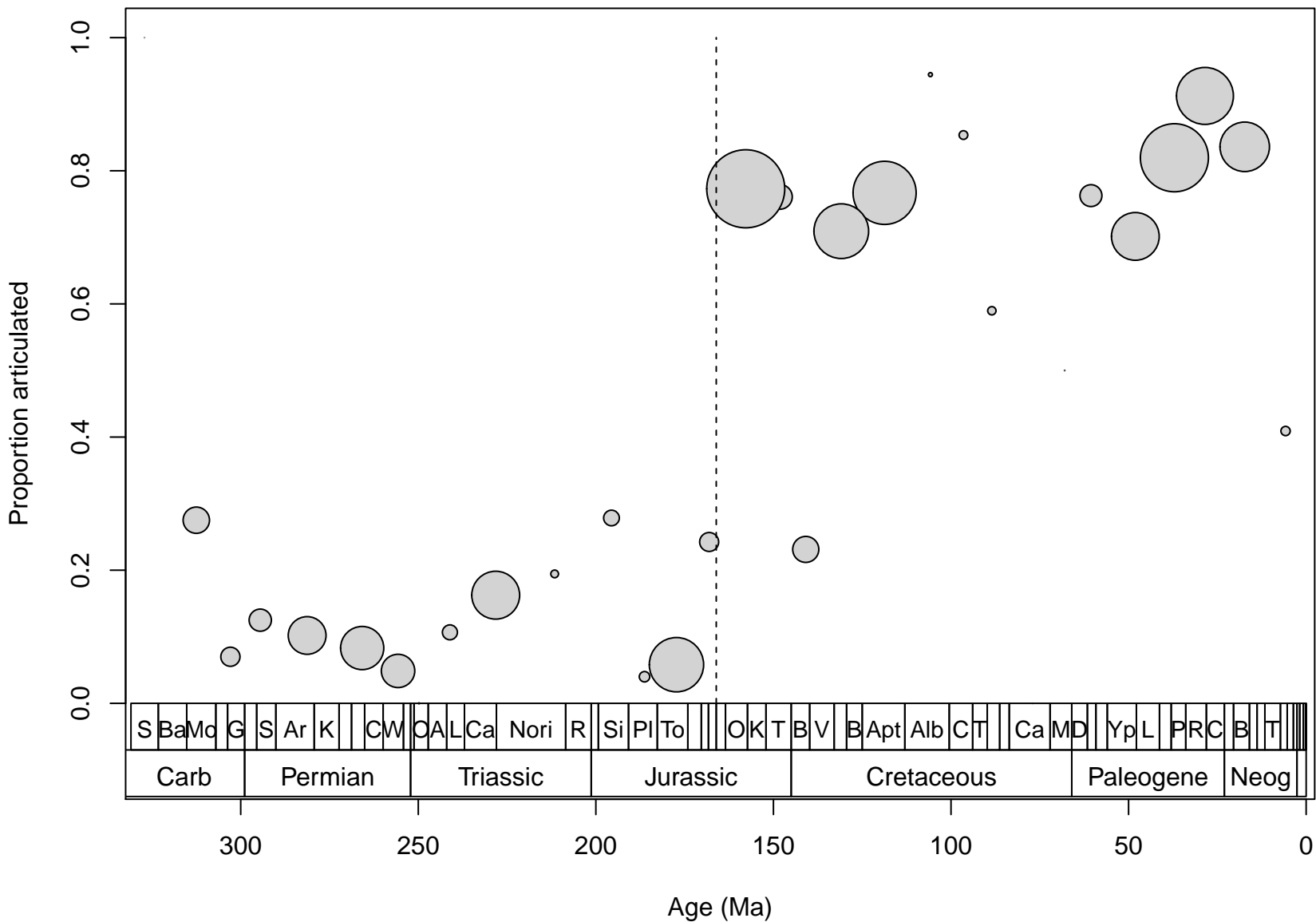
727 **Fig. 6.** Occurrences of insect holotypes in the Phanerozoic with logistic regression
728 model fits relating articulation as a function of tested parameters. Dashed lines
729 represent different regression models holding different combinations of the three
730 predictors (environment, morphology, size) constant. Bars indicate deep lake
