Causes and consequences of extinction and survival in fossil marine invertebrates with a special focus on the Crinoidea (Phylum Echinodermata)

by

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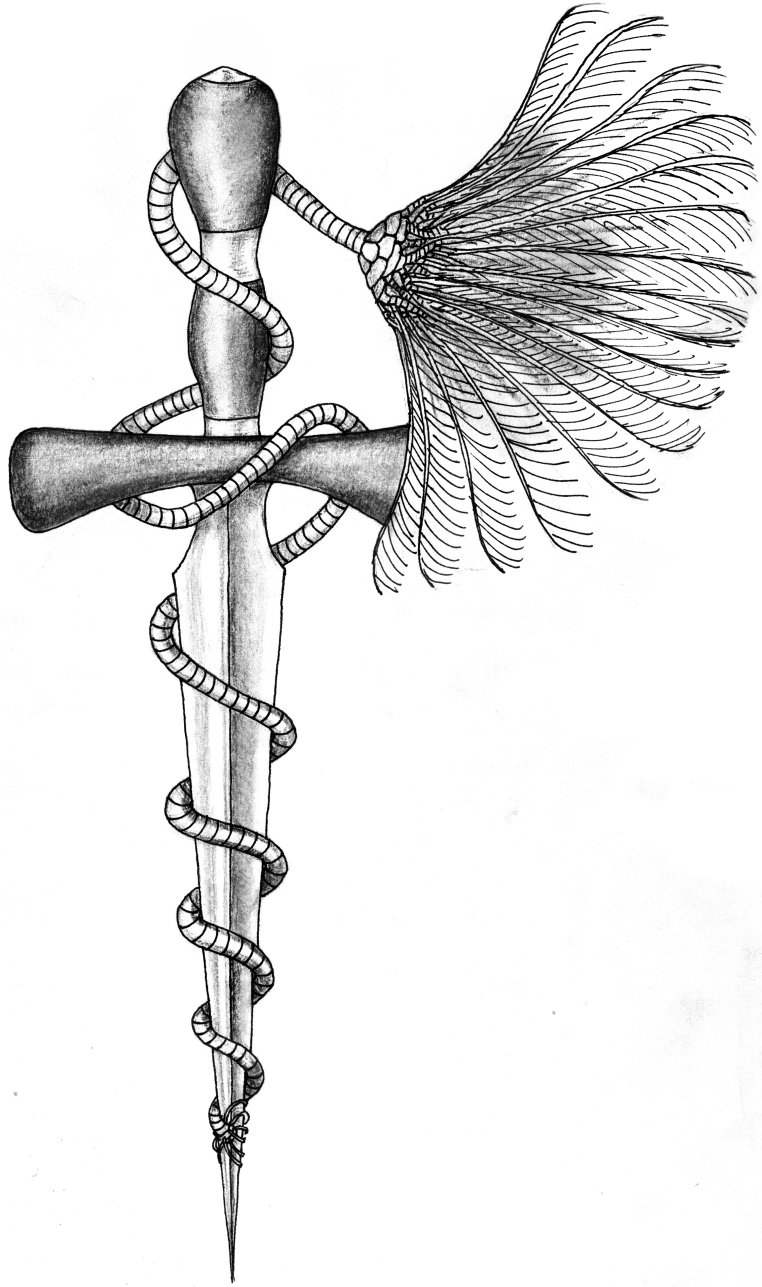
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Chapter IV would not have been possible without many colleagues, including

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ABSTRACT

Causes and consequences of extinction and survival in fossil marine invertebrates
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In the geologic past, certain traits increased the chance of survival of some marine invertebrate taxa, which means that extinction did not occur randomly. However, it has been claimed that these traits buffer less against extinction at mass extinction events. Herein, a method for detecting selective extinction shows that during both background and mass extinction times, extinction of marine invertebrate genera was non-random for most of the Phanerozoic Eon. The two best-known mass extinctions, the Cretaceous-Paleogene (K-Pg), and the Permian-Triassic (P-Tr), appear to have been highly selective. It is shown that extinction will appear random at the genus level with respect to the number of species in a genus when extinction is highly selective at the species level.

A phylogenetic analysis of 51 crinoid species (Phylum Echinodermata: Class Crinoidea) addresses major, unresolved questions in crinoid evolutionary history: how many lineages survived the P-Tr extinction event? Did extinction selectivity affect crinoids during this event? The phylogeny supports a single surviving lineage of crinoids at the P-Tr extinction event. However, crinoids were likely reduced in diver-

sity before the P-Tr boundary, which brings into question whether they experienced extinction selectivity at the P-Tr extinction event.

Lastly, crinoid biodiversity since the P-Tr extinction event is investigated. Modern crinoids are dominated by the stalkless comatulids (Order Comatulida), notable for their ability to crawl and swim. It has been claimed that these abilities are anti-predatory adaptations that aided comatulid survival in the face of increased predation pressure during the Mesozoic marine revolution (MMR). Recently, relatively rapid crawling has been shown in stalked crinoids, which means that only swimming is unique to comatulids. A biomechanical model and functional morphology shows that stalk loss and other traits are required for swimming. The swimming capability of extinct comatulids is considered, revealing that the earliest comatulids may have been swimmers. Swimming may have evolved in response to benthic predation pressure. Comatulid species that can only crawl likely represent lineages that lost the ability to swim. The possibility that the MMR and the number of reef sites may have affected the diversity of crawling and swimming comatulids is considered.

CHAPTER I

Introduction

One of the great achievements of the late 20th century "paleobiological revolution" was the shift in paleontology from a mostly descriptive science to a field that actively uses rigorous hypothesis testing, in other words, the formation of a discipline in which the driving focus is to adhere to the laws of nature, known as a "nomothetic" discipline (Ruse, 2009). Thirty years ago paleobiologists were encouraged to answer questions without relying on inductivist philosophy, and limited approaches that imitate those used in biology, instead of using novel, paleontological methods (Schopf, 1979; Gould and Calloway, 1980). This dissertation follows this tradition by testing hypotheses surrounding supposed causes of extinction and survival in the fossil record of marine invertebrates, through new methods of analysis of fossil databases, and observation of living and fossil marine invertebrates.

This work unites five manuscripts with overlapping themes that all seek to answer a simple question with not so simple answers: why have some species failed while others have succeeded? To answer this question multiple methods and case studies were examined. Novel approaches for the detection of extinction selectivity using taxonomic databases were developed. Extinction selectivity is a description of what went extinct, that is, were some species or or less likely to go extinction, as opposed to extinction intensity, which is a measure only of the size of an extinction

event. The methods for detecting exintction selectivity were applied to marine invertebrate data from the Paleobiology Database (PaleoDB; http://www.paleodb.org), an international collaborative effort by paleontologists to compile global occurrence information for fossil organisms.

Additionally, major unresolved questions within one specific group of marine invertebrates with an extensive fossil record, crinoids (Class Crinoidea, Phylum Echinodermata), were considered. A comprehensive phylogeny of crinoids across the Permian-Triassic mass extinction (P-Tr) was produced, and the potential role of extinction selectivity in the face of this largest of all extinction events (Bambach et al., 2004; Alroy, 2008) was evaluated. An investigation was also undertaken to determine if the modern species composition of crinoids is best explained by the traditional explanation of predator-prey driven interactions during the late Mesozoic and the ability of the species-rich stalkless crinoids to swim and/or crawl. Alternatively, the possibility that increases in diversity may have been associated with of reef sites is considered.

I begin by stepping back from the question of why species have failed or succeeded, and ask if there is even a significant pattern to explain. The idea, using a null hypothesis of random chance, is not new to paleontology (Raup, 1978; Schopf, 1979). This principle is applied in a new way in Chapter II by noting that under random extinction, the probability of a supraspecific taxon going extinct is a function only of its number of component lower taxa. By studying deviations from this random expectation, extinction selectivity can be revealed.

Databases like the PaleoDB are heavily used to study the history of diversity (e.g., Alroy et al., 2008; Alroy, 2010a), and have helped spur a growth in analytical methods for detecting extinction intensity through time (e.g., Alroy, 2008, 2010b). Yet the development of analytical methods for detecting extinction intensity has not been matched by methods for detecting extinction selectivity of taxa. Most of the latter approaches rely on correlating extinction intensity of taxa with traits, without

considering data limitations as thoroughly as has been done for extinction intensity. For example, the ability to detect selectivity using this approach depends on the preservation of traits that led to selectivity, and that those traits will be observable in fossil samples. Additionally, while selectivity on a large number of traits will cause greater extinction selectivity of taxa, it may be harder to detect than if one or a few, easily measured, traits caused extinction selectivity. Thus, testing for correlations of traits with extinction probability does not allow paleontologists to say whether, for example, background extinctions are generally more or less selective than mass extinctions.

By applying the new method of detecting exinction selectivity to data from the PaleoDB, Chapter II shows that extinctions in the Phanerozoic marine invertebrate fossil record have rarely been random, disproving the "field of bullets" hypothesis, the idea that at some times extinction may have been entirely random (Raup, 1991). Chapter III expands on the method by using the principle of statistical likelihood (Edwards, 1992) to detect the strength of support for selective extinction at a given extinction event. The likelihood approach allows a test of whether the selectivity was due to regional extinction rate differences (regional selectivity), or if the extinction selectivity is entirely attributable to other selective causes (possibly ecological selectivity). This new method, applied in Chapter III to data on the P-Tr and the Cretaceous-Paleogene (K-Pg) extinction events from the PaleoDB, demonstrates that the strong extinction selectivity at these events was not due to regional extinction rate differences; this may mean that ecological selectivity was particulary strong at those times. Combined with the observations in Chapter II, it appears that extinctions have been selective during both background and mass extinction times.

Chapters IV-VI focus on testing traditional explanations for diversity patterns in fossil and modern crinoids. Chapter IV tackles one of the major, unresolved questions in crinoid evolutionary history: how many and which lineages survived the P-Tr

extinction event and why? I show using phylogenetic analysis that a single lineage survived the P-Tr extinction event, a lineage which would then give rise to all subsequent crinoid diversity, including the approximately 600 extant species of crinoids.

Chapter V presents new biometric data on species from the Smithsonian Institution National Museum of Natural History Invertebrate Zoology collections, which contains the largest collection of extant crinoids in the world. The data were collected to constrain a biomechanical model that would allow description of morphology that would allow a crinoid to swim. The elegant swimming of comatulid crinoids is sometimes treated as the pinnacle of crinoid evolution, as crinoids are seen as a mostly sessile group, once uniquely classified among living echinoderms in the Subphylum Pelmatozoa ("pelma" = stalk, "zoa" = animals, and thus stalked and attached animals), in contrast to the remaining echinoderms which are traditionally assigned to Eleutherozoa ("eleuthero" = free, thus free-living animals). In order to determine the traits that typically characterize swimming crinoids, Chapter V uses a modern biomechanical paradigm (Plotnick and Baumiller, 2000), and tests conditions under which a crinoid could swim. Further, contrasts were drawn between swimming and non-swimming comatulids, adding to the observations of the functional morphology that could characterize extinct swimming crinoids.

A first look at the fossil record of putative swimming crinoids was made possible through insights provided by biomechanical modelling and new observations of functional morphology, a view presented in Chapter VI. I show that swimming likely appeared early in comatulid history, possibly in the first comatulid, and during the first phase of innovation of the Mesozoic marine revolution (Vermeij, 2008). Meanwhile, clades of obligate crawling comatulids may have diversified in concert with the expansion of reef sites (Kiessling, 2009), and these crawling taxa do not represent an intermediate stage between stalked crinoids and swimming comatulids. The ability to swim may have been lost in some diverse, comatulid clades, which implies that in

some environments the ability to crawl may have been sufficient or better for survival, and thus that the ability to swim was not always crucial for comatulid success.

CHAPTER II

Evidence for extinction selectivity throughout the fossil marine invertebrate fossil record

2.1   Abstract

The fossil record has been used to show that in some geologic intervals certain traits of taxa may increase their survivability, and therefore that the risk of extinction is not randomly distributed among taxa. It has also been suggested that traits which buffer against extinction in background times do not confer the same resistance during mass extinction events. An open question is whether at any time in geologic history extinction probabilities were randomly distributed among taxa. Here we employ a method for detecting random extinction to demonstrate that during both background and mass extinction times extinction of marine invertebrate genera has been non-random with respect to species richness categories of genera. A possible cause for this non-random extinction is selective clustering of extinctions in genera consisting of species which possess extinction-biasing traits. Other potential causes considered here include geographic selectivity, increased extinction susceptibility for

species in species-rich genera, or biases related to taxonomic practice and/or sampling heterogeneity. An important theoretical result is that extinction selectivity at the species level does not smoothly extrapolate upward to genera; the appearance of random genus extinction with respect to species richness of genera results when extinction has been highly selective at the species level.

2.2 Introduction

In recent decades increased attention has been paid to extinction in the fossil record. This research on extinction has been inspired by numerous factors including the availability of global, synoptic fossil databases (e.g., Sepkoski's genus compendium [Sepkoski, 2002]; the Paleobiology Database [Alroy et al., 2001]). The publication of the Alvarez et al. (1980) hypothesis of an impact-induced, catastrophic cause of extinction at the K-Pg boundary, and the widespread belief that we are in a "sixth mass extinction" (e.g., Thomas et al., 2004), have increased the attention focused on mass extinction events. While there has been a dramatic increase in research output associated with the "Big Five" mass extinctions (Twitchett, 2006), the community has debated whether mass extinctions form a distinct mode separate from "background" extinction (Bambach et al., 2004), or if they form part of a continuous distribution distinguished only by an arbitrary cut-off (Raup, 1994; "continuity of magnitude" in Wang, 2003). The general acceptance that at certain intervals of time mass extinctions occur, suggested by the weight of research output on these intervals, prompts the question as to whether the rules governing extinction probability vary depending on extinction intensity.

Extinction selectivity, "non-random or selective survival" (Kitchell et al., 1986, p. 504), and hence non-random and selective extinction, has been the focus of considerable recent research with increased recognition that many of the traits which promote survival during background extinction times do not confer survivability across mass

extinction events (Jablonski, 2005; Payne and Finnegan, 2007). The scenario in which extinction probability during mass extinction events is non-random but is not predictable from those traits thought to promote survivorship during background times was dubbed "wanton extinction" by Raup (1991). He contrasted this with the model of selectivity that operated during normal, background extinction times, which he called "fair game," and which would represent Darwinian extinction leading to survival of the fittest. Raup further contrasted the selective extinction models of "wanton extinction" and "fair game" scenarios from a third model, the "field of bullets," which is a hypothesis that at certain times traits of species do not promote survivability, and that the disappearance of lineages can be attributed to stochastic fluctuations. In this work we test for random extinction (no selectivity, the "field of bullets" model) versus non-random extinction (with selectivity, be it "wanton extinction" or "fair game" scenarios). Eble (1999) has presented a discussion of the contrast between evolutionary and statistical notions of chance, only the latter of which is addressed here.

Few evolutionary biologists, be they focused on paleontology or ecology, would a priori assume that extinction is random, but three decades ago we were asked to consider random extinction as a null model to be rejected (Raup, 1978; Schopf, 1979). This was explicitly in a macroevolutionary context which attempted to avoid the deterministic assumption that common traits had doomed species in certain higher taxa to extinction (e.g., blastoids), while allowing others (e.g., crinoids) to survive. The notion of stochastically equal probability of extinction across taxa was codified in some work (e.g., the "MBL program" [Gould et al., 1977]; the reverse rarefaction method [Raup, 1979; McKinney, 1995]), partly as a necessarily simplifying first step. A large body of research accumulated since that time demonstrating that extinctions among species, genera, or clades have not been random in geologic history (Jablonski, 2005 and references therein; Smith and Roy, 2006; Payne and Finnegan, 2007;

Leighton and Schneider, 2008; Peters, 2008). An open question is whether at any time in the geologic past extinction has actually been statistically random. That is, has the history of life ever experienced a "field of bullets", be it during background or mass extinctions?

A test of the random extinction hypothesis was devised by McKinney (1995) in the context of Raup's reverse rarefaction method which "is based on the assumption that species are killed at random" (Raup, 1991, p. 72). The reverse rarefaction method involved constructing rarefaction curves for living echinoderm taxa and then interpolating to estimate the proportion of species that would have to go extinct to produce the observed values of higher taxon extinction seen in the fossil records of well-skeletonized marine animals if extinction had been random (Raup, 1979). McKinney analyzed a fossil echinoid dataset (Kier and Lawson, 1978) and determined that the extinction of genera was not random with respect to species richness categories, with the likely cause being nesting of traits promoting extinction within some genera, i.e., selectivity (1995).

Here we expand on McKinney's method to demonstrate that the same evidence for selectivity is seen in the marine invertebrate dataset of the Paleobiology Database (PaleoDB), and that extinctions appear to be non-random through the Phanerozoic during background and mass extinction times. We discuss possible explanations for these observations including non-random extinction caused by clustering species extinctions in some genera, geographic selectivity via regional extinction rate heterogeneity, a mechanism of selectivity in which extinction probability of member species is correlated with species richness of genera, and biases introduced by taxonomic procedure. We find that clustering species extinctions within genera can explain the pattern that we report here, supporting the growing body of literature that demonstrates extinction selectivity in the geologic past, and the non-random distribution of extinction risk for extant species in phylogenies (e.g., Purvis et al., 2000) and
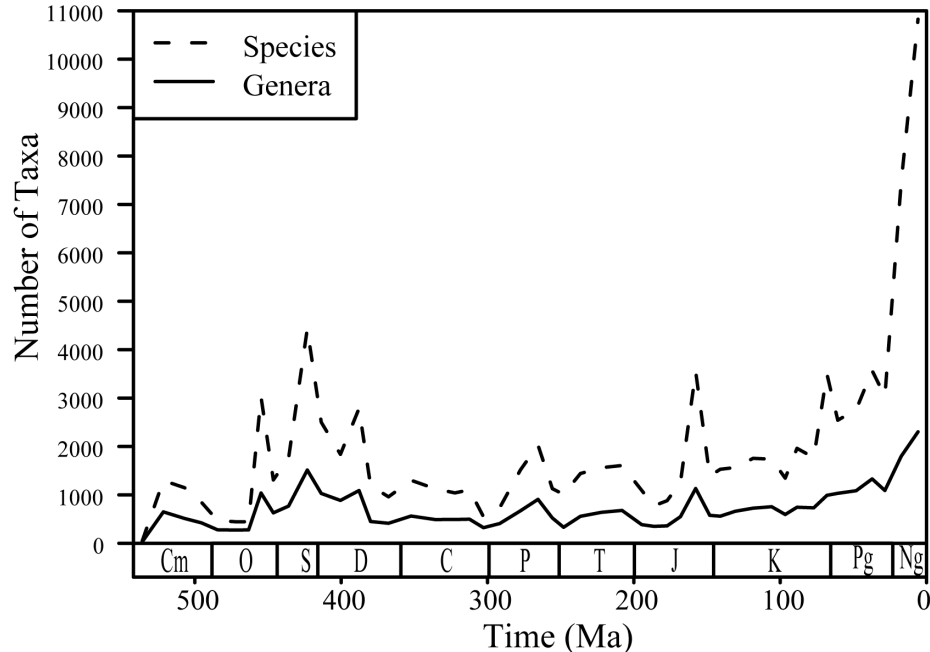
Figure 2.1: Sampled-in-bin genus and species diversity curves with species-level taxonomic designations from the PaleoDB in ~11-Myr intervals of the Phanerozoic. Cm, Cambrian; O, Ordovician; D, Devonian; S, Silurian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene. Timescale from Gradstein and Ogg (2004).

taxonomies (e.g., Lockwood et al., 2002). We find little evidence for stochastically random extinction as the dominant pattern in the Phanerozoic. And we recognize that highly selective, non-random extinction of species results in the *appearance* of random genus extinction with respect to species richness.

2.3 Data and Methods

The results reported here are based on fossil marine invertebrate occurrences from the PaleoDB (Alroy et al., 2001, http://www.paleodb.org/), downloaded on January 4th, 2009. Occurrences not assigned to the approximately 11-Myr bins of the PaleoDB were excluded when analyzed. The dataset was reduced to those unique occurrences that were identified to species-level; cf., sp., and other modifiers were excluded, as were abbreviated genera (e.g., "A."). These culling procedures did not substantially

alter the diversity data when compared to the sampled-in-bin genus diversity of the PaleoDB (for ~11-Myr bins: Spearman's $\rho = 0.88$, $p < 10^{-16}$), though, as expected, the volatility in species-level diversity is greater than that seen in genera (Fig. 2.1). The first Cambrian time bin ("Cambrian 1") was excluded due to very small sample size. Extinction rates were calculated as the percent of genera which went extinct in a time bin, which normalizes for the number of genera present in that bin (Raup and Boyajian, 1988). Comparable results were produced for alternative binning protocols (stages, epochs, periods); only ~11-Myr bin data are reported here (94,886 unique occurrences). Normalizing for absolute time by combining shorter bins, as has been advocated for stages (Raup and Boyajian, 1988), is accomplished by employing the PaleoDB ~11-Myr bins. All analyses were written and run in R version 2.3.1 (R Development Core Team, 2006).

If we assume that species extinctions are equally probable regardless of genus membership, it is possible to use simple sampling probability and the observed extinction rate of monospecific genera to predict the extinction rates that should be observed in genera with more than one species (McKinney, 1995). We can then compare the predicted extinction rates for the genera with more than one species to their observed extinction rates. The approach is straightforward: given an extinction rate for genera with one species in a time bin, q_1, the predicted extinction rate for genera with two species, q_2, is $(q_1)^2$; for genera with three species, the predicted extinction rate, q_3, is $(q_1)^3$; etc. The predicted extinction rate of the genera with more than one species is equal to the extinction rate of the genera with one species raised to the power of the number of species in those genera (their "species richness category"). An example of the method of calculation on a hypothetical dataset is presented in Figure. 2.2. Eighteen species belonging to ten genera were assigned to species richness categories, with species richness categories determined by the number of species present in the time bin of interest (in the case of the example, Bin 1). Extinction rates for each

species richness category of genera were observed, and predicted extinction rates assuming random species extinction were determined from the observed extinction rate of genera with one species. No lineages were added based on phylogenetic information and no ranges were extended due to genealogy or sampling correction (Foote, 1996).

An extinction model demonstrating the relationship of observed to predicted extinction rates is shown for two and five-species genera in Figure 2.3. The solid line of slope one represents a scenario in which extinction of species is random, and thus there is a one-to-one correspondence between the observations and the extinction predictions derived via the method described above. For example, a random species extinction of 50% should correspond to a 25% extinction probability for genera with two species ($0.5^2 = 0.25$), and approximately 3% for genera consisting of five species ($0.5^5 = 0.03125$). The data points will scatter around the line of slope one if species extinctions occur randomly across all genera.

The random extinction scenario described above can be contrasted to the predicted extinction rates of genera when species extinctions are clustered among genera. The dashed (two species) and dotted (five species) lines represent scenarios where there is maximum selectivity, occurring when all species extinctions are clustered among the fewest number of genera resulting in the highest possible genus extinction rate. Under this scenario the extinction rate of genera is the same regardless of the number of species contained within a genus, e.g., 50% of species go extinct, resulting in 50% genus extinction for genera with one species and also 50% extinction for genera with more than one species. Perhaps counterintuitively, this is also the expected result of random generic extinction, i.e., extinction of genera independent of their species richness. In other words, random extinction at the generic level with regard to species richness can be caused by intense selectivity with maximum clustering of species extinctions in genera.

The areas below the respective patterned regions and the line of slope one cor-

Species Richness Category of Genus	Observed Extinction Rate of Genera	Predicted Extinction Rate of Genera
One species (includes genera *B., C., D., E., F.*)	q_1 = 3 out of 5 (60.0%)	q_1 = 60.0%
Two species (includes genera *G., H., I.*)	1 out of 3 (33.0%)	$q_2 = (q_1)^2 = (3/5)^2 = 36.0\%$
Three species (includes genera *J., L.*)	1 out of 2 (50.0%)	$q_3 = (q_1)^3 = (3/5)^3 = 21.6\%$
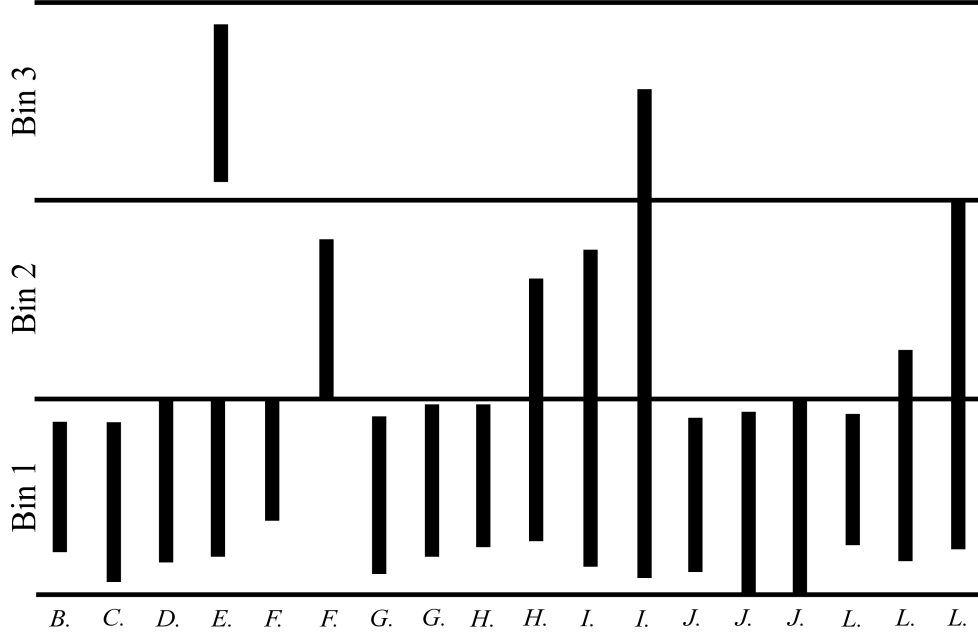
Figure 2.2: The method used here for detecting nonrandom extinction is applied to Bin 1 in this hypothetical dataset to demonstrate particulars of the methodology. Letters correspond to unique species of genera, and vertical lines represent the observed stratigraphic ranges of those taxa with no corrections to ranges (e.g., range extensions). In this case, genera are assigned to species richness categories and extinction rates are calculated as the number of genera that went extinct out of the number of genera present for Bin 1. The species richness category is based on the number of constituent species in the genus in the time bin of interest. Genera B., C., D., E., and F. are in the one-species richness category for Bin 1. Genus F. contains a species in Bin 2 that is not present in Bin 1, and therefore does not affect the species richness category assignment for genus F. in Bin 1. The presence of this species in Bin 2 does diminish the observed extinction rate for one-species genera. Genus E. is not counted as extinct despite absence in Bin 2 because it reappears in Bin 3 (the genus is presumed to range through this interval of non-preservation/non-recovery). For the one-species richness category, three out of five genera (B., C., and D.) went extinct ($q_1 = 60.0\%$). Predicted extinction rates are calculated from the extinction rate of genera with one species such that the predicted extinction rate of two-species genera is $q_2 = (60.0\%)^2 = 36.0\%$, and for three-species genera is $q_3 = (60.0\%)^3 = 21.6\%$.
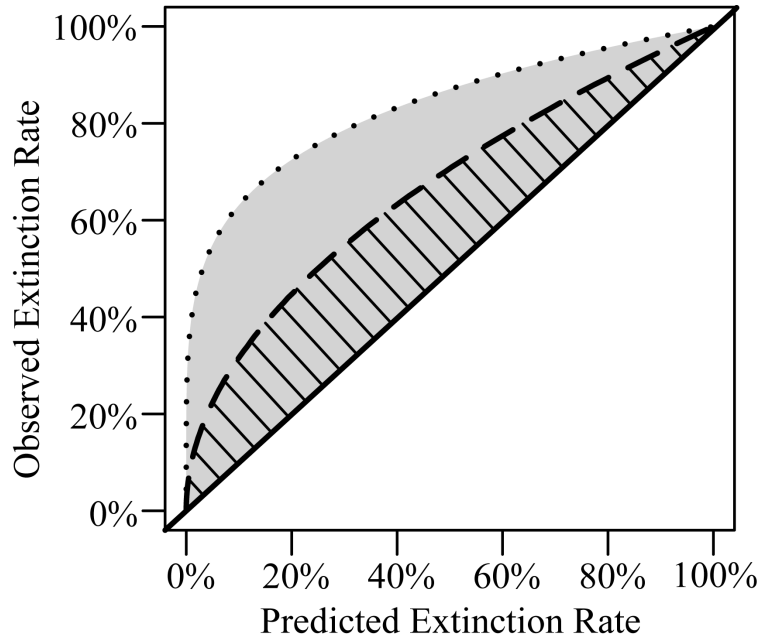
Figure 2.3: Extinction simulation of the observed extinction rate of genera with multiple species plotted against the predicted extinction rate derived from monospecific genera when extinction is random (solid line). The broken lines represent the observed extinction rates in the multi-species richness categories when extinction occurs in a maximally selective scenario (two-species genera, dashed; five-species genera, dotted).

respond to a scenario when fewer genera go extinct than would be expected under random species extinction. This would occur if species one-species genera were more liable to extinction than species in species rich genera. Based on the data and arguments for selectivity presented here there is little evidence for this scenario.

2.4 Results and Discussion

In order to see whether extinction selectivity is evident in the fossil record the predicted extinction rates for genera with different numbers of species (species richness categories) under a random species extinction scenario were plotted against the observed extinction rates of those genera for the PaleoDB marine invertebrate dataset. Figure 2.4 is a plot of observed versus predicted extinction rates of genera grouped into ~11-Myr bins for the Phanerozoic; data are plotted for four different species rich-

ness categories. Identical to the extinction simulation in Figure 2.3, in Figure 2.4, the line of slope one (solid) represents random species extinction. Under a random species extinction scenario points would fall on the line of slope one, whereas under a selective extinction scenario the points would fall above the line. It is clear in Figure 2.4 that virtually all of the points fall above the line.

The present analysis does not suggest that genera with one species have lower extinction rates than genera with more than one species. Rather, the opposite is true, species richness generally contributes to the survivability of genera (Table 2.1). However, genera with more than one species do not resist extinction to the degree that is expected if extinction had occurred randomly across species. These results corroborate those found by McKinney (1995, see Fig. 3) for a smaller, taxonomically and temporally restricted dataset. Given these two similar results, it is worth considering factors that could cause the observed patterns.

A possible explanation for this pattern is that species extinctions throughout the Phanerozoic have not been random with respect to genus membership, which could occur if shared ecological traits of species caused extinctions to be clustered within genera (McKinney, 1995). Under a random species extinction scenario we would expect the observed versus predicted extinction rates of the genera to plot around the line of slope one in Figure 4. By clustering extinctions among species, the observed values of extinction for genera will be higher than predicted, producing a pattern like that seen in Figure 2.4.

As in Figure 2.3, the regions of selectivity are plotted in Figure 2.4 (shaded areas under the dashed, curved lines and above the line of slope one). The dashed lines represent the maximum selectivity, i.e., clustering of species extinctions in the fewest possible genera. It is clear that the region of selectivity in the graphic method employed here is larger for genera in higher species richness categories, i.e., the shaded region of selectivity for the three-species genera is larger than the shaded region for
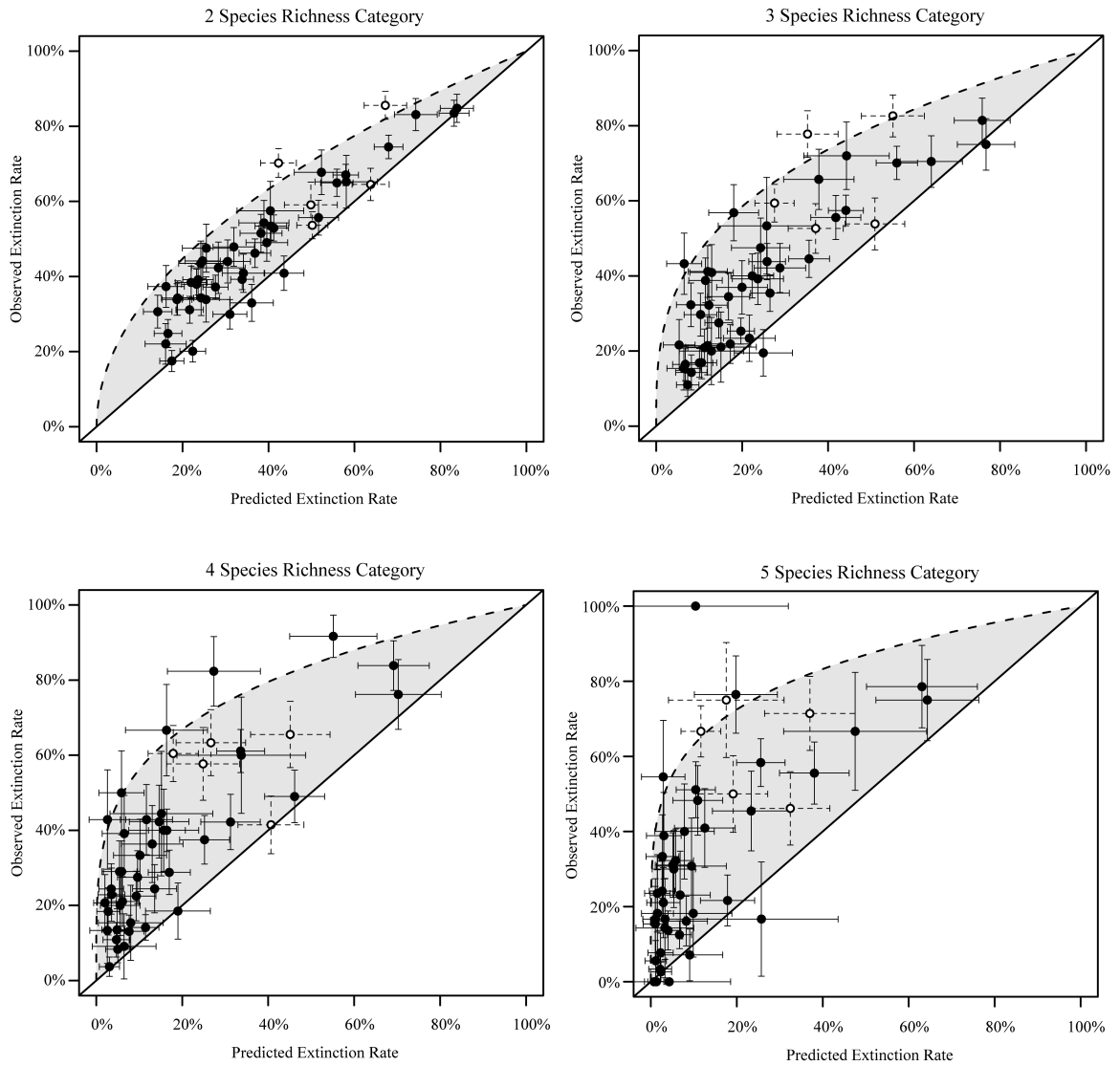
Figure 2.4: Observed versus predicted extinction rates for genera in ~11-Myr bins of the PaleoDB with predicted rates calculated as in the text. Error bars are binomial estimates of one standard error calculated as $((p*q*n)^{0.5})/n$ (cf. McKinney, 1995: Fig. 3), where q is the predicted proportion of genera that go extinct, p is the predicted proportion of genera that survive, and n is the number of genera in that time bin for that species richness category. Figures are plotted separately by species richness category for clarity. Note that nearly all points fall above the line of slope one, indicating nonrandom extinction. Time bins representing the "Big Five" mass extinctions are plotted with open symbols and dashed error bars.

two-species genera. In addition to falling above the line of slope one, we see that most of the points in Figure 2.4 fall within the regions of selectivity. This is the expected outcome when extinctions of genera result from a combination of stochastically random species extinction and selective extinction of species clustered within some genera. Under a state of perfect knowledge (e.g., complete sampling of occurrences, extinctions, etc.), we would expect no points to fall above the region of selectivity, or below the dashed line of random extinction (if selectivity always existed). The 'fit' of the points to this predicted region of selectivity for each species richness category appears surprisingly good given incomplete knowledge.