731 environments in column A, beetles in column B, and small size in column C. The
732 thick line represents the predicted articulation where values of the three predictors are
733 simulated to represent the actual fossil record as they change through time. Size
734 changes from 1.54 to 0.83 (\log_{10} mm), morphology (proportion of beetles) changes
735 from 0.0 to 0.26, and environment (proportion of deep lakes) changes from 0.0 to
736 0.82. (one column)

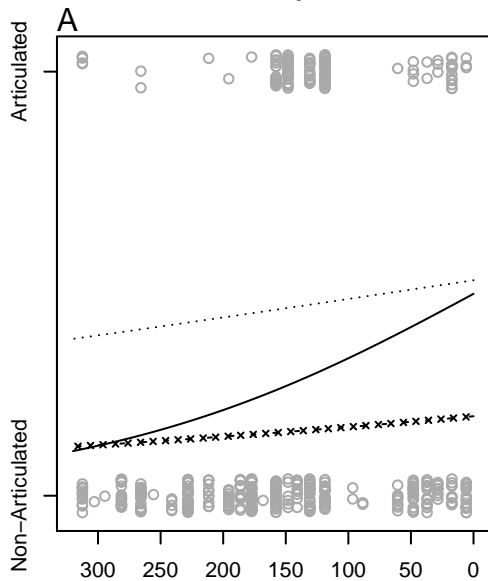
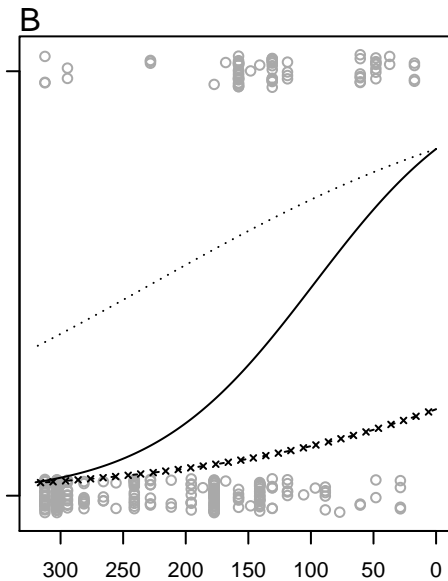
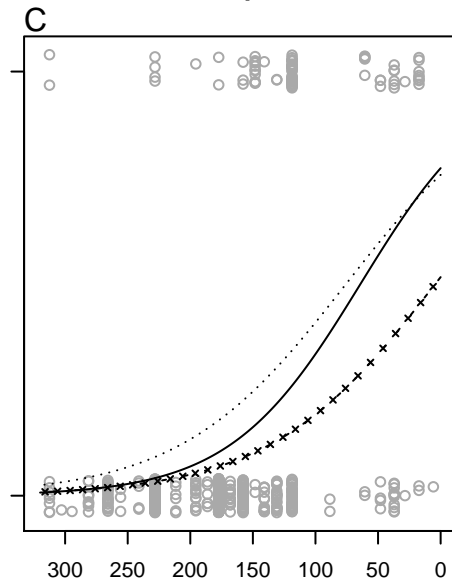
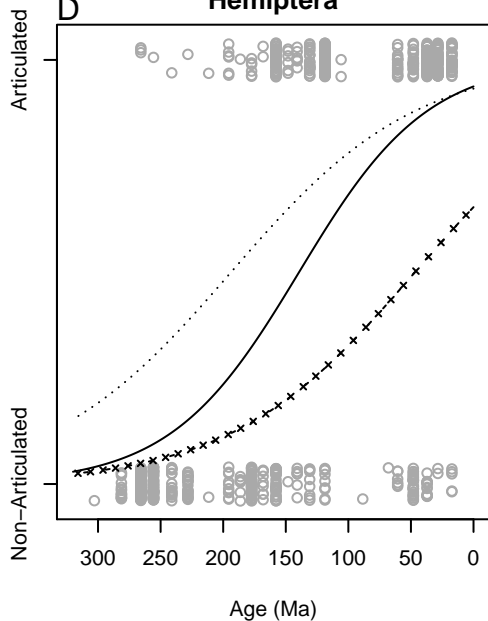
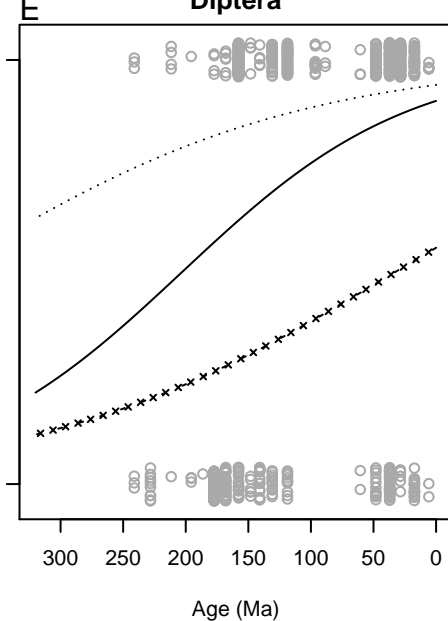
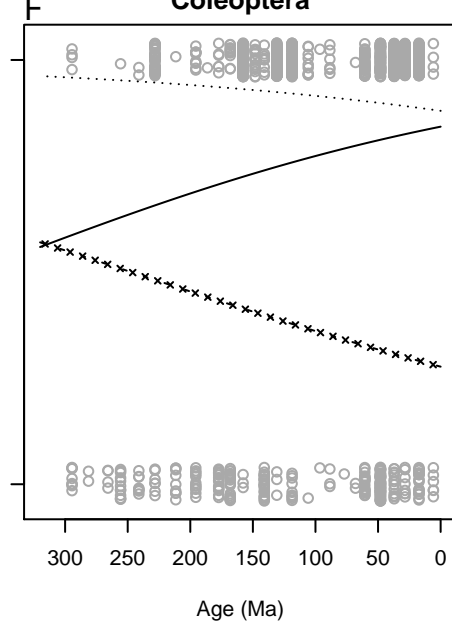