Another way in which the patterns in Figure 2.4 might result is if extinction probabilities of species are biased by genus membership such that there is an increased likelihood of extinction of species in genera with many species compared to species in genera with fewer species. A possible cause of this is if an attribute that buffers against extinction (e.g., wide geographic range, great abundance of individuals, or other life-history traits) is correlated with membership in a genus with one or a few species. For example, this could occur if genera with many species alive at one time are composed of species with limited geographic ranges, whereas a genus with a single or few species would be less limited in geographic range, and thus more resistant to extinction.

If this correlated species richness effect exists it would not violate the method employed here for detecting selectivity, but it would negate an explanation based exclusively on clustered species extinctions in genera via selectivity. This effect would also run counter to the expectation of diminished extinction probability for genera in higher species richness categories. If the member species of genera in the higher species richness categories have greater extinction probabilities than member species in genera in lower species richness categories, it would reduce the greater survivability of the higher species richness category genera conferred by being composed of many

species. There would be a trade-off at the genus level: decreased extinction risk with the addition of species, but a diminishing added buffering against extinction for each additional species.

Table 2.1: Extinction rate of genera by species richness category compared with predicted extinction rate derived from the extinction rate of monospecific genera.

~11-Myr Bin	Extinction Rate in percent	Species Richness Category				
		One	Two	Three	Four	Five
Cambrian 2	Observed	91	83	81	84	79
	Predicted	91	83	76	69	63
Cambrian 3	Observed	92	85	75	76	75
	Predicted	92	84	77	70	64
Cambrian 4	Observed	86	83	70	92	67
	Predicted	86	74	64	55	48
Ordovician 1	Observed	76	65	72	60	17
	Predicted	76	58	44	34	26
Ordovician 2	Observed	64	58	53	67	100
	Predicted	64	40	26	16	10
Ordovician 3	Observed	53	42	21	15	0
	Predicted	53	28	15	8	4
Ordovician 4	Observed	71	54	45	38	22
	Predicted	71	50	36	25	18
Ordovician 5	Observed	72	56	53	63	50
	Predicted	72	52	37	27	19
Silurian 1	Observed	56	30	22	28	30
	Predicted	56	31	17	10	5
Silurian 2	Observed	76	67	57	61	58
	Predicted	76	58	44	34	26
Devonian 1	Observed	64	53	35	29	48
	Predicted	64	41	26	17	11
Devonian 2	Observed	61	46	40	24	16
	Predicted	61	37	22	14	8
Devonian 3	Observed	82	74	70	49	56
	Predicted	82	68	56	46	38
Devonian 4	Observed	71	59	78	58	75
	Predicted	71	50	35	25	18
Devonian 5	Observed	62	54	48	44	31
	Predicted	62	39	24	15	9
Carboniferous 1	Observed	62	52	39	42	7
	Predicted	62	38	24	15	9
Carboniferous 2	Observed	58	41	37	43	23
	Predicted	58	34	20	12	7
Carboniferous 3	Observed	63	49	20	40	18
	Predicted	63	40	25	16	10
Carboniferous 4	Observed	60	33	23	36	40
	Predicted	60	36	22	13	8
Carboniferous 5	Observed	50	34	20	9	14
	Predicted	50	25	13	6	3
Permian 1	Observed	40	22	15	13	15
	Predicted	40	16	6	3	1
Permian 2	Observed	47	38	30	14	8
	Predicted	47	22	10	5	2
Permian 3	Observed	75	65	56	42	45
	Predicted	75	56	42	31	23

| | Extinction Rate | Species Richness Category | | | | |
~11-Myr Bin	in percent	One	Two	Three	Four	Five
Permian 4	Observed	82	86	83	66	71
	Predicted	82	67	55	45	37
Triassic 1	Observed	72	68	66	82	76
	Predicted	72	52	38	27	20
Triassic 2	Observed	56	48	57	33	32
	Predicted	56	32	18	10	6
Triassic 3	Observed	66	41	42	19	41
	Predicted	66	44	29	19	13
Triassic 4	Observed	80	65	54	41	46
	Predicted	80	64	51	41	32
Jurassic 1	Observed	40	37	43	43	17
	Predicted	40	16	6	3	1
Jurassic 2	Observed	49	43	21	50	55
	Predicted	49	24	12	6	3
Jurassic 3	Observed	51	48	41	39	17
	Predicted	51	26	13	7	3
Jurassic 4	Observed	38	31	22	21	0
	Predicted	38	14	5	2	1
Jurassic 5	Observed	64	53	44	40	51
	Predicted	64	41	26	16	10
Jurassic 6	Observed	55	44	34	23	31
	Predicted	55	30	17	9	5
Cretaceous 1	Observed	49	34	41	29	21
	Predicted	49	24	12	6	3
Cretaceous 2	Observed	49	39	39	20	33
	Predicted	49	24	11	6	3
Cretaceous 3	Observed	48	38	21	29	24
	Predicted	48	23	11	5	3
Cretaceous 4	Observed	50	44	32	21	39
	Predicted	50	25	12	6	3
Cretaceous 5	Observed	43	34	14	23	18
	Predicted	43	19	8	4	2
Cretaceous 6	Observed	43	34	32	24	24
	Predicted	43	19	8	3	2
Cretaceous 7	Observed	41	25	16	18	6
	Predicted	41	17	7	3	1
Cretaceous 8	Observed	65	70	59	60	67
	Predicted	65	42	28	18	12
Cenozoic 1	Observed	47	31	17	11	3
	Predicted	47	22	10	5	2
Cenozoic 2	Observed	47	20	17	8	3
	Predicted	47	22	11	5	2
Cenozoic 3	Observed	53	37	28	13	14
	Predicted	53	28	15	8	4
Cenozoic 4	Observed	42	17	11	4	0
	Predicted	42	18	7	3	1
Cenozoic 5	Observed	58	39	25	14	13
	Predicted	58	34	20	11	7

Investigating the data surrounding the K-Pg extinction event lends evidence against this correlated species richness effect and toward a model of non-random extinction via selectivity. It has been shown that at the genus level numerous factors supposed to buffer against extinction in other geologic intervals do not correlate with survivability at the K-Pg extinction event, including species richness of genera (Jablonski, 2005). However, as stated above, random extinction of genera with regard to species richness category results when there is highly clustered, selective extinction of the member species of genera.

For the latest Cretaceous time bin ("Cretaceous 8"), the observed extinction rates of genera across species richness categories are roughly equivalent (Table 1), confirming previous observations that genus extinction rates are not influenced by species richness at the K-Pg boundary (Jablonski, 2005). Meanwhile, the predicted extinction rates of the two-to-five species richness categories of genera based on the extinction rate of genera in the one- species richness category are much lower than the observed extinction rates, suggesting non-random extinction. An alternative way to consider this problem is to recognize that for the observed extinction of 67% of genera in the five-species richness category to have occurred by random extinction of species would require the extinction of 92% of species ($0.67^{1/5} = 0.92$). The observed random extinction of genera with respect to species richness category requires a greater, and non-random, extinction of species in the five-species richness category of genera relative to the one-species richness category. This non-random component could be provided by the aforementioned species richness effect if we were willing to accept that extinction of member species in the genera in the five-species richness category is much more likely than extinction of the member species in the one-species richness category (92% versus 67%).

It seems implausible that species extinction rates would be so dramatically increased simply by membership in high species richness genera, and conversely that

membership in low species richness genera would buffer so effectively against species extinction. However, based on the data presented here the correlated species richness effect cannot be entirely dismissed, and it could contribute to the pattern in Figure 4. Regardless, the effect constitutes non-random extinction and evidence against the "field of bullets" model.

While results presented here for the K-Pg extinction event as well as the data for the other "Big Five" suggest that mass extinctions have been selective (Fig. 2.4), it must be mentioned that the methodology employed here does not assume that all of the extinctions took place at the end of the time bin of interest. In the ~11-Myr time bins of the PaleoDB the latest Cretaceous time bin is represented by the Maastrichtian stage. Therefore, the highly selective species extinctions required to explain the observations here do not allow us to distinguish between a sudden extinction mechanism such as the bolide impact (Alvarez et al., 1980) and a more protracted interval of extinction that persisted throughout the stage, and culminated with the K-Pg boundary event. Additionally, the results presented here do not distinguish between the "fair game" and "wanton extinction" scenarios, but rather confirm previous observations that regardless of the intensity of the extinction events taking place, some form of selectivity has operated (Jablonski, 2005).

The issue of whether species extinction probability is biased upward by its inclusion in a genus with many species leads one to consider whether the results reported here might be the product of taxonomic practice rather than biological reality. In investigating "taxonomic wastebaskets" Plotnick and Wagner identified characteristics possessed by common genera in the PaleoDB (2006). Among those traits with potential implications for the data presented here are that common genera in the PaleoDB may be inflated by being speciose, having a high number of occurrences, a wide geographic distribution, and a long geologic range. While these traits of common genera may reflect their underlying reality, Plotnick and Wagner's suggestion

is that genera meeting these criteria may require systematic review to ensure that they are not artificially inflated by one of these biases. However, if we assume that these common genera, which are typically speciose, are indeed inflated temporally, the effect should run counter to that proposed here as it is the genera with the greater number of species (in the highest species richness categories), that do not appear to live as long as random extinction of species would predict.

An explanation for the observations presented here that could be caused by this taxonomic wastebasket effect is if very short-lived species in monospecific genera have been lumped into wastebasket genera instead of designated as distinct genera. Lumping short-lived species into a wastebasket genus likely will not extend the geologic duration of that genus, but will alter the predicted value of extinction for the wastebasket genus since the present analysis depends on the use of extinction rates in monospecific genera. This lumping, if it occurred, would lower the average extinction rate of monospecific genera, and therefore produce a lower predicted extinction rate for genera in higher species richness categories. Any factor related to taxonomic practice that instills a bias in the extinction rates of genera with one species will affect the predicted extinction rates for higher species richness categories of genera. Additionally, the wastebasket genus will shift to a higher species richness category raising the exponent in the prediction calculation, lowering its predicted extinction rate.

One way to circumvent this problem is to not use the extinction rates of monospecific genera, but instead to predict the extinction rates via the observed extinction rate of a higher species richness category of genera. For example, if $q_2 = (q_1)^2$, and $q_3 = (q_1)^3$, then $q_3 = (\sqrt{q_2})^3$, $q_4 = (\sqrt{q_2})^4$, etc. In this fashion we can define the predicted random extinction rates for higher species richness categories of genera in terms of the observed extinction rate of genera in the two-species richness category (or higher richness category) of genera. These new predicted extinction rates can
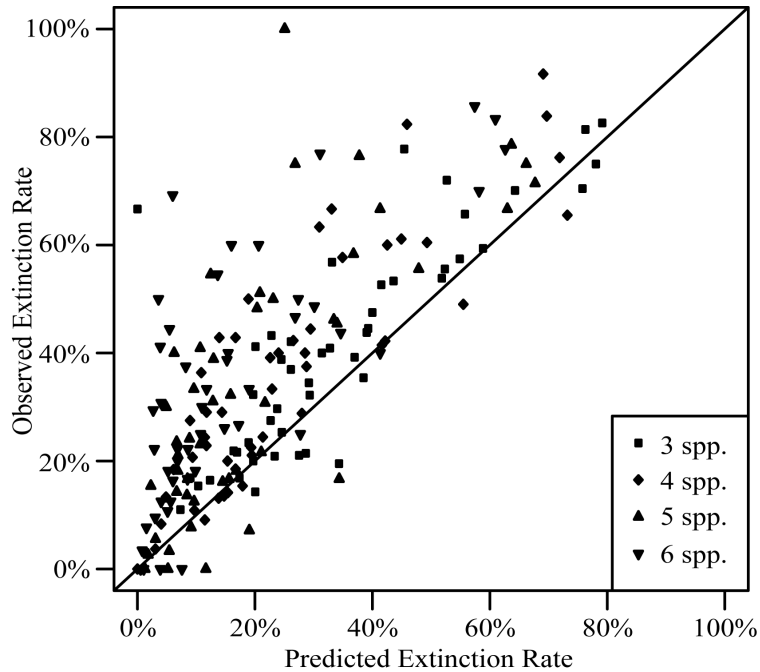
Figure 2.5: Observed versus predicted extinction rates for genera in ~11-Myr bins of the PaleoDB with predicted extinction rates calculated for genera with three to five species using the observed extinction rate of genera in the two-species richness category. As with the method using the extinction rates of monospecific genera, most points fall above the line of slope one, suggesting that more genera went extinct than if extinction had been applied randomly across species.

then be plotted against the observed extinction rates, as was done for Figure 2.4. The results of this analysis are similar to those seen previously (Fig. 2.5); most points fall above the line of slope one that defines the random extinction expectation. This result is maintained regardless of whether the observed extinction rate of genera with three, four, and five species is employed. Thus if the results presented here are a product of taxonomic practice, the pattern is not as simple as preferential diminution of the extinction rates for genera with only one species, but must apply across the taxonomy of fossil species and genera.

Another potential explanation for the pattern presented here which merits future investigation is whether the result could be produced by incomplete sampling due to non-preservation or non-recovery of some taxa. It is not clear how such incompleteness would result in the appearance of greater observed extinction probability than

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predicted for genera with more than one species. The apparent non-random extinction appears in all intervals of time, whether poorly or well-sampled. As presented, the result is particularly strong for the late Cretaceous, an interval that has merited considerable focus and is the best documented extinction event (Raup and Jablonski, 1993; Twitchett, 2006). However, given the known incompleteness of the K-Pg fossil record (MacLeod et al., 1997), factors related to sampling and incompleteness should be more fully investigated.

The analysis is agnostic about the cause of extinction selectivity and does not distinguish ecological selectivity from other mechanisms, e.g., geographic selectivity. One reviewer pointed out the possibility that regional differences in extinction rate and/or sampling heterogeneity could create the pattern observed here. This could occur as follows: consider two regions, A and B, each containing 100 genera with one species and 100 genera with two species. In region A, the observed extinction rate of one-species genera is 90%, resulting in a predicted extinction rate of 81% for the two-species genera (81 of 100 genera). In region B, the observed extinction rate of one-species genera is 30%, with a predicted extinction rate of 9% for the two-species genera (9 of 100 genera). In total for regions A and B, 45% of the two-species genera (90 of 200 genera), are predicted to go extinct. However, in the pooled dataset combining region A and B, the observed extinction rate for one-species genera of 60% would result in a prediction of 36% extinction for two-species genera (72 of 200 genera), a lower predicted value. In this example, regional extinction rate heterogeneity creates non-random extinction in the pooled dataset, with no explanation based on ecological clustering of extinctions merited.

In order to test for the possibility that the observed pattern could be driven by regional extinction rate heterogeneity, we ran the analysis on separate regions represented by continents and paleocontinents as assigned in the PaleoDB. In all regions, a pattern similar to that observed in Figure 2.4 resulted (results available

upon request). The evidence for selectivity presented here does not appear to be driven by regional differences in extinction rate (Appendix A). The possibility of within-region extinction rate heterogeneity cannot be dismissed. This would still represent extinction selectivity and evidence against the "field of bullets" model, albeit geographic and not ecological selectivity. Within-region sampling heterogeneity similarly cannot be dismissed and merits further testing.

Additionally, as this study was undertaken in a non-phylogenetic context, it does not account for pseudoextinction of genera (Leighton and Schneider, 2008), or other effects created by employing a non-phylogenetic approach to measuring extinction intensities (MacLeod et al., 1997). Further work should investigate whether the appearance of non-random extinction could result from lack of recognition of surviving genera due to pseudoextinction or lack of accurate phylogenies.

2.5 Conclusion

We used data from the PaleoDB to test for randomness in the Phanerozoic record of marine invertebrate extinctions. The results indicate that extinctions have been nonrandom with respect to species-richness categories of genera throughout the Phanerozoic, during background extinction and mass extinction events. Although many studies have demonstrated that extinctions are nonrandom by revealing differential survivorship of taxa that possess extinction-biasing traits, this approach demonstrates nonrandom extinction without appeal to correlated traits, complementing the findings of these analyses. These results do not allow us to determine whether similar selective regimes operated during both background and mass extinction times, but they do suggest that an exclusive "field of bullets" scenario did not operate frequently, if at all, on a geologic time scale.

Future work should further explore the proposed explanations presented here for the evidence against random extinction. These explanations include whether nonran-

dom extinction can be attributed entirely to nesting of traits promoting extinction within some genera, whether it could result from correlation of traits buffering against extinction with membership in a genus with fewer species, and whether geographic selectivity contributes to the pattern. Further consideration should be given to whether the method used here for detecting nonrandom extinction could result from sampling or taxonomic artifacts. These potential explanations could have implications for future analyses using the PaleoDB. Additionally, it is worth recognizing that not all patterns apparent at higher taxonomic levels represent smooth extrapolations from the species level. Nonrandom extinction of species via selective, clustered species extinctions will give the appearance of random extinction of genera with regard to their species richness.

2.6 Acknowledgments

CHAPTER III

Extinction selectivity at the Permian-Triassic and Cretaceous-Paleogene mass extinctions

3.1 Abstract

Extinction selectivity during mass extinction events is still poorly understood, with some studies suggesting that mass extinctions exhibit less selectivity than exists during background extinction. Herein, I provide an expansion of a probabilistic method that uses the number of species in a genus to predict the probability of its extinction in the absence of extinction selectivity. Using this method, I present evidence that the two most-studied mass extinctions of the Phanerozoic, the Permian-Triassic and Cretaceous-Paleogene extinction events, show strong evidence for extinction selectivity. A newly developed method based on a likelihood ratio test shows that regional selectivity did not cause the observed extinction selectivity, which may suggest that ecological or some other form of trait selectivity was particularly strong during these intervals. This observation accords with the dramatic faunal turnover at these boundaries of geological eras. I also show that species richness has a particular effect on genus survivorship. When species richness has failed to predict genus survivorship at an extinction event, it has been claimed as evidence against extinction selectivity for species-rich genera. Here I show that the mathematical expectation of

extinction electivity is such that as selectivity for any trait increases, species richness declines in its ability to reduce extinction probability. Therefore, when species richness does not predict genus survivorship it may be a prima facie indicator of a time of high extinction selectivity.