737 **Fig. 7.** Comparison of actual and modeled insect articulation for bins with at least 100
738 occurrences. Actual articulation proportions (open circles) are calculated from
739 holotype specimens in each time bin. Modeled articulation proportions (filled circles)
740 are predicted from the logistic regression model using the proportion of deep-lake
741 occurrences, proportion of Coleoptera, and average size in each time bin. (one
742 column)

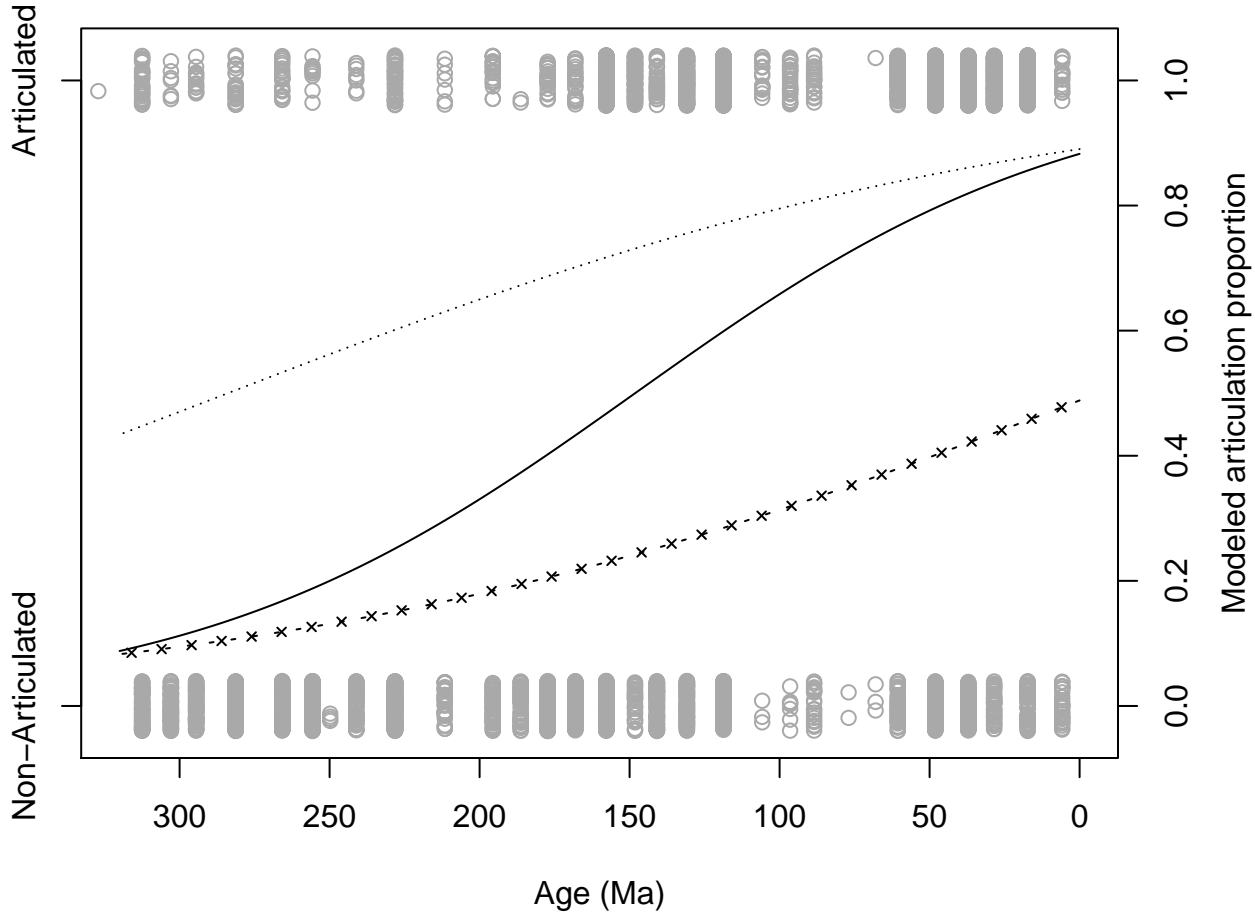
743 **Fig. 8.** Phanerozoic occurrences of Coleoptera (grey circles) for all holotypes or only
744 those described in the literature after 1950 with logistic regression models fit relating
745 articulation as a function of age in all environments (black line), fit to only deep lake
746 environments (dotted line) and fit to only non-deep lake environments (hashed line).
747 (one column)

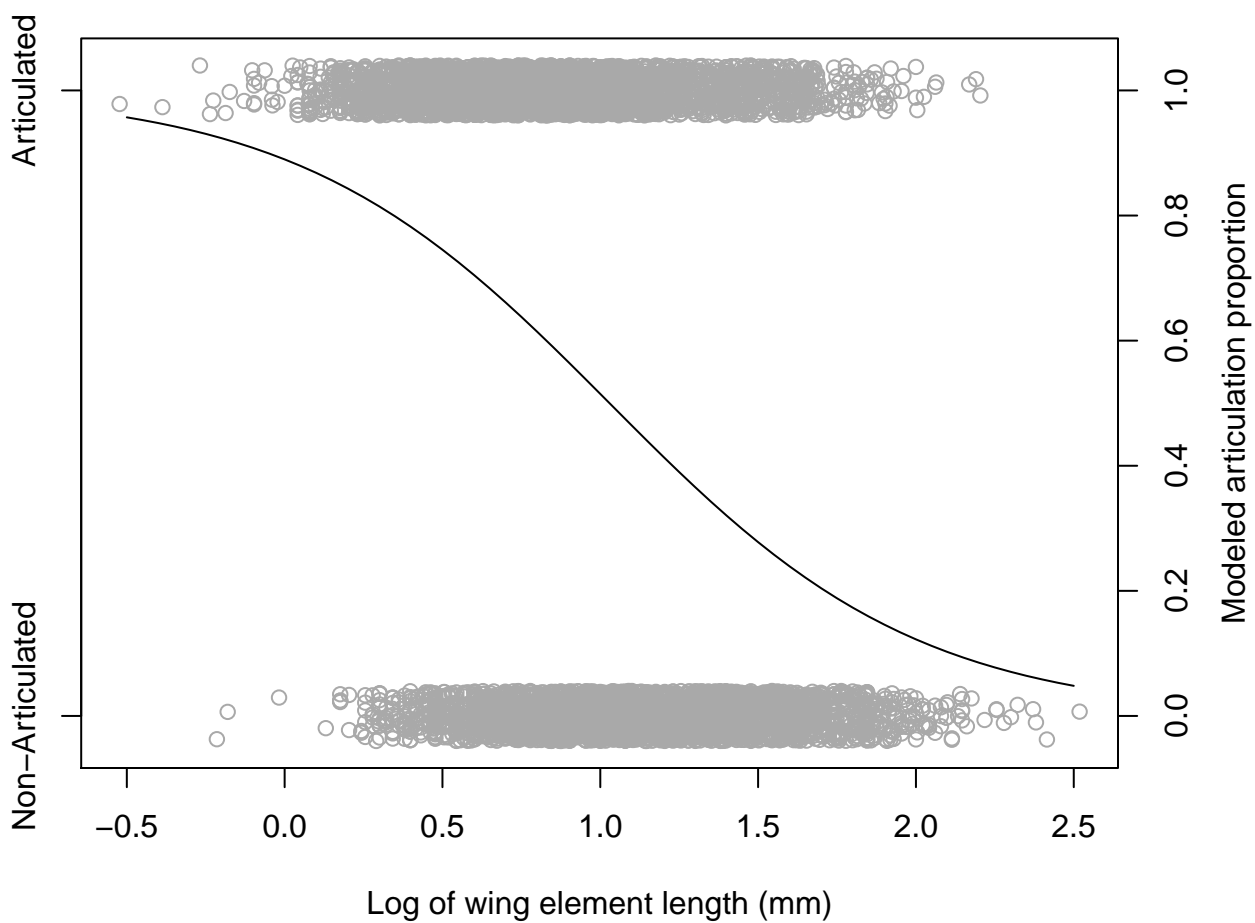
748 **Fig. 9.** Articulation of insect (solid line) and only Coleoptera (dashed line) holotypes
749 as a function of publication year. Beetles described in older papers are much more