3.2 Introduction

The fossil record is the best resource for understanding the dynamics of extinction, with evidence that extinction intensity, the magnitude of extinction, and extinction selectivity, the non-random extinction of species, have varied through time (Jablonski, 2005). Faced with the prospect that we may be in a sixth mass extinction due to the great number of threatened species (Wake and Vredenburg, 2008), and that the loss of evolutionary history is much greater if extinction is not randomly distributed across taxa (Purvis et al., 2000; Vamosi and Wilson, 2008), it is important to understand whether past mass extinctions were similarly selective in order to properly compare the past and current extinction crises. Despite a surge in research output on mass extinctions, particularly the Permian-Triassic (P-Tr) and Cretaceous-Paleogene (K-Pg) events (Twitchett, 2006), few generalities about mass extinctions and extinction selectivity have emerged (Jablonski, 2005).

Certain studies have shown that traits that reduced extinction probability during background times did not correlate with reduced extinction probability at the K-Pg mass extinction event (Banerjee and Boyajian, 1996; Jablonski, 1986; Payne and Finnegan, 2007), leading some to conclude that mass extinction events generally exhibit less selectivity than background extinction times (Raup, 1994; Brusatte et al., 2008), or that selectivity may operate with reduced effectiveness during mass extinctions (Jablonski, 2005, 2008). However, trait inference for fossil taxa can be difficult or even impossible, and the absence of significant correlations between the traits that are measured and extinction of taxa does not suggest absence of extinction selectivity

at the extinction event. Rather, the traits creating selectivity may not have been observed, and extinction selectivty may have been strong for one or more traits that were not preserved or studied.

Using a probabilistic method oreviously applied to marine invertebrates for the entire Phanerozoic (Janevski and Baumiller, 2009), I show that the two most-studied mass extinctions in the history of life show strong extinction selectivity on marine invertebrates. I formulate and apply a likelihood ratio test to demonstrate that geographic extinction rate heterogeneity (regional selectivity) explains little of the observed extinction selectivity. Unstudied ecological traits may have contributed to the intense extinction selectivity. I also show that species richness is a characteristic unlike other traits of genera. The effect of species richness on the selectivity of genus extinctions correlates inversely with selectivity on other other traits, such that as extinction selectivity increases (on one your more traits), species richness predictably declines in its ability to predict survivorship of genera. Under strong extinction selectivity, species richness will entirely cease to predict genus survivorship. The observation that species richness does not predict survivorship of genera during some time intervals is thus evidence for increased, not reduced, extinction selectivity.

The genus is often the unit of analysis in paleontological studies of biodiversity and extinction. This approximation of species-level patterns usually suffices as the primary intent in most studies is to determine relative rather than absolute changes in diversity or extinction (e.g., was Paleozoic species richness lower than Cenozoic species richness?). Most marine invertebrate genera in the PaleoDB consist of only one species, and thus raw counts of fossil genera and species track each other (Janevski and Baumiller, 2009). However, the use of genera creates some difficulties for studies of extinction selectivity. Some traits of a genus (e.g., geographic range or number of habitats occupied) are expected to co-vary with the number of species in the genus. In order to determine whether these traits have an effect on genus survivorship inde-
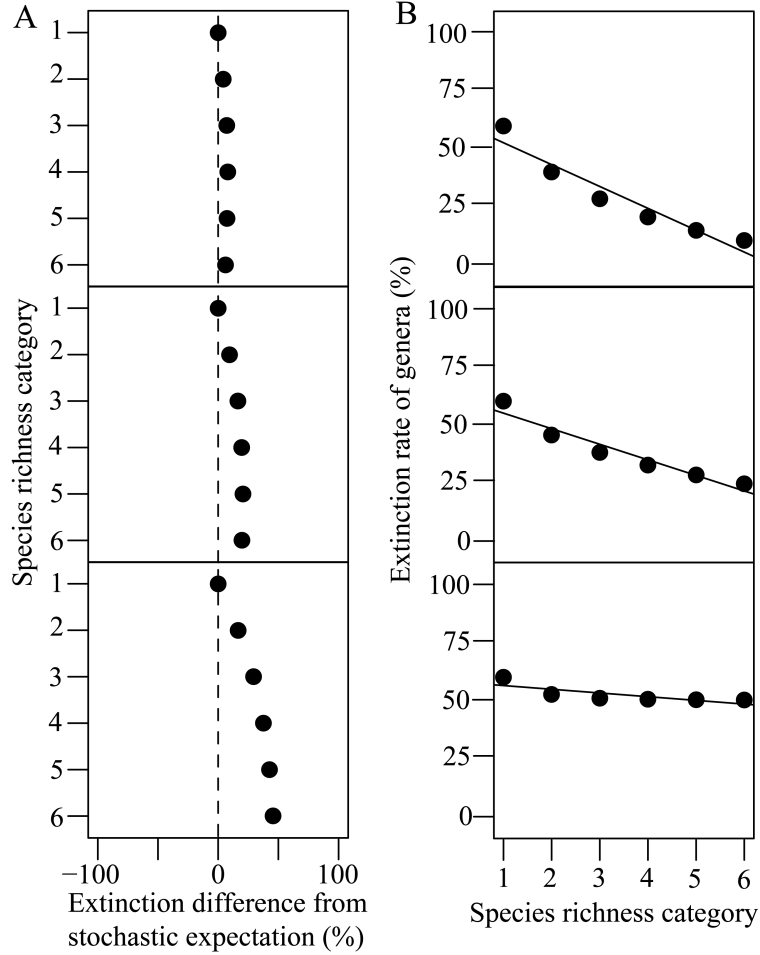
Figure 3.1: Extinction simulation on a model dataset showing the reduced ability of species richness to predict genus survivorship as extinction selectivity increases. Solid circles represent observed extinction rates by species richness category. See text for discussion.

pendent of species richness, a confounding variable, it is often necessary to explicitly consider the covariance of species richness (Payne and Finnegan, 2007; Finnegan et al., 2008).

3.3   Data and Methods

3.3.1   Data

The data are of fossil marine invertebrate occurrences downloaded from the Paleobiology Database (PaleoDB). Included occurrences were only of determinate species

that contained temporal (PaleoDB ~11-Myr bins) and geographic (paleolatitudinal and paleolongitudinal coordinates) information (325,405 occurrences). The dataset was filtered to include only unique occurrences and to exclude species with abbreviated genera (e.g., "A."). For further culling protocol see Janevski and Baumiller (2009). The analysis was restricted to the P-Tr and K-Pg extinction events, arguably the two largest mass extinctions of the Phanerozoic (Bambach et al., 2004). The K-Pg time bin is equivalent to the last stage of the Cretaceous (Maastrichtian), while the P-Tr time bin combines the last two stages of the Permian (Wuchiapingian and Changhsingian).

3.3.2 Interaction of species richness and extinction selectivity

I use the principle that under non-selective (stochastic) species extinction, species richness will contribute to the probability of a genus surviving an extinction event in a manner dictated by binomial sampling probability (McKinney, 1995; Purvis, 2008; Janevski and Baumiller, 2009); conversely, maximum selectivity results in no correlation between species richness and genus survivorship. These stochastic and selective extinction probabilities form explicit, mathematical expectations that can be compared to observed extinction data.

A special relationship exists between species richness and extinction selectivity on other traits. As selectivity on these traits increases, species richness diminishes in its contribution to genus survivorship. Figure3.1 presents a model to show this effect. In the model, there is no selectivity against multi-species genera - extinction intensity is the same for all species richness categories of genera. Extinction is simulated on a model dataset under three scenarios of differing extinction selectivity. Selectivity was simulated by subjecting half of the species to a higher extinction rate, and half to a lower rate; total species extinction probability remained the same in each scenario. The number of surviving genera was tallied to determine the genus extinction rate.

In Figure 3.1A, dashed lines representing stochastic extinction expectation for genera are plotted for reference. The observed genus extinctions differ from this stochastic expectation more greatly with increased extinction selectivity of species. Species richness of genera is decreasingly able to predict survivorship as selectivity increases (Fig. 3.1B). Multi-species genera appear more extinction-prone when species experience selective extinction, without direct selection against those genera. The null assumption for species richness is opposite to that of other traits: In the absence of selectivity for any trait, species richness is expected to be a significant predictor of genus survivorship; when selectivity for other traits is strong, species richness is expected to diminish in significance and thus lose its ability to predict extinction (Fig. 3.1). This relationship follows a predictable form: when all species extinctions are clustered in the fewest possible genera (maximal selectivity), equivalent extinction intensity occurs across genera with respect to their species richness.

3.3.3 Extinction intensity and selectivity

Extinction rates were calculated as the per-genus extinction rate in the time bin, a requirement for the method of detecting selectivity described here, though more advanced metrics for occurrence-based calculation of extinction rate exist (e.g., Alroy, 2010b). Under a null hypothesis of no selectivity for any organismal or species-level trait (ecological, regional, etc.), survivorship of a genus is due only to stochastic effects, and is predicted by the number of species in that genus (McKinney, 1995; Purvis, 2008; Janevski and Baumiller, 2009). Survivorship can be mathematically represented as p^n, where p is the species extinction rate, and n is the number of species in a genus. The extinction rate of genera with one species, p_1, is p^1, and the stochastic expectation of extinction of genera with n species is $p_n = p_1^n$. Further, for a given p, the maximum value p_n can take is p, and this result occurs only when species extinctions are clustered in the fewest number of genera possible. Extinction

selectivity, which is non-random extinction, causes deviations from the stochastic expectation until selectivity reaches a maximum such that all species in some genera go extinct, and no species in other genera go extinct.

3.3.4 Likelihoods given data

The expectations formulated above allow direct comparison of the stochastic (H_1 : $p_n = p_1^n$) versus selective ($H_2 : p_n = p_1$) extinction hypotheses using the principle of statistical likelihood (Edwards, 1992). A likelihood ratio test compares the relative support for a model in which extinction of taxa was entirely stochastic and a model in which extinction was selective. The test begins with a likelihood function, which for the binomial probabilty case represented by the two models, is formulated as $L[p|y, x, binomial] = \binom{x}{y} p^y (1 - p)^{x-y}$ (Burnham and Anderson, 2002), where p is the extinction probability, x is the number of genera present, and y is the number of extinct genera. The log-likelihood ratio (support; LR) of the two hypotheses is then $LR[\frac{p^n}{p}|y, x, binomial] = y(n - 1)(ln(p)) + s[ln(1 - p^n) - ln(1 - p)]$, where s is the number of surviving genera ($x - y$), and n is the number of species in the genera.

A positive LR indicates stronger support for H_1 while a negative LR favors H_2. By convention, a LR of $2(-2)$ is a conventional value sometimes used as strong evidence in favor of $H_1(H_2)$ (Royall, 1997) (i.e., analagous to $p < 0.05$). An important component of LR is that the results are additive when drawn on independent datasets (Edwards, 1992). This allows the LR across genera of varied n to be summed for a given time interval to determine whether extinction was generally selective in the time interval. Table 3.1 shows the LR comparing the stochastic and selective extinction models for marine invertebrate taxa from the PaleoDB for the P-Tr and K-Pg extinction events. In the two-to-six species category, 228 of 360 genera go extinct at the K-Pg (63%), and 156 of 195 at the P-Tr (80%). The highly negative LR suggest strong support for the selective extinction hypothesis.

The LR represents a general test that should be widely applicable to determine whether extinction events better support stochastic or selective extinction. Importantly, it allows detection of selective extinction even in the absence of knowledge of organismal or species-level traits. Such a characteristic is useful for paleontological data where trait inference for fossil taxa can at times be difficult or impossible (e.g., for traits that are not preserved). The absence of significant correlations between extinct taxa and studied traits does not suggest absence of selectivity on the whole, as the trait causing selectivity may not have been observed. The method for detecting extinction selectivity used here, which is explicitly agnostic about taxon traits, allows detectiong of selectivity in the absence of trait knowledge, but may also be a guide toward particularly selective extinction events for which the traits of interest are as yet undiscovered.

Additionally, the LR can be used to test the contribution of regional selectivity to observed extinction selectivity. The operation consists of calculating LR for a series of paleolatitudinal/-longitudinal grids of constant size (global) but of increasing grid resolution (cell number). Fossil occurrences are plotted in grid space. The LR is first determined for the entire global dataset. The data are then divided into a 2×2 grid of equal cell size; the LR is determined for each grid cell and then summed for the whole grid. The operation continues with the next, finer resolution grid (3×3). The global grid combines regions that may have experienced disparate extinction intensity. By subdividing the globe, differences in extinction rate by region will be revealed, and the contribution of geographic extinction rate heterogeneity to the LR can be shown. The expectation is that the LR will increase (i.e., more strongly favor the stochastic hypothesis, H_1) as finer resolution grids are analyzed. The operation proceeds through more finely divided grids until an 18×18 grid is formed ($10°$ paleolatitude and $20°$ paleolongitude), at which point most grid cells will be unoccupied.

Table 3.1: Observed extinction rates and predicted extinction rates under stochastic and selective extinction scenarios. n=number of species in genus, LR=likelihood ratio.

Extinction Event	Extinction Probability	n						LR
		1	2	3	4	5	6	
K-Pg	observed: p_n	61%	60%	55%	65%	56%	45%	
	stochastic: p_1^n	61%	37%	22%	14%	8%	5%	-127
	selective: p_1	61%	61%	61%	61%	61%	61%	
P-Tr	observed: p_n	82%	85%	84%	85%	81%	79%	
	stochastic: p_1^n	82%	67%	55%	45%	37%	30%	-55
	selective: p_1	82%	82%	82%	82%	82%	82%	

3.4 Results

Figure 3.2 presents the mathematical expectations when extinction is entirely stochastic, and when extinction is maximally selective. For comparison, the results of genus extinction in simulation of stochastic species extinction is also presented. In general, a reasonable expectation is that species extinction with be both a product of selectivity and stochastic effects. Species extinction may be driven by selection against certain traits, while the contribution to extinction for some species may have more to do with being in the wrong place at the wrong time (e.g., chance effects). I compared the mathematical expectations of stochastic and selective extinction to the actual extinctions of fossil marine invertebrate genera in the PaleoDB for the P-Tr and K-Pg extinction events: selectivity appears very high at these extinction events.

3.5 Discussion

3.5.1 Regional selectivity

Extinction selectivity has been described as trait, taxonomic, or geographical (McKinney, 2001). Geographical selectivity has herein been referred to as regional selectivity. Taxonomic selectivity may be a product of shared traits, often ecologi-
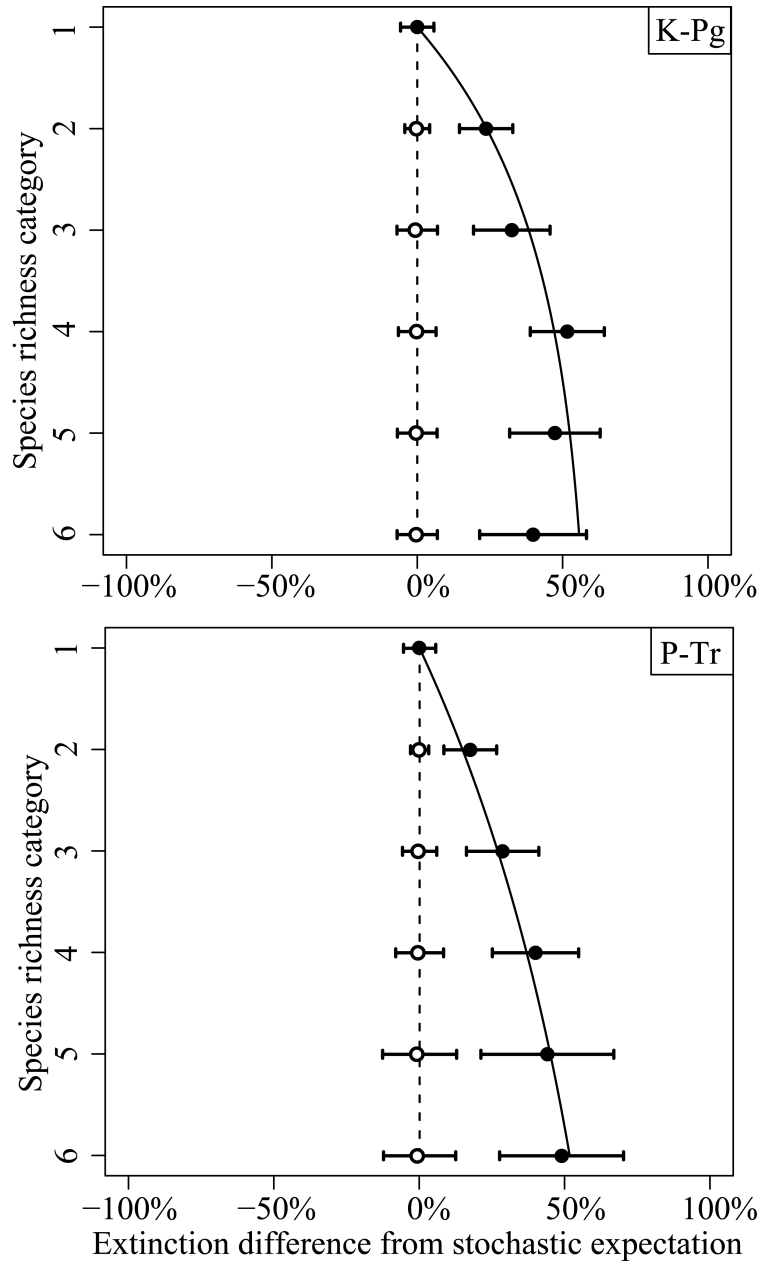
Figure 3.2: Observed extinction rates of genera by species richness category for the K-Pg and P-Tr extinction events (solid circles) compared to a stochastic extinction simulation (open circles). Error bars are 95% binomial confidence limits. In the stochastic simulation, extinction if species was simulated randomly for 10,000 trials to determine the median expected genus extinction (error bars represent 95% of the observed genus extinctions in the simulation). The dashed line represents the mathematical expectation of stochastic extinction. The solid line represents the mathematical expecation of genus extinction when species extinctions are highly selective. The observed genus extinctions differ greatly from the stochastic extinction expectation and fall very close to the expectation for a highly selective extinction event.
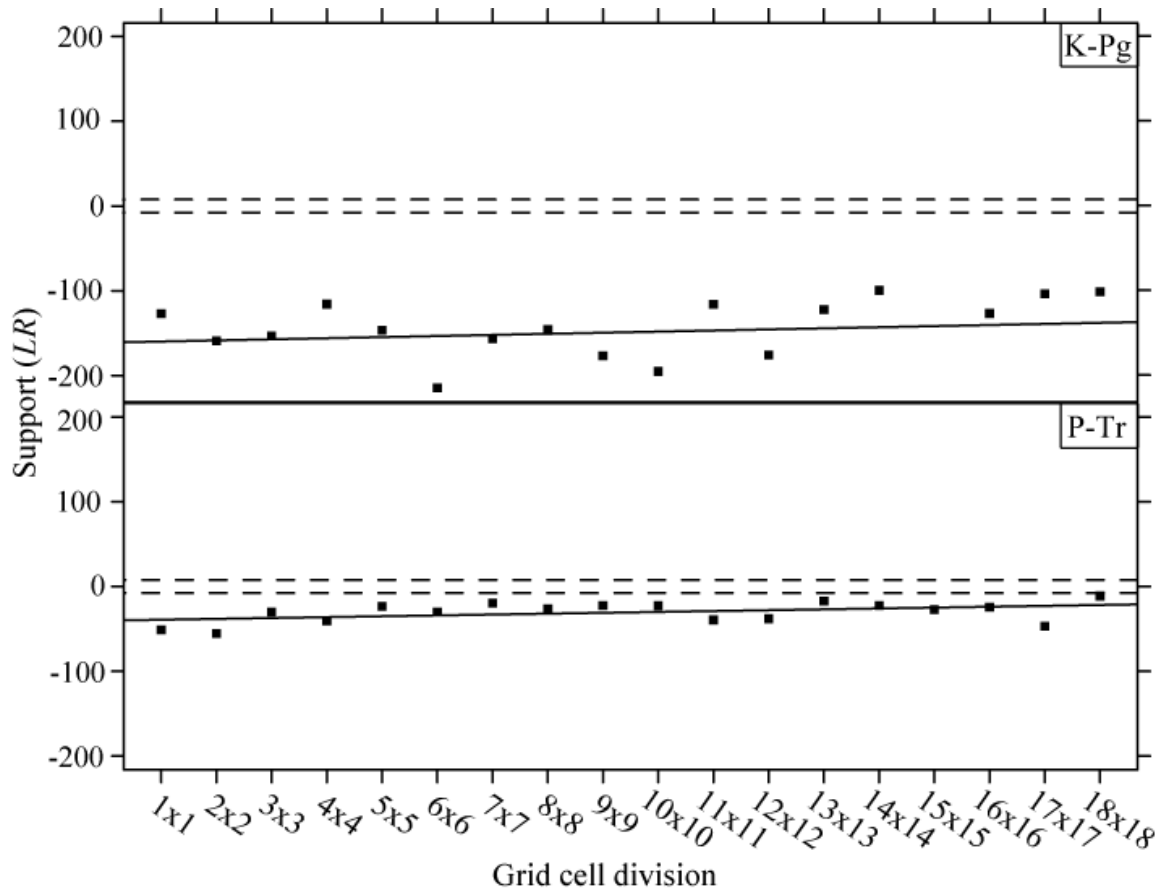
Figure 3.3: Plots of LR calculated across global paleolatitudinal and paleolongitudinal grids to determine the contribution of regional selectivity to observed extinction selectivity patterns. All points are highly negative, showing strong evidence in favor of H_2, selective extinction.

cal, or regions among related taxa. Regional selectivity occurs when extinction rates differ between geographic areas. A caveat to the LR formulation is that the selective extinction revealed here by taxonomic extinction could be partly a product of regional rather than trait selectivity, if extinction rates vary geographically (Janevski and Baumiller, 2009). In order to determine the relative contribution from regional selectivity, i.e. that it is due to geographic rate disparities, I tested if the LR for the P-Tr and K-Pg extinctions more strongly supported stochastic extinction when geographic extinction rate heterogeneity was taken into account.

Figure 3.3) shows the results of the reduction in LR as geographic extinction rate heterogeneity is taken into account. The LR for the global grids are all highly

negative, showing strong evidence in favor of H_2, selective extinction, even when this effect of regional selectivity is taken into account. Dashed line marks values of support for random and selective extinction models at 8 and -8, which are analagous to p-values of < 0.001, representing very high support for a model. Even at the finest scale of resolution, the LR for both extinction events still strongly favors selective extinction. Solid lines are linear regressions. Both grids reveal slight increases in the LR as the geographic extinction rate heterogeneity is taken into account, suggesting that geographic extinction rate heterogeneity marginally contributes to the selectivity of extinction for the pooled, global dataset, though this increase is not statistically significant for either extinction event (K-Pg $p-value : 0.496$; P-Tr $p-value : 0.062$).

The low geographic extinction rate heterogeneity revealed here supports other studies which found a similar lack of geographic extinction rate differences at the K-Pg extinction event (Raup and Jablonski, 1993). Alternative gridding strategies produced similar results. As shown in Figure 3.4, it is necessary to divide grids both latitudinally and longitudinally. Restricting to only latitudinal or longitudinal grid division will not reveal extinction rates that vary only orthogonally to the direction of division.

3.5.2 Taxonomic practice

In studies that analyze taxonomic databases, it may be necessary to evaluate if taxonomic practice contribute to the observed patterns. Evaluating taxonomic practice is particularly important for this study as counts of species richness are used to determine the probability of a genus going extinct. However, problems of taxonomic practice are not unique to this study. The null assumption of species richness as a determinant of genus extinction probability used here should probably be applied to any study of extinction selectivity that uses higher taxonomic categories. For example, the frequently reported observation that size of geographic range occupied
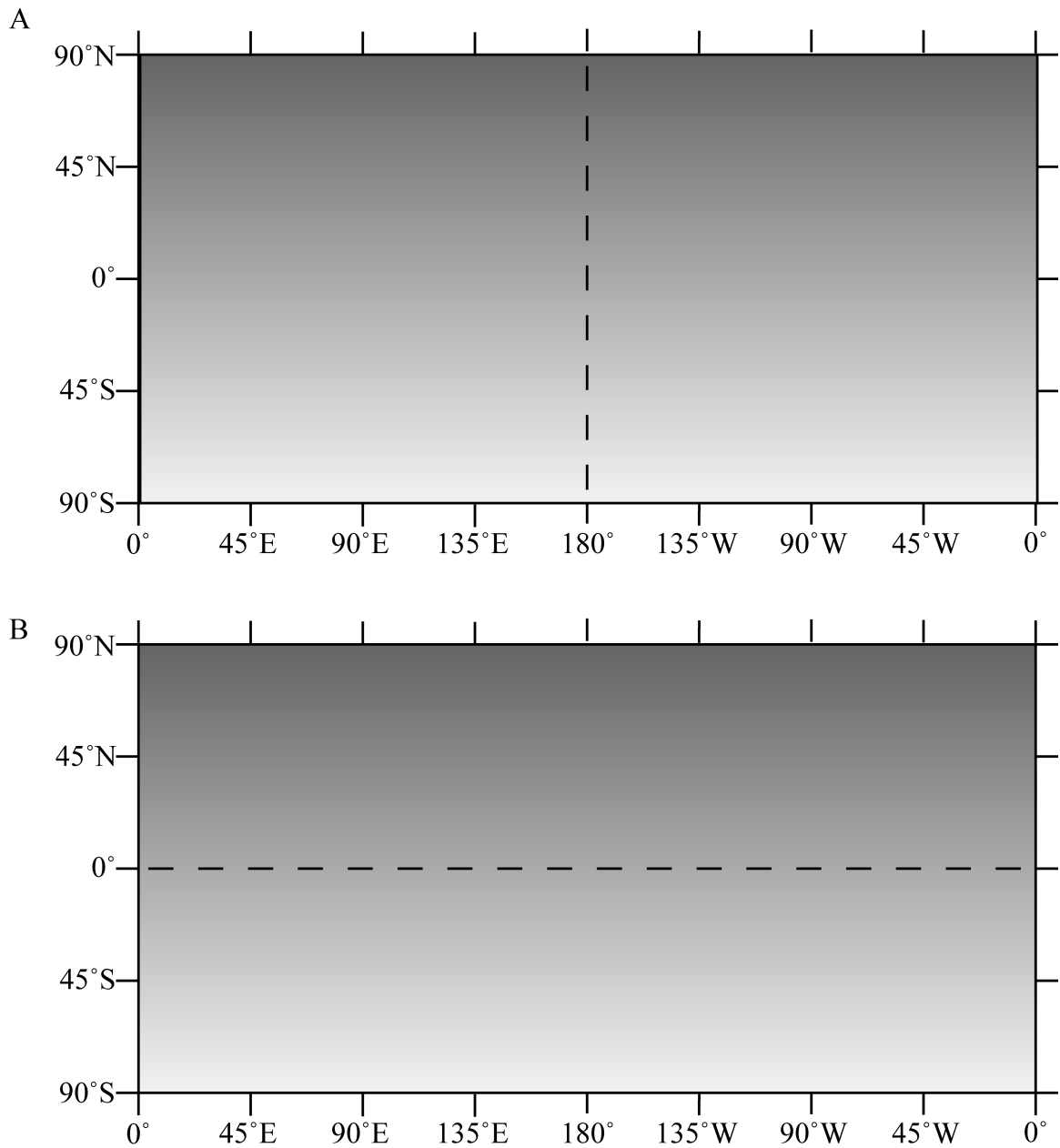
Figure 3.4: The effect of gridding protocol on detecting geographic extinction rate heterogeneity is illustrated with a simple latitudinal extinction gradient (shading). In A, the longitudinal grid division results in equivalent average extinction rates in each half of the grid, despite the obvious extinction heterogeneity. In B, the latitudinal grid division properly reveals extinction rate heterogeneity. Dividing grids both latitudinally and longitudinally will reveal geographic extinction rate heterogeneity.

is the most consistent predictor of genus survivorship is only demonstrable when species richness, which should co-vary with geographic range occupied, is explicitly taken into consideration (Payne and Finnegan, 2007). And thus taxonomic practice may affect all such studies.

Further, it has been asserted that all studies of extinction rate require taxonomic standardization (Roy et al., 2009). However, every dataset, whether standardized or not, contains errors. What is important is whether the errors are non-random (i.e., whether the data are unbiased), and sufficiently error-free to answer the question considered.

A few lines of evidence, explicit and implicit, suggest that taxonomic practice does not create the pattern of selectivity observed here. The analysis relies on the extinction rate of genera with one species, p_1, to predict the extinction probability of genera with more than one species, p_n. Thus if p_1 is biased by taxonomic practice to artificially extend stratigraphic ranges, lowering the extinction rate, the stochastic extinction predictions for p_n will be artificially lower than actually observed. However, based on observations of marine invertebrate data from the PaleoDB, is has been claimed that multi-species genera ($n >> 1$) are more likely to have artificially extended ranges (Plotnick and Wagner, 2006). This effect runs counter to the observed evidence for selectivity as it is the higher species genera that do not survive as long as their species richness should allow. Additionally, it is possible to reformulate the extinction probabilities such that they do not use p_1 (considering the possibility that p_1 is uniquely biased), instead relying only on multispecies genera. If only the higher species richness genera are used, the evidence for selectivity persists (Janevski and Baumiller, 2009).

The fossil record of species is less complete and species-level taxonomy more unstable than that of higher taxa (Sepkoski, 1998). On probabilistic grounds the fossil record of species is necessarily less complete than that of higher taxa as species dis-

covery represents a rarefaction problem in which discovery of additional species is decreasingly likely to reveal new higher taxa (Raup, 1975). The use of species to predict the extinction rate of genera was chosen partly because species may be usefully regarded as the fundamental unit of macroevolution (Stanley, 1998). It has yet to be determined that species-level taxonomy in large-scale databases like the PaleoDB is biased in a way that necessarily makes it less valid in all kinds of analyses than the use of higher taxa. However, species-level taxonomy can be avoided completely if the analysis is changed to use the observed extinction rate of families with one genus to predict the extinction rate of multi-genus families. This higher taxonomic level reduces sample sizes, but the predictions and assumptions are similar to the lower taxonomic level. Again, strong evidence for selective extinction at both extinction events is evident at this higher taxonomic level (Fig. 3.5).

3.6   Conclusion

Studies of extinction selectivity at mass extinctions have often treated species richness of genera as a trait to be analyzed similar in kind to other traits, and interpreted a lack of significance of species richness in predicting genus extinction to mean the absence of selectivity for species richness (Jablonski, 1986; Smith and Jeffery, 1998; Leighton and Schneider, 2008; Powell, 2008). The lack of an advantage to genera with more species in surviving the K-Pg mass extinction has been described as ironic (Raup, 1986). Instead, properly formulated in this probabilistic framework the expectation when extinction selectivity is operating heavily is that species richness will fail to predict genus survivorship. It is thus unsuprising that the studies that found no correlation of genus extinction with low species richness found selectivity operating on other factors (Jablonski, 1986; Smith and Jeffery, 1998; Leighton and Schneider, 2008; Powell, 2008).

The method I used here to detect selectivity can be caused by ecological trait
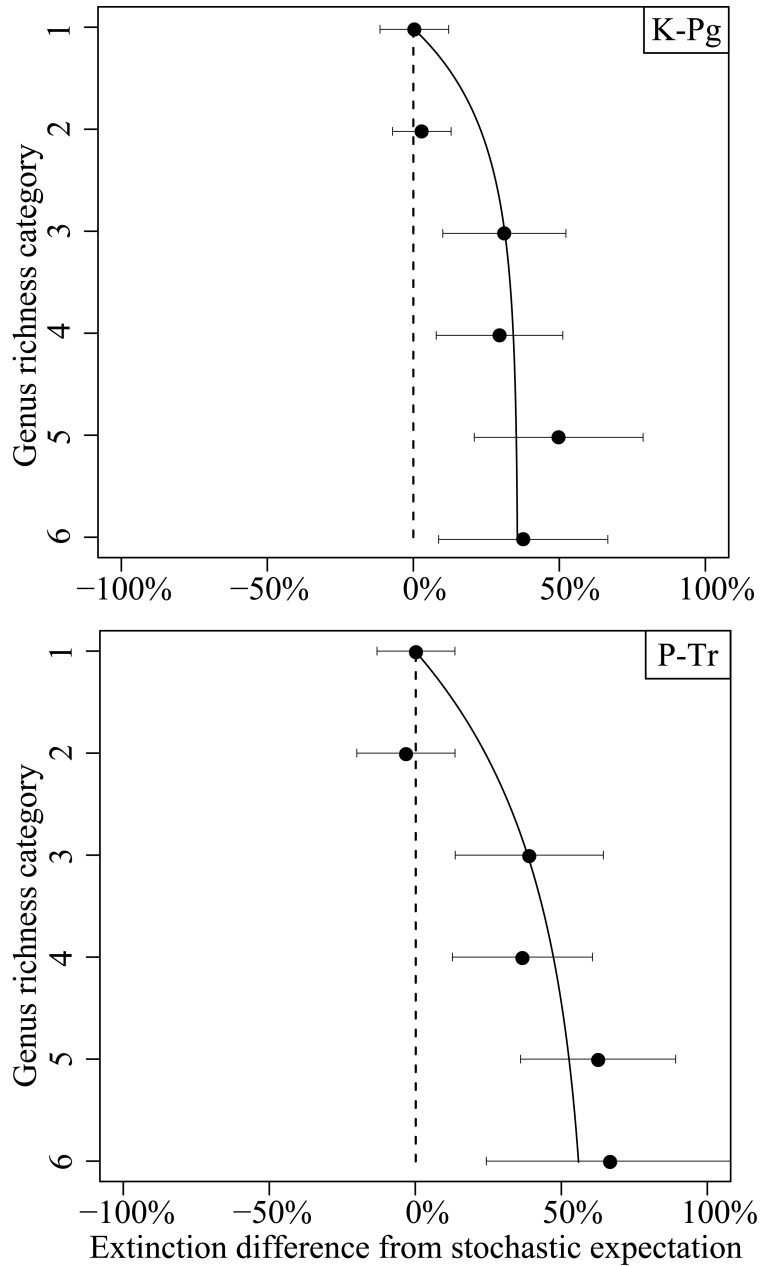
Figure 3.5: Observed extinction rates of families by genus richness category for the K-Pg and P-Tr extinction events (solid circles). Error bars are 95% binomial confidence limits. The dashed line represents the stochastic expectation of extinction. The solid line represents the family extinction expected when extinctions are highly selective. The observed family extinctions fall very close to the expectation for a highly selective extinction event.

selectivity or regional selectivity (Janevski and Baumiller, 2009). Yet the *LR* approach was able to show that there is little evidence that regional selectivity is the primary contributor to selectivity at the P-Tr and K-Pg extinction events (Fig. 3.3). One general rule for these mass extinctions may be general homogeneity of geographic extinction rates. Untested possibilities are that strong ecological trait selectivity or high global extinction intesnity increases geographic extinction rate homogeneity.