750 likely to be based on isolated elytron holotypes, but there is no trend in holotype
751 articulation among insects as a whole. (one column)

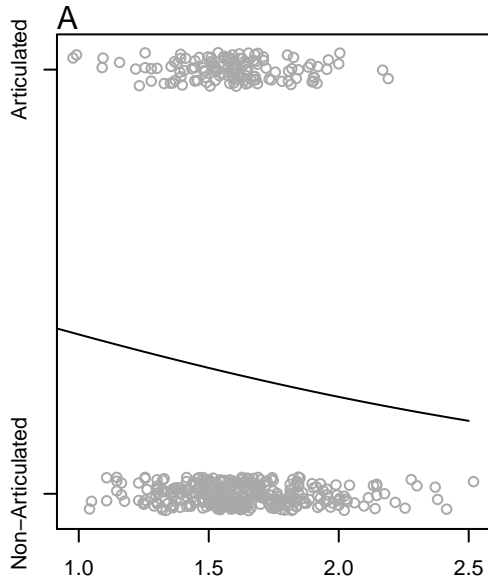
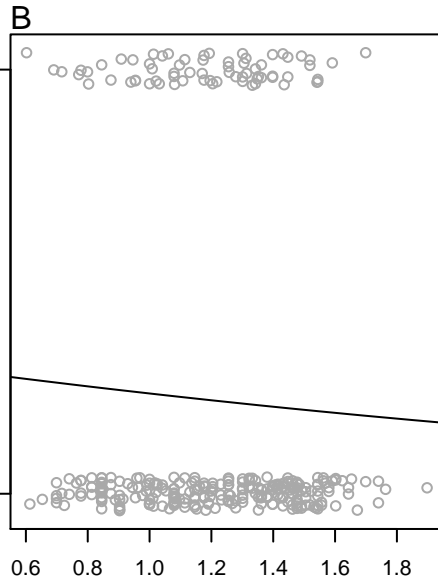
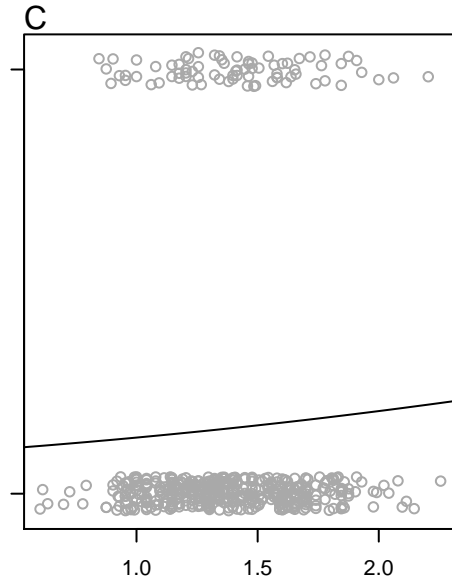
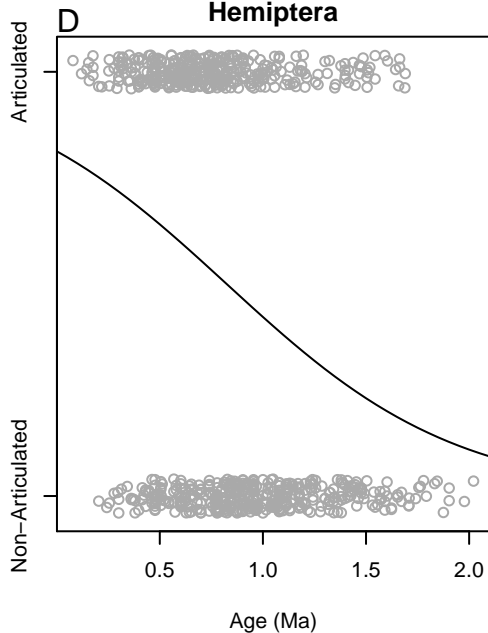
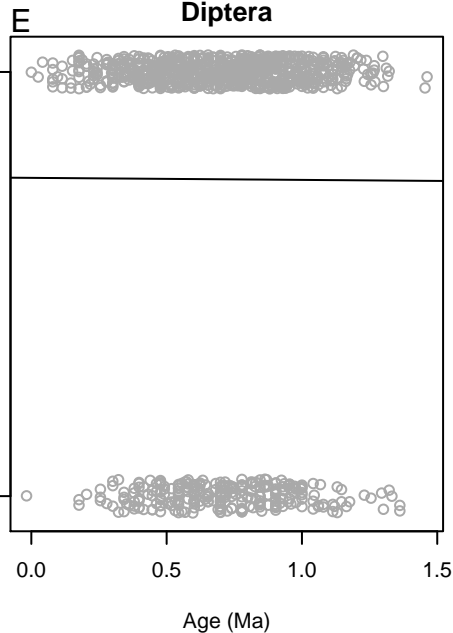
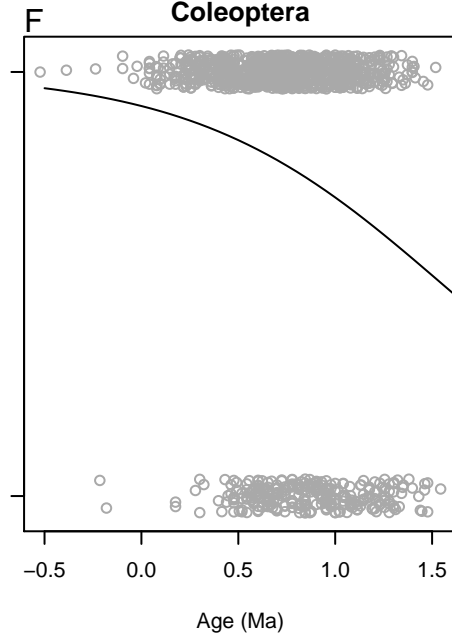