The results presented in Figure 3.2 do not appear to be a product of taxonomic practice. While I considered here the extinction of genera as a function of their number of constituent species, the analysis can be easily extended to higher taxonomic levels (e.g., genera within families) with similar predictions. The results at this higher taxonomic level are qualitatively similar (Fig. 3.5). Further, by employing species I was able to show that species richness of genera differs from other traits of genera by having opposite predictive expectations when extinction is selective. In fact, when species richness fails to buffer against the extinction of genera, it may be inferred that there was strong extinction selectivity operating at the species level for other traits.

Further, when species richness fails to predict survivorship of genera it is not evidence that the rules of selectivity have changed (Jablonski, 1986, 2005). Instead, it may suggest that the extinction event was an increase in both intensity and selectivity of extinction, under the same or alternative rules of selectivity from those that operated during background times. If mass extinctions subject species to a unique selective regime, discovery of the traits on which selectivity operated may be hampered by a bias toward looking for traits that typically contribute to selectivity during normal background times, when most extinction has occurred. While the evidence for selectivity demonstrated here does not rule out a change in selective regime for the P-Tr and K-Pg mass extinctions, it does suggest that these two mass extinctions were highly selective.

3.7 Acknowledgments

CHAPTER IV

Paleozoic to post-Paleozoic crinoid phylogeny and the Permian-Triassic extinction event

4.1 Abstract

The first phylogeny of Paleozoic to post-Paleozoic crinoids found via numerical phylogenetic methods is proposed. Phylogenetic analysis is based on 51 species and 39 binary and multistate morphological characters. The monophyly of post-Paleozoic crinoids is supported, and retention of the subclass Articulata to describe this clade is recommended. The work expanded on previous attempts to ascertain relationships of Paleozoic to post-Paleozoic crinoids, in particular by the inclusion of diverse Mesozoic crinoid species. Further work should expand on the character matrix, in order to counter the apparent rampant homoplasy among crinoids, and to better ascertain relationships among species. Discovery of less fragmentary late Permian crinoid specimens may shed further light on the origin of the Articulata. The phylogenetic analysis helps shed light on extinction intensity and selectivity at the Permian-Triassic extinction event. At present it appears likely that crinoid diversity was reduced by the end of the Guadalupian epoch, which calls into question the use of crinoid extinction as evidence for or against extinction selectivity at the Permian-Triassic extinction event. However, the earliest post-Paleozoic crinoids share biological characteristics, includ-

ing small size, capacity for mobility, and adaptation to soft substrates, which may have aided survival during the extinction event.

4.2 Introduction

There are approximately 600 living species of crinoids (Hess and Ausich, 1999), and all are assigned to the subclass Articulata Miller 1821 (e.g., Simms et al., 1993). Articulata is one of five crinoid subclasses and the only one thought to have survived the Permian-Triassic (P-Tr) extinction event (Simms, 1999). Articulata has often been used to refer to post-Paleozoic crinoids, implying that the latter form a monophyletic clade. However, monophyly for post-Paleozoic crinoids has not been demonstrated using numerical phylogenetic analysis. Some of the most important unresolved questions in crinoid evolutionary history are whether or not post-Paleozoic crinoids are monophyletic and the identity of the sister taxa to their most recent common ancestor(s).

In order to understand the intensity of an extinction event, one must know how many lineages survived it. For example Jeffery (2001) calculated the intensity of the Cretaceous-Paleogene extinction event on heart urchins and found that extinction was dramatically lower than previously thought when true lineage extinction and pseudoextinction is taken into account in a phylogenetic context. At present it is unknown how many crinoid lineages survived the P-Tr extinction event. If a single crinoid lineage survived the P-Tr extinction event and gave rise to all post-Paleozoic crinoid diversity, this seemingly improbable scenario would lead to important questions: was the demise of all other crinoid higher taxa due to bad luck resulting from the dramatic loss of species, or were the extinct lineages selected against due to possession of particular attributes (e.g., ecological traits, biogeographic distribution)? Or was the lineage that survived especially adapted for the conditions that characterized the late Permian? If multiple lineages survived, did this occur because of shared char-

acteristics? In order to understand selectivity during the extinction event, one must know the characteristics of the lineages that survived. Both extinction selectivity and intensity can be better understood within the context of a phylogeny of Paleozoic and post-Paleozoic taxa.

Here I present a phylogenetic analysis based on an unpublished, species-level morphological character matrix focused on late Paleozoic crinoids (Holterhoff and Baumiller, 1996). The matrix was expanded by the inclusion of multiple post-Paleozoic crinoid species, covering many major Triassic crinoid higher taxa, to determine if there was a single common ancestor for post-Paleozoic crinoids. This analysis builds on previous attempts at reconstructing crinoid phylogeny across the P-Tr boundary. The analysis sheds further light on the frequent homoplasy within clearly unrelated crinoid lineages (Simms and Sevastopulo, 1993), and represents a step toward a comprehensive crinoid phylogeny using many diverse characteristics for evaluating systematics rather than relying on the presence of one or a few traits to define clades. Further, I discuss issues revealed on the measurement of extinction intensity and inference of extinction selectivity for the P-Tr extinction event using published taxonomic databases, in particular the low number of late Permian crinoid lineages.

4.2.1 Previous cladistic analyses

Since the last major consideration of crinoid phylogenetic systematics across the P-Tr boundary (Simms and Sevastopulo, 1993), it has been accepted that post-Paleozoic crinoids are monophyletic and may be taxonomically placed in the Articulata (e.g., Simms, 1999; Brower, 2007). Common usage of the Articulata has excluded all or most Paleozoic crinoids, and included all post-Paleozoic crinoids, which implies that post-Paleozoic crinoids are derived from a single common ancestor (the P-Tr extinction event survivor). However, this relationship has not been established through a numerical phylogenetic analysis. Simms and Sevastopulo (1993) proposed a phylogeny

relating Paleozoic crinoids to post-Paleozoic crinoids. They developed a morphological character and taxon matrix of 14 taxa of subclass to genus taxonomic rank and scored them for 9 binary and multi-state morphological characters. They inferred evolutionary relationships among the taxa. However, inferring phylogeny without computational methods is unlikely to reveal the best- supported trees (14 taxa give $> 3 \times 10^{11}$ possible unrooted trees, and more than an order of magnitude more rooted trees). In applying Bayesian tree inference to their data matrix, I have confirmed support for monophyly of post-Paleozoic crinoids in their data (Fig. 4.1). However, this relationship is upheld with low posterior probability (31%).

The analysis by Simms and Sevastopulo (1993) was a major step toward a resolved crinoid phylogeny across the P-Tr boundary. However, the analysis had some limitations. For example, the relatively small numbers of taxa and characters in their analysis, 14 and nine, respectively, and the choices of specimens and characters, do not allow for a comprehensive exploration of phylogeny. Figure 4.1 shows the clade uniting the post-Paleozoic genera. However, the analysis includes only three post-Paleozoic crinoid genera. Given the high diversity of crinoids in the Middle Triassic (Hagdorn, 2010), it must be determined if some had independent roots in the Paleozoic. Additionally, terminal taxa were of differing taxonomic rank, from genus to subclass level. It has been argued on philosophical and practical grounds that species are superior as terminal taxa (Prendini, 2001). And it has been shown that supraspecific taxa can alter inferred phylogenetic relationships relative to a species-level analysis (Bininda-Emonds et al., 1998). A species-level analysis avoid these problems as well as any that may arise from using taxa of differing rank (e.g., the need to first establish monophyly of the higher taxa used as terminals).

Systematists now generally accept that post-Paleozoic crinoids are derived from one or more lineages of the ampelocrinids, Family Ampelocrinidae Kirk 1942, with some authors referring to the putative ancestors as stem-group articulates (Simms and
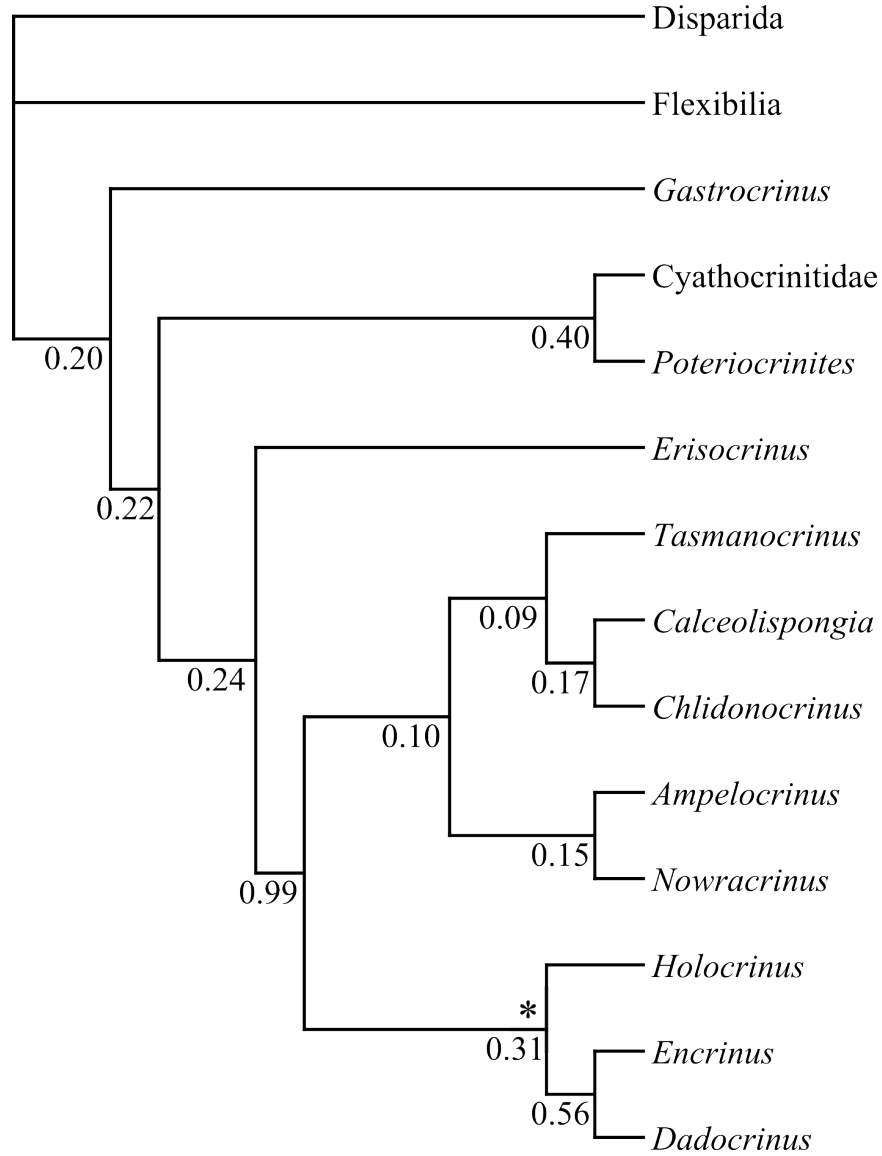
Figure 4.1: Consensus tree based on data matrix of Simms and Sevastopulo (1993) showing all compatible groupings found via Bayesian analysis (100,000 generations, sampled every 10 generations, burnin of first 2500 trees discarded). The numbers are the posterior probabilities of the Bayesian analysis. * indicates the clade of post-Paleozoic crinoids (subclass Articulata).

Sevastopulo, 1993) or proto-articulates (Holterhoff and Baumiller, 1996). Figure 4.1 shows strong evidence for this relationship with high posterior probability (0.99). However, with relatively few ampelocrinids in the phylogeny, Figure 4.1 is ultimately unsatisfying because post-Paleozoic crinoids may have descended from multiple lineages of ampelocrinids. They would appear to have branched subsequent to the P-Tr extinction event in the absence of taxa that are more closely related to their multiple ancestral lineages. To remedy this problem, Holterhoff and Baumiller (1996) began an expanded phylogenetic analysis with wide taxonomic coverage of ampelocrinids (33 species). Their unpublished morphological character matrix for late Paleozoic crinoids assessed relationships of late Paleozoic to post-Paleozoic crinoids, with preliminary parsimony analyses suggesting monophyly for post-Paleozoic crinoids (Holterhoff and Baumiller, 1996). However, as in Figure 4.1, their analysis also suffered from few post-Paleozoic taxa (two of 21 genera analyzed).

The earliest preserved major radiation of post-Paleozoic crinoid species took place in present-day Europe during expansion of the Tethys Ocean (Hagdorn, 1995). These crinoids rebounded from the lows of the late Permian and Early Triassic, and diversified dramatically with Middle Triassic crinoids attaining a diversity of 33 diagnosed fossil genera in 16 families and five orders (Hagdorn, 2010). To determine if any of these taxa had independent roots in the Paleozoic, they must be included in a phylogenetic analysis together with their potential ancestors. In order to create this more comprehensive analysis and to test whether post-Paleozoic crinoids are monophyletic, early Mesozoic crinoids were studied and added to the character-taxon matrix of Holterhoff and Baumiller (1996). Morphology was scored for exemplars of sixteen Triassic crinoid species representing the taxonomic diversity of the group. The current analysis provides greater comprehensiveness than previous P-Tr phylogenetic analyses for crinoids by adding coverage of Triassic crinoids in order to demonstrate if they originated from a single common ancestor.

4.2.2 Taxonomic debate

In recent years a new interpretation of the Articulata has arisen with the observation that as the taxon was originally described (Miller, 1821), numerous Paleozoic crinoids can be diagnosed as articulates (Webster and Jell, 1999). Simms and Sevastopulo (1993) made the same observation; however, they preferred to retain the Articulata to refer to the monophyletic clade of post-Paleozoic crinoids, in the sense that most authors had come to refer to articulates. They redefined the Articulata based on the presence of a cup with no anal plate and an enclosed entoneural system with one or two axial canals in the radials and brachials. Using the presence of syzygial paired brachials (syzygial pairs) as the defining characteristic of crinoids, Webster and Jell (1999) instead chose to regard numerous Paleozoic crinoids as articulates. Most recently this redefinition has resulted in the inclusion of the Middle Devonian genus *Logocrinus* Goldring 1923 in the Articulata, which extends the stratigraphic range of the subclass 140 Ma deeper in time (see Webster and Lane, 2007, for discussion). No full evaluation of the distribution of syzygial pairs among Paleozoic taxa has taken place and no cladistic analysis of these putative articulates has been completed. It is thus unclear if syzygial pairs unite a monophyletic clade, or if such a clade should constitute a revised usage of the taxon Articulata.

Table 4.1: Taxon list with primary references and time period of occurrence.

Taxon	Primary Reference	Period
Encrinus liliiformis	Lamarck 1801	Triassic
Pentacrinites briareus	Miller 1821	Jurassic
Millericrinus milleri	Schlotheim 1823	Jurassic
Dadocrinus gracilis sp. 1	von Buch 1845	Triassic
Dadocrinus kunischi	Wachsmuth and Springer 1886	Triassic
Encrinus aculeatus	von Meyer 1851	Triassic
Encrinus robustus	Assmann 1926	Triassic
Chelocrinus schlotheimi	von Quenstedt 1835	Triassic
Holocrinus acutangulus	von Meyer 1847	Triassic
Holocrinus dubius	Goldfuss 1831	Triassic
Traumatocrinus caudex	von Dittmar 1866	Triassic
Dadocrinus gracilis sp. 2	von Buch 1845	Triassic
Encrinus brahli	Overweg 1971	Triassic
Somphocrinus mexicanus	Peck 1948	Triassic
Carnallicrinus carnalli	von Beyrich 1856	Triassic
Apiocrinites rotundus	Miller 1821	Triassic
Corythocrinus insculptus	Kirk 1946	Carboniferous
Armenocrinus tenuidactylus	Worthen 1882	Carboniferous
Aesiocrinus deliculatus	Lane and Webster 1966	Permian
Aesiocrinus francisensis	Strimple and Moore 1971	Carboniferous
Aesiocrinus harii	Miller and Gurley 1890	Carboniferous
Aesiocrinus magnificus	Miller and Gurley 1890	Carboniferous
Allosocrinus bronaughi	Strimple 1949	Carboniferous
Allosocrinus ivanovi	Yakovlev and Ivanov 1956	Carboniferous
Ampelocrinus mundus	Kirk 1942	Carboniferous
Ampelocrinus kaskaskiensis	Kirk 1942	Carboniferous
Armenocrinus watersi	Strimple and Horowitz 1971	Carboniferous
Belashovicrinus ghzelensis	Arendt and Zubarev 1993	Carboniferous
Calceolispongia sp.	Teichert 1949	Permian
Cambellicrinus compactus	Jell and Willink 1993	Permian
Chlidonocrinus echinatus	Strimple and Watkins 1969	Carboniferous
Chlidonocrinus ornatus	Strimple and Moore 1971	Carboniferous
Cymbiocrinus cherribunensis	Unknown	Permian
Cymbiocrinus grandis sp. 1	Kirk 1944	Carboniferous
Cymbiocrinus grandis sp. 2	Kirk 1944	Carboniferous
Cymbiocrinus gravis	Strimple 1951	Carboniferous
Jimbacrinus bostocki	Teichert 1954	Permian
Moundocrinus luxuris	Strimple 1951	Carboniferous
Moundocrinus osagensis	Strimple 1939	Carboniferous
Moundocrinus patens	Unknown	Carboniferous
Nowracrinus ornatus	Willink 1979	Permian
Oklahomacrinus loebelichi	Moore 1939	Carboniferous
Oklahomacrinus spicatulus	Strimple and Watkins 1969	Carboniferous
Oklahomacrinus supinus	Moore 1939	Carboniferous
Paracymbiocrinus ormandi	Burdick and Strimple 1973	Carboniferous
Paragassizocrinus caliculus	Moore and Plummer 1938	Carboniferous
Paragassizocrinus tarri	Strimple 1938	Carboniferous
Polusocrinus amplus	Lane and Webster 1966	Permian
Polusocrinus avanti	Strimple 1951	Carboniferous

Taxon	Primary Reference	Period
Polusocrinus ochelataensis	Strimple 1952	Carboniferous
Proallosocrinus glenisteri	Moore and Strimple 1973	Carboniferous

4.3   Materials and Methods

Holterhoff and Baumiller (1996) assembled a morphological character matrix based on late Paleozoic crinoids that assessed relationships of crinoids across the P-Tr boundary with preliminary parsimony analyses suggesting monophyly for post-Paleozoic crinoids. A modified version of Holterhoff's morphological characters was the basis for the present analysis (Appendix B contains a list of character and state descriptions). For consistency in coding, cup shape characters were reduced in the number of states and defined based on measurements. Character states that did not occur were removed. Characters that could not be reliably coded were removed from the analysis. Character states were recoded to reflect inferred evolutionary polarity. The data matrix was expanded to include more thorough coverage of Triassic crinoid diversity (Table 4.1, with seven Triassic families represented. This resulted in a matrix of 51 species scored for 39 morphological characters (Appendix C).

Bayesian tree inference was completed with MrBayes v.3.1.2 (Ronquist and Huelsenbeck, 2003). MrBayes was used because strength of nodes could be easily assessed using posterior probabilities. Bayesian analysis was run using the Mk model of Lewis (2001) for 2,000,000 generations with a sampling frequency every 10 generations. A "burnin" of 50,000 was used to remove the first 25% of trees, and thus achieve stable likelihood values . A consensus tree of all compatible groupings was generated from the 150,000 remaining trees.

Currently, MrBayes allows specification of only a single outgroup. However, other outgroup choices were investigated to determine the effect on post-Paleozoic

crinoid monophyly (Appendix B). Numerous exploratory analyses were run with post-Paleozoic species iteratively removed in order to determine if their presence or absence had an effect on post-Paleozoic crinoid monophyly. To confirm basic tree topology, parsimony analyses were also run in PAUP* v. 4B10 for Windows. Heuristic searches were run using the tree bisection-reconneciton (TBR) search algorithm. The effect on overall tree topology of outgroup choice was also investigated by selecting multiple outgroups in parsimony analyses.

4.4 Results

Bayesian tree inference on the full data matrix shows high posterior probability for a single clade uniting post-Paleozoic crinoids (81%, Fig. 4.2). The lineage leading to post-Paleozoic crinoids appears as a sister taxon to a clade that unites most of the remaining ampelocrinids, though posterior probability for this relationship is low. Relatively high posterior probability is also shown for a clade uniting all ampelocrinids, with the genus *Ampelocrinus* Kirk 1942 as sister taxon to the clade that unites ampelocrinids and post-Paleozoic crinoids. The remaining ampelocrinids form a clade that is sister taxon to post-Paleozoic crinoids, implying a relatively ancestral divergence for the ancestor of post-Paleozoic crinoids.

Heuristic searches in PAUP* produced four equally parsimonious trees, all with 287 steps. A strict consensus of the equally parsimonious trees shares the major topological features with the phylogeny inferred form bayesian methods (Fig. 4.2), including a monophyletic clade of post-Paleozoic crinoids. Topological differences were few and occurred only at nodes that have low posterior probability in Figure 4.2. Because the primary goal of this study was to test whether post-Paleozoic crinoids monophyletic, and because the parsimony analysis confirmed the presence of this clade, for simplcity the strict consensus tree is not shown here. The Bremer support for the clade of post-Paleozoic crinoids is two. The consistency index (CI) is 0.26
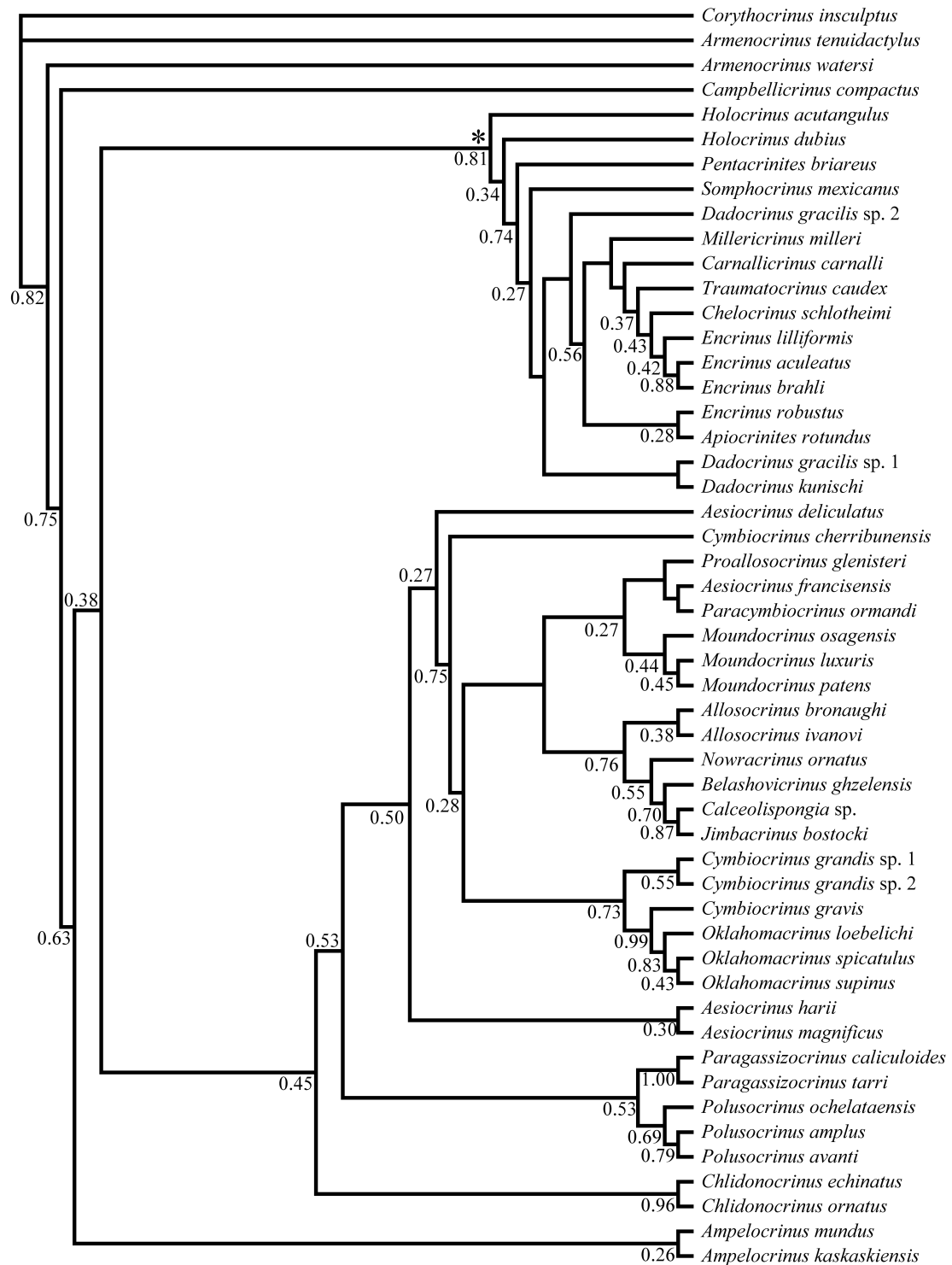
Figure 4.2: Consensus tree found via protocol described in text. The numbers are the posterior probabilities of the Bayesian analysis (> 25% shown). * indicates the clade of post-Paleozoic crinoids (subclass Articulata).

and the retention index (RI) is 0.70. A high RI with low CI has been interpreted in echinoids as evidence that once acquired, clades tend to retain characters (high RI), but that individual characters often have reversals (low CI) (Kroh and Smith, 2010).

Alternative outgroup choices did not substantially alter tree topology. The post-Paleozoic crinoid clade was retained when using alternative outgroups in MrBayes, and when multiple outgroups (Appendix B) were used in parsimony analyses .

This analysis includes some derived Jurassic species of familes that are thought to have originated in the Triassic (e.g., Pentacrinitidae Gray 1842 and Millericrinidae Jaekel 1918), for which complete Triassic specimens are rare or unknown. The Jurassic species may have descended from lineages that were present in the Triassic, based on described disarticulated elements (Hagdorn, 1995), and were thus included to add comprehensiveness to the analysis. These highly derived taxa, having expanded into and reoccupied morphospace not occupied by Triassic crinoids, could lower overall support for post-Paleozoic crinoids by adding homoplasy. However, iterative analyses with the removal of these taxa did not alter overall tree topology found in MrBayes. Their inclusion consistently raised posterior probability for the clade uniting post-Paleozoic crinoids. These species are part of the monophyletic clade that descended from a single surviving P-Tr boundary-crossing crinoid lineage.

The phylogenetic analysis supports monophyly for many named fossil genera (Fig. 4.2), often with high posterior probability. Additionally, structure revealed by the data includes a biogeographic and temporal clustering of some species, discussed further below.

4.5   Discussion

The major goal of this analysis was to add Triassic crinoid diversity to a phylogenetic analysis that includes the Paleozoic ancestors of post-Paleozoic crinoid species in order test whether post-Paleozoic crinoids are monophyletic. Phylogenetic infer-

ence through both bayesian (Fig. 4.2), and heuristic parsimony searches, support the hypothesis that a single clade unites all post-Paleozoic crinoids. Although posterior probability for the clade of post-Paleozoic crinoids is high, Bremer support is low, making the support for the clade somewhat equivocal. The relatively low number of characters in the analysis, and the high homoplasy revealed by the low CI, likely explain the low Bremer support.

Crinoids are prone to homoplasy (Ausich, 1998; Kammer, 2008), and also suffer from character exhaustion (Wagner, 2000), both of which may be problems for a study such as this one, which covers a long span of geologic time. Character exhaustion refers to the observation that new character states are not added continuously throughout clade history, and that intrinsic biological constraints or repeated selection for particular states increases the tendency to homoplasy over the course of clade history. Characters that are sometimes convergent, such as biserial appendages, should not be excluded from phylogenetic analyses. Some characters may be locally informative, though known to be homoplasious over a larger clade in a phylogenetic analysis: i.e., biseriality does not unite all crinoids with biserial appendages, but it appears to unite the encrinids among articulates. A choice could be made to code such characters as uniquely derived where the evidence is clear, but careful study of such traits should be undertaken to demonstrate convergence. For example, stalk loss in adult crinoids has occurred repeatedly in separate crinoid lineages, creating superficial similarity among unrelated crinoid lineages, e.g., *Paragassizocrinus* Moore and Plummer 1940 and members of the Comatulida Clark 1908a, with the latter truly stalkless as the centrodorsal represents fused columnals (Simms, 1988a). A character matrix coded for "stalk presence/absence" would clearly not indicate homology in this case. Coding each of these stalk-loss events as unique characters could reduce potential homoplasy present in analyses that instead remain entirely agnostic about character homology. The widespread presence of other characters thought to be con-

vergent in crinoids further suggests the need for such careful homology assessments (Simms and Sevastopulo, 1993).

The phylogeny supports monophyly of many crinoid genera, and also some traditional crinoid higher taxa. For example, the Australian taxa *Nowracrinus ornatus* Willink 1979, *Calceolispongia sp.* Teichert 1949, *Jimbacrinus bostocki* Teichert 1954, along with the Russian *Belashovicrinus ghzelensis* Arendt and Zubarev 1993, form a clade with high posterior probability. This clade is a sister taxon to *Allosocrinus* Strimple 1949, and these two clades (though not *Belashovicrinus ghzelensis*) are currently united in Calceolispongidae Teichert 1954 by Webster and Jell (1999). Thus the phylogeny upholds this traditional classficiation, and suggests that *Belashovicrinus* may also belong in Calceolispongidae.

However, caution should be exercised in interpreting relationships from the phylogeny presented here where posterior probability is low (e.g., $< 50\%$). For example, Figure 4.2 suggests that members of the genus *Encrinus* Lamarck 1801 are polyphyletic, but only weak posterior probability supports this topology. This situation could almost certainly be resolved by considering additional characters of phylogenetic relevance for the derived encrinids and other derived post-Paleozoic taxa. The original character matrix was based on Paleozoic crinoids, and the post-Paleozoic crinoids have been added to this analysis without full consideration of characters that might help resolve post-Paleozoic relationships. Adding these characters would require a full re-assessment of the Paleozoic species studied by Holterhoff and Baumiller (1996), which is beyond the scope of the present study. Importantly, adding these characters without re-studying all Paleozoic species would cause post-Paleozoic species to group together due to the absence of coded characters in Paleozoic taxa. Thus the posterior probability supporting post-Paleozoic crinoid monophyly may be conservative since characters of a stronger post-Paleozoic focus have not been incorporated.

Future work should evaluate more characters that are important for post-Paleozoic crinoid systematics, and the distribution of those characters in Paleozoic crinoids. For example, biserial appendages among members of the Encrinidae Dujardin et al. 1862 are thought to unite these taxa (Hagdorn, 1995). This character was treated as of sufficient importance to have the genus *Encrinus* be the lone post-Paleozoic genus classified with Paleozoic crinoids in the Treatise (Moore et al., 1978). However, this taxonomic assignment to the Erisocrinacea Wachsmuth and Springer 1886 ignored other characters of the Encrinidae, such as the first arm branching on primibrach 2, rather than primibrach 1, which is found in Erisocrinacea. This example clearly shows the importance of comprehensive phylogenetic analyses and character selection instead of reliance on single characters for taxonomic assignment. Encrinids have a suite of highly derived traits, yet this most diverse family of Triassic crinoids convergently attained a Paleozoic aspect in some traits. Furthermore, recent work on encrinids has demonstrated a trend toward biseriality among more derived encrinids (Hagdorn, 2010), which suggests that this trait was actively being selected for and of recent acquisition among encrinids. Additional characters of post-Paleozoic crinoid species would help determine the relationships of these taxa, and these may also one day be aided by molecular phylogenetic approaches as the phylogenetic split of many extant crinoids is thought to have occurred in the Triassic (cf. Simms, 1999, fig. 61).

All post-Paleozoic crinoids have the entoneural system enclosed within the cup and arms, resulting in radials and brachials pierced by at least one entoneural canal. There is usually a single radial canal, but there are dual canals in Early Triassic crinoids, such as the holocrinids (Family Holocrinidae Jaekel 1918) and dadocrinids (Family Dadocrinidae Lowenstam 1942) and many ampelocrinids (Simms and Sevastopulo, 1993). However, even among the encrinids, a single canal may be found in some brachials, and occasionally the developmental progression toward a single canal is shown by a peanut-shaped single canal representing the merger of two canals. As

advocated by Simms and Sevastopulo (1993), entoneural canals may be a character of phylogenetic utility for future analyses. This was beyond the scope of the present study as it would require a full reassessment of disarticulated material of the previously studied Paleozoic crinoids, as articulation surfaces of brachials and radials are rarely described or figured in publications on Paleozoic crinoids which often show the most complete crowns.

Post-Paleozoic crinoids are united by the presence of distinctly outward-sloping radial muscular articulations and the absence of an anal plate from the cup. Other characters are frequently shared among many of the species, but have undergone loss or reversal in derived members of the clade. The presence of an anal plate in juveniles of post-Paleozoic crinoids, as well as in two aberrant, adult specimens of post-Paleozoic species that typically lack anal plates as adults (Simms and Sevastopulo, 1993), provides evidence that this plate was lost in the ancestor to post-Paleozoic crinoids. Character loss has been treated with some skepticism by some phylogeneticists (Sereno, 2007). It has been claimed via a complex, epistemological argument that character loss is not useful as a concept in phylogenetic reconstruction (Fitzhugh, 2008). Fitzhugh presents an example of legless lizards and argues that rather than treating legs as an absent or lost character, the species could instead be coded as having smooth body margins. An analog in the present analysis is that taxa with no anal plate could have been coded as having a cup with perfect pentaradiate symmetry. Such a coding strategy would not alter the phylogenetic results presented here.

Anal plate loss has occurred in lineages of Paleozoic crinoids that are not closely related to post-Paleozoic crinoids (Simms and Sevastopulo, 1993). Among advanced cladids there is often a reduction of anal plate size and number; however, complete loss is not known in any species (Kammer, 2008). It is possible that this tendency toward reduction could have produced a polyphyletic group of post-Paleozoic crinoids, if mutiple lineages of ampelocrinid ancestors underwent parallel evolution of anal plate

loss. This would imply ancestry of the articulates from within a relatively closely related few species, and is a hypothesis to be tested in future work.

Reduction in the number of anal plates in advanced cladids to one plate has been associated with traits that lead to relatively paedomorphic adult crinoids (Kammer, 2008). Complete loss of anal plates could also be a product of increased paedomorphosis in post-Paleozoic crinoids. This applies in particular to the Early Triassic holocrinids and dadocrinids, which are very small. These taxa may represent additional evidence for the Lilliput effect, reduction in average body size, that may have characterized other benthic marine invertebrates at the P-Tr extinction event (Twitchett 2007; see Brayard et al. 2010 for an exception to the Lilliput effect).

4.5.1 Extinction selectivity

It is unclear whether crinoids suffered extinction selectivity at the P-Tr extinction event. It has been suggested that crinoids were part of a heavily skeletonized group of marine invertebrates that suffered preferential extinction at the P-Tr extinction event due to hypercapnia (Knoll et al., 2007). The hypercapnia hypothesis suggests that elevated levels of dissolved CO_2 in oceans led to increased stress on animals that precipitate carbonate skeletons, with some evidence that animals with larger carbonate requirements experienced elevated extinction rates (Knoll et al., 2007, Table 1) The relatively small size of the Early Triassic crinoids accords with this hypothesis.

Post-Paleozoic crinoids are notable for their motility, in particular crawling and swimming, which contrasts with the likely more sessile Paleozoic crinoids (Baumiller et al., 2010). However, the presence of traits that allow crawling (muscular articulations with transverse ridge acting as fulcrum in the arms, cirri with transverse ridge fulcrums along the stalk, and lack of permanent attachment) is seen in some Paleozoic crinoids, with the P-Tr extinction event representing a transition in the relative diversity dominance of motile and sessile species (cf., Baumiller, 2008, fig.