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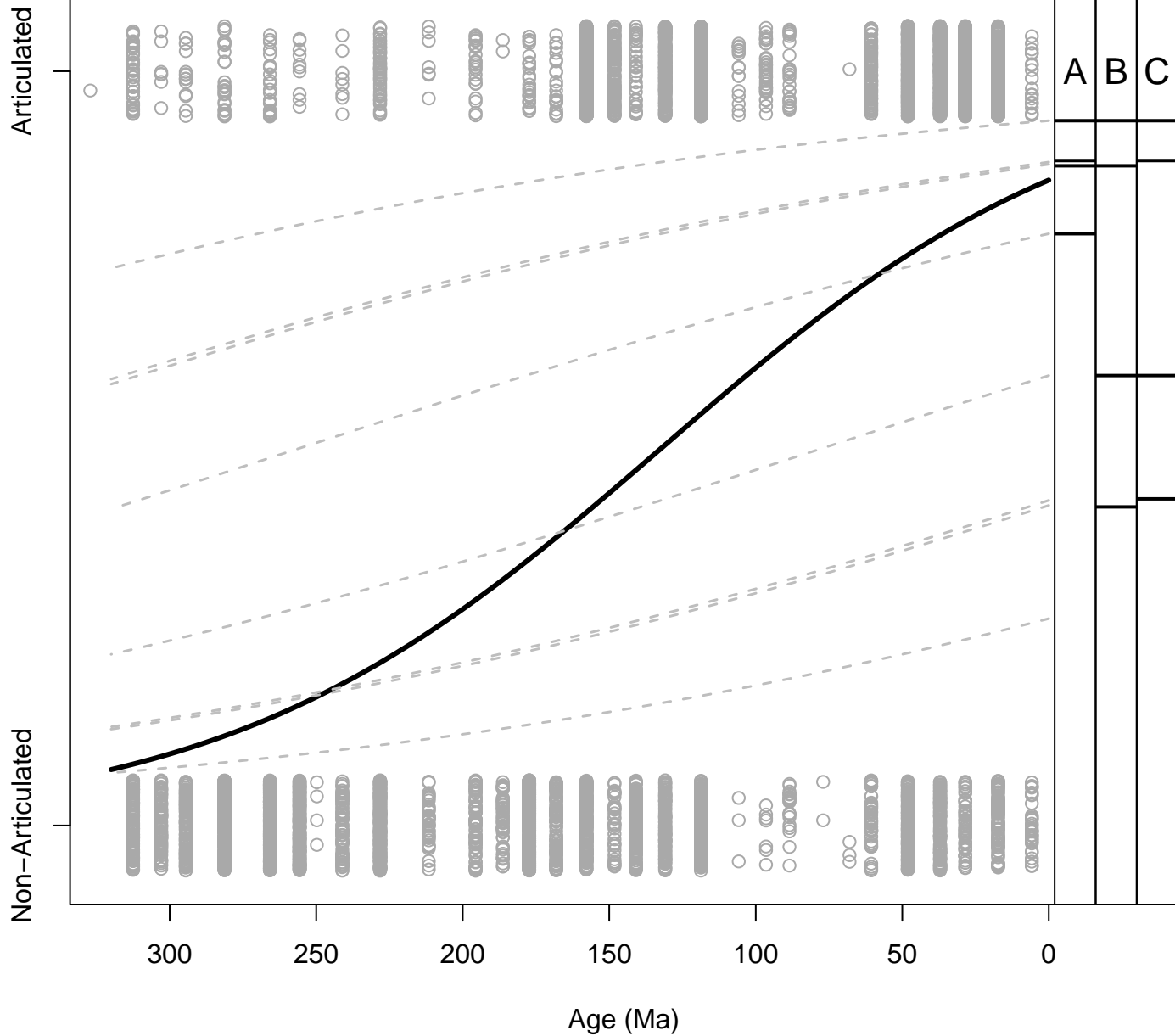


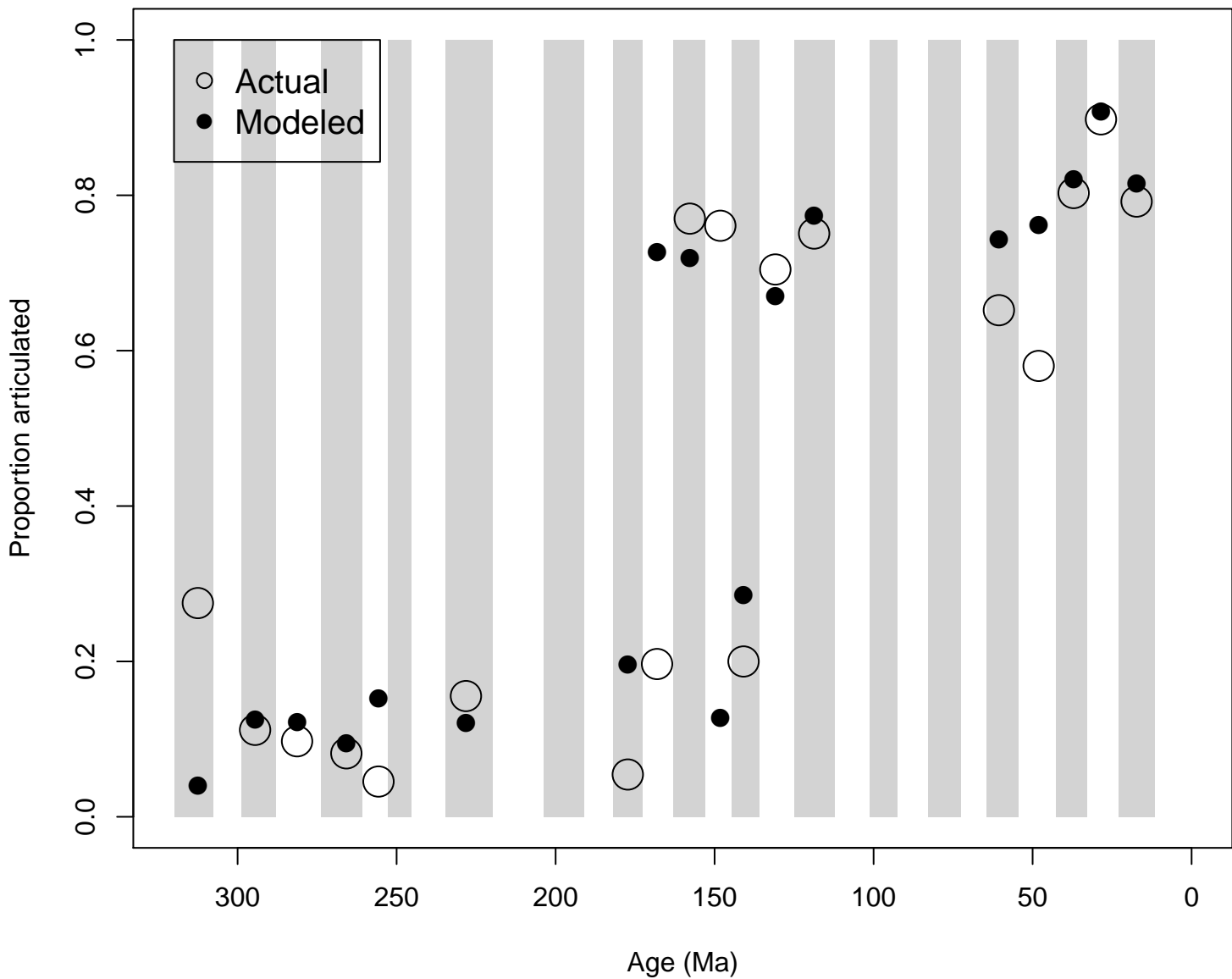
Odonoptera**Blattodea****Orthoptera****Hemiptera****Diptera****Coleoptera**



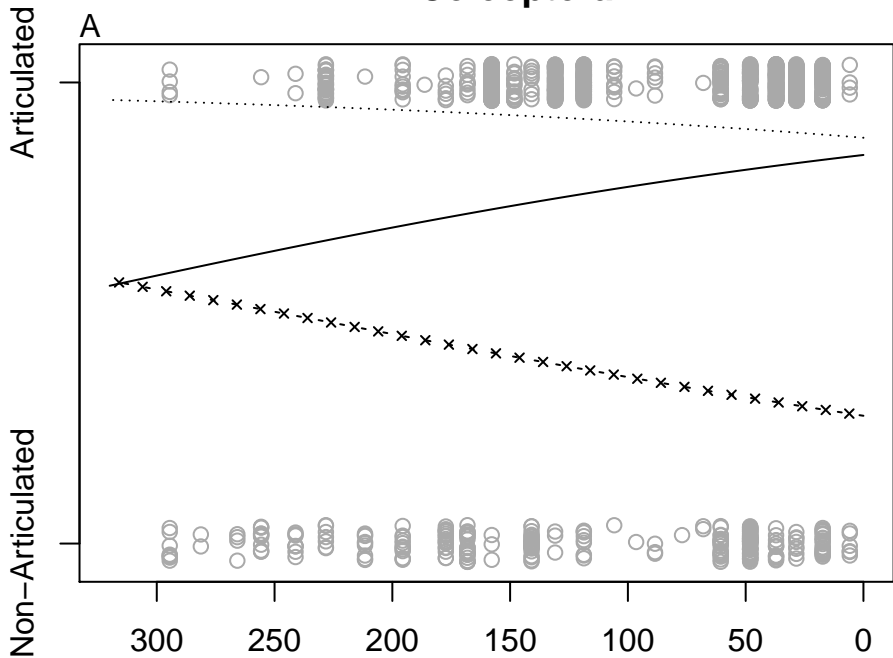


Odonatoptera**Blattodea****Orthoptera****Hemiptera****Diptera****Coleoptera**





All Coleoptera



Post-1950 Coleoptera