12). Ampelocrinids are included within the group of potentially crawling Paleozoic crinoids. *Holocrinus* Wachsmuth and Springer 1886 was likely capable of stalk autotomy, may have had the ability to crawl, to relocate, and with its cirri would have been capable of reattachment (Baumiller and Hagdorn, 1995). The outward sloping radial muscular articulations that characterize post-Paleozoic crinoids may have a functional explanation. The reorientation of radial articular faces outward in post-Paleozoic crinoids may have been an adaptation for motility in crinoids around the time of the P-Tr extinction event. *Holocrinus* was well-adapted for soft substrates, but had no obvious functional features that would have prevented it from also living on hard substrates. *Dadocrinus* von Meyer 1847, which lacked cirri and possessed a holdfast, likely did not locomote as an adult. Nonetheless, it has been argued that *Dadocrinus* tended to live on soft substrates where they attached to other individuals or to bivalves (Hagdorn, 1996). Adaptation to a wide range of substrate types may have affected crinoid survival at the P-Tr boundary.

However, whether the putative Lilliput effect, the proposed hypercapnia cause of extinction, motility behavior or substrate adaptation affected survivorship of crinoids is unresolved due to the poorly known late Permian crinoid record. Testing for extinction selectivity in crinoids at the P-Tr boundary is difficult due to the equivocal diversity pattern for crinoids across the P-Tr boundary. A full assessment of taxonomic diversity for crinoids is needed, as most analyses rely on the range-based Sepkoski database (Sepkoski, 2002, accessible at http://strata.geology.wisc.edu/jack/start.php). The database contains no crinoids in the earliest Triassic Induan stage, and only two genera in the Tatarian, which is equivalent to the Wuchiapingian and Changhsingian stages of the late Permian. It is unclear if these assignments are accurate, as the genus *Cymbiocrinus* Kirk 1944 is only known from the Mississippian, while the genus *Neocamtocrinus* appears to be a nomen dubium for *Neocamptocrinus* Willink 1980, which is an early Permian genus. The late Permian record of crinoids is so

depauperate that it is highly plausible that crinoids actually suffered nearly complete extinction at the end-Guadalupian extinction instead of at the P-Tr boundary.

4.5.2   Paleozoic ghost lineage and fragmentary late Paleozoic taxa

The phylogeny in Figure 4.2 implies an early divergence of post-Paleozoic crinoids. By calibrating the phylogeny against the stratigraphic record of crinoid genera, a very long ghost lineage is shown in the lineage leading to post-Paleozoic crinoids (Fig. 4.3). Post-Paleozoic crinoids, which generally lack a large, tightly sutured calyx that is common in many Paleozoic crinoids, may suffer from relatively low preservation probabilities. Lower preservation probablity also may have affected their Paleozoic ancestors. The small body size of early post-Paleozoic crinoids may imply that their Paleozoic ancestors were similarly small, which also may have affected their preservation potential. Relatively poor preservational potential may have led to the ghost lineage in Figure 4.3.

Alternatively, the absence of late Paleozoic sister taxa to post-Paleozoic crinoids may be due to the spotty nature of the crinoid fossil record. The relatively complete crinoid specimens that are required for species-level diagnoses and that are useful in systematics research are recovered from particular basins, at particular times. Most late Paleozoic crinoids are described from modern day North America, many Permian crinoids from Australia, and most post-Paleozoic crinoids from Europe. Although a full consideration of biogeography is beyond the scope of this study, the previously-discussed evidence for a clade of Australian species of Calceolispongidae suggests that closely related species once lived in paleogeographic proximity. The lack of late Paleozoic sister taxa to post-Paleozoic crinoid species that re-diversified in a remote, epicontinental basin of the Tethys Ocean may simply be a product of an absence of fossil record from major regions of the ocean. The possibility of this 'mega-sampling bias' affecting crinoid systematics may be an avenure for future research, and may

have had a greater effect during times of low global biodiversity.

Nonetheless, two poorly preserved late Paleozoic species may help fill the gap in the ghost lineage. Webster and Jell (1999) described *Archaeoisocrinus occiduaustralis*, a poorly preserved, early Permian specimen lacking most of the stalk and arms, and assigned it to the Isocrinidae, which had been previously known only from the Middle Triassic to the Recent. However, Twitchett and Oji (2005) noted that this specimen possesses characters not present in any isocrinids and disagreed with its assignment to the Isocrinidae. Although too fragmentary to be useful in the current phylogenetic analysis, a few features suggest that instead of being an isocrinid, this specimen may be part of the lineage leading to post-Paleozoic crinoids. Dual entoneural canals and first arm branching on the 2nd primibrach are plesiomorphic for post-Paleozoic crinoids and place *Archaeoisocrinus* within the ampelocrinids. Webster and Jell (1999) saw no evidence for an anal plate in the specimen, which would potentially place it as sister taxon to the clade of post-Paleozoic crinoids presented here. Confirmation of this placement would require acquisition of specimens with better preservation; stalk and cirrus articulations may be particularly informative for assessing the relationship to post-Paleozoic crinoids.

Late Permian crinoids are extraordinarily rare. Walter (1953) described fragmentary columnals from the late Permian Rustler Formation of West Texas. Recent field visits to the site have revealed additional disarticulated ossicles with occasional pluricolumnals and pluricirrals. Radials and brachials have been identified, but no complete crowns have been found. As in ampelocrinids and *Archaeoisocrinus*, dual entoneural canals are present in radials and brachials. Columnals appear to be pentalobate. Cirral articulations are of a type not known in any other crinoid species, having a synarthrial and symplexial half at the cirral/cirrinodal articulation. This implies one primary direction of flexure for the cirrus, more evolved for efficient grasping than cirri typical of Paleozoic crinoids, which more frequently are symplexial, though
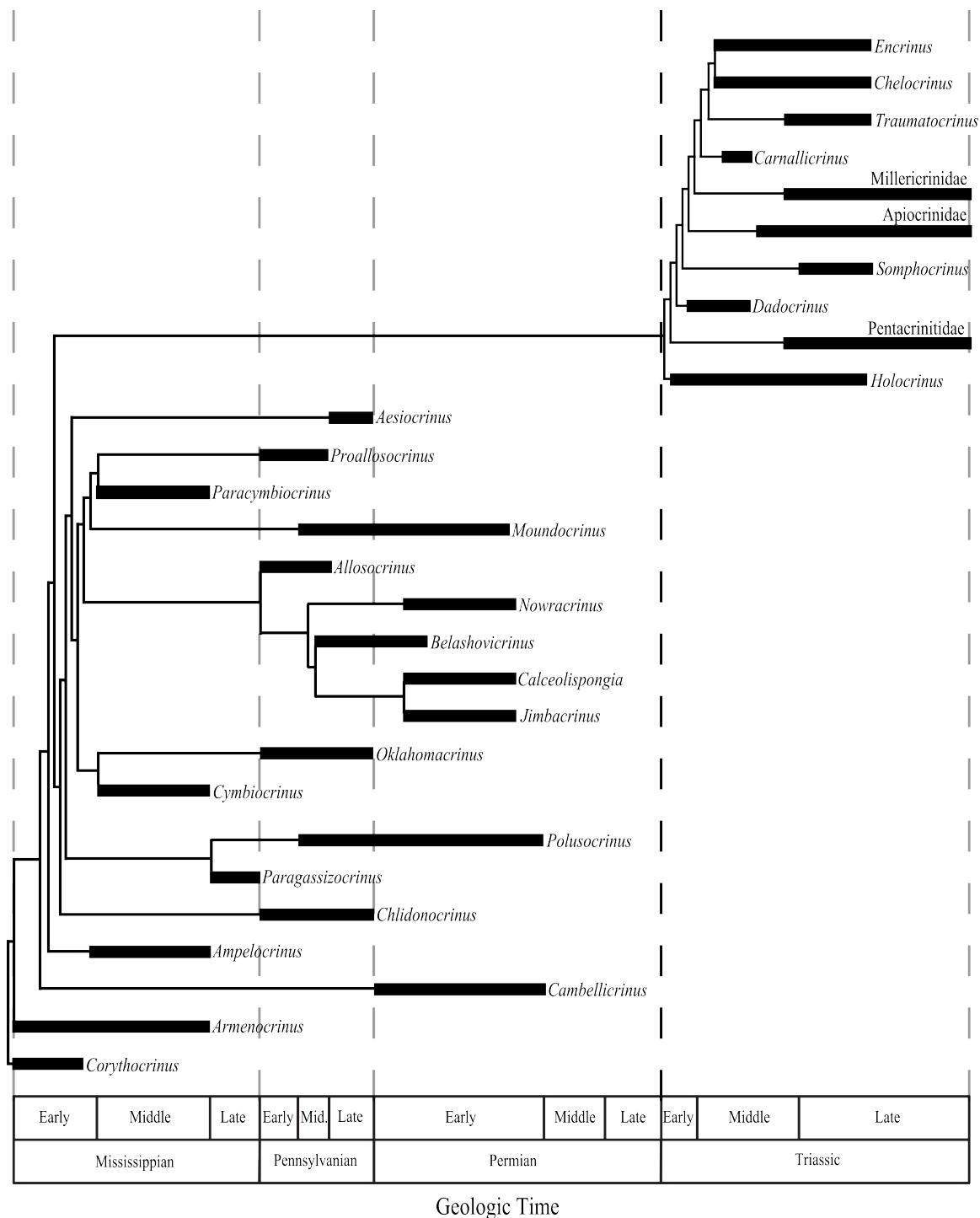
Figure 4.3: Evolutionary tree constructed by calibrating the cladogram shown in Figure 4.2 against the observed fossil record. A small amount of inferred range was added where necessary to show branching relationships. Heavy solid lines = observed fossil record; thin solid lines = inferred missing fossil record; grey dashed lines = period boundaries; black dashed line = era boundary.

synarthrial articulations are present in some ampelocrinids and may have evolved more than once (Simms and Sevastopulo, 1993). This specimen may also lie in a transitional stage from fully symplexial to fully synarthrial cirrus articulations.

Cirri with synarthrial articulations are common in post-Paleozoic crinoids, but cirri may have been secondarily lost in some taxa. The rare presence of vestigial cirri in some encrinids suggests that cirri were lost in this clade (Hagdorn, 2010). Symplexial cirri articulations are found in some post-Paleozoic crinoids, synarthrial cirri articulations are found in some ampelocrinids of the Paleozoic, and the genus *Chlidonocrinus* Strimple and Watkins 1969 has cirri which proximally have synarthrial articulations, and distally are symplexial (Simms and Sevastopulo, 1993). At present, it seems that cirri gain and loss, and the transition from symplexial to synarthrial articulations (and maybe vice versa), is relatively common among crinoids.

4.5.3 Classification

A new classification of crinoids based on preliminary phylogenetic work, particularly where tree support is minimal, is not yet warranted. However, this and other analyses have demonstrated support for a monophyletic clade of post-Paleozoic crinoids. As this relationship continues to be upheld, it is reasonable to refer to this clade by what has become a standard accepted epithet: I recommend that the subclass Articulata be retained in its usage for the clade of post-Paleozoic crinoids.

I caution against reclassifying taxa on the tree presented here, at least where support for clades is not strong. For example, many traditional genera are upheld in the analysis with high posterior probability (e.g., *Oklahomacrinus* [Moore, 1939]), while others are shown to be polyphyletic (e.g., *Aesiocrinus* [Miller and Gurley, 1890]), but with low posterior probability. Where node support is high for traditional classifications greater confidence may be placed on relationships. I also caution against accepting relationships within the Articulata depicted here, especially where posterior

probability is low, until a phylogenetic analysis is completed that contains characters of direct relevance to assessing articulate relationships.

4.6 Conclusion

Numerical phylogenetic analysis demonstrates support for post-Paleozoic crinoid monophyly, despite the frequent homoplasy exhibited by crinoids. Retention of the term Articulata to refer to this monophyletic clade of crinoids is warranted. Future research should include a full consideration of characters of relevance for post-Paleozoic crinoid systematics and the distribution of those characters among Paleozoic crinoids.

A single-survivor lineage is upheld for the P-Tr extinction event. However, crinoid diversity may have been dramatically reduced before the P-Tr boundary, likely at the end-Guadalupian extinction event, with crinoids existing at very low diversity throughout the late Permian. Synoptic studies evaluating the role of extinction selectivity at the P-Tr extinction event should exercise caution in inferring patterns from the crinoid record in current taxonomic databases. Study of new Permian crinoid specimens and description of fragmentary material may improve our understanding of P-Tr extinction selectivity. At present, it is unclear if crinoids suffered preferential extinction among lineages or as a whole group at the P-Tr extinction event.

4.7 Acknowledgments

Could a stalked crinoid swim? A biomechanical model and characteristics of swimming crinoids

5.1 Abstract

Modern stalked crinoids represent a relict fauna of once considerably higher diversity, as seen in their extensive fossil record. Comatulid crinoids, which lack a stalk and dominate modern crinoid diversity, have been interpreted as an evolutionary success story due to the increased mobility afforded by stalk loss. This mobility includes effective crawling and also swimming, often interpreted as anti-predatory escape strategies. Until recently it was assumed that stalked crinoids were incapable of active locomotion, but observations of an extant isocrinid have demonstrated that some can crawl relatively rapidly, perhaps in order to escape from benthic predators. Because the mechanics of crawling in stalked crinoids resemble the mechanics of swimming in comatulids, it is worth investigating whether a stalked crinoid would be capable of swimming. The feasibility of this scenario is tested using a biomechanical model of swimming in a stalkless crinoid and by applying the model to a stalked
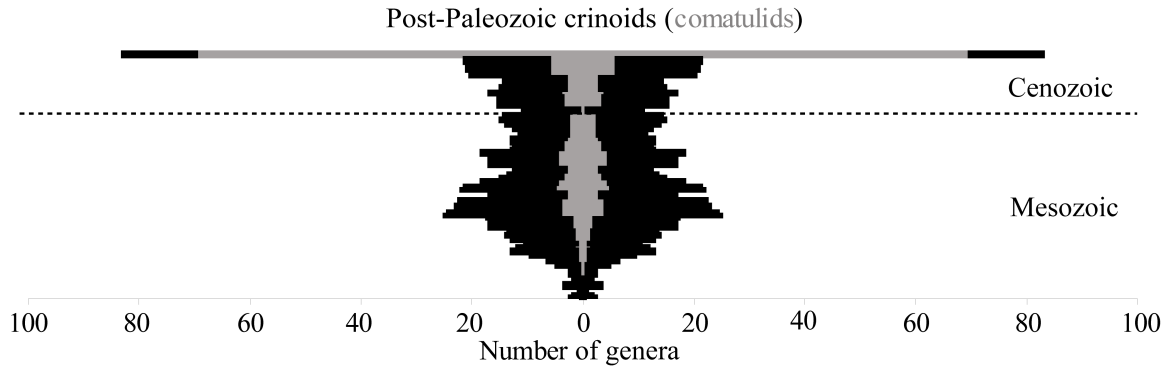
Figure 5.1: Diversity of post-Paleozoic crinoid genera, with the subset of comatulid diversity shown in gray. Note the dramatic increase in comatulid diversity in the Recent.

crinoid. The model demonstrates that the stalk imposes a heavy burden that limits the ability of a stalked crinoid to swim. Evolutionarily this might suggest that stalk loss was a key innovation that facilitated swimming; however, stalk loss alone is not sufficient to allow a crinoid to swim. Swimming would have allowed greater capability for escape from benthic predators than crawling. An evolutionary scenario is considered in which swimming evolved in a stalked crinoid to allow more effective escape from benthic predators subsequent to evolution of rapid crawling, precipitating eventual stalk loss.

5.2   Introduction

Swimming is a rare method of locomotion among extant echinoderm species and was likely rare for echinoderms during the geologic past. Swimming is known in a few deep-sea species of holothurians (Miller and Pawson, 1990) and a handful of ophiuroid species (Hendler and Miller, 1991). It is only among the extant stalkless, comatulid crinoids that swimming is a relatively common capability.

The ability of comatulids to locomote, through crawling and swimming, forms part of the widely cited explanation for modern crinoid diversity; it has long been thought that the comatulids diversified while stalked crinoids declined in diversity

due to the presence of anti-predation adaptations in the former (Meyer and Macurda, 1977). The primary evidence for this interpretation is the contrast between the fossil record of crinoids, often characterized by high diversities of stalked crinoids, and the dominance of stalkless comatulids in modern seas (Fig. 5.1). The decline in stalked crinoid diversity was accompanied by relegation to progressively deeper, offshore environments during the Late Cretaceous-Paleogene (Bottjer and Jablonski, 1988; Oji, 1996), while many stalkless comatulid species thrive in modern shelf environments (Messing, 1997). Given evidence for increased predation during the Mesozoic marine revolution (MMR, Vermeij, 1977, 1987), this provided an explanation for the relative success of comatulids compared to stalked crinoids (Meyer, 1985). The inferred predators were primarily nektonic forms, such as teleost fish, based on the presence of lethal and sublethal damage on crinoids, crinoid material in fish guts, and observed fish attacks on comatulids (Meyer and Macurda, 1977; Meyer, 1985).

The anti-predatory adaptations possessed by stalkless crinoids include relatively rapid crawling and swimming, as well as morphological traits that aid or allow motility, such as increased musculature, reduction of the calyx, and lack of a stalk. Whereas crawling is not rapid enough to escape most nektonic predators, nocturnal activity and refuge seeking during daylight have been interpreted as adaptations against visual hunters such as diurnal fish (Meyer and Macurda, 1977). It is less clear how the slow swimming of stalkless crinoids could provide defense against rapidly swimming nektonic predators like fish. The movement of invertebrates is detectable by predaceous fish using their lateral line systems and swimming could attract predators to the crinoids.

Recent in situ observations on the stalked crinoid, *Neocrinus decorus* Wyville Thomson (Order Isocrinida), taken via submersible, have demonstrated crawling speeds two orders of magnitude greater than previously recorded, $\sim 10 - 30 \frac{mm}{sec}$ (Baumiller and Messing, 2007). Coupled with inferences of cidaroid predation on isocrinids

due to close association and the presence of isocrinid remains in the guts of cidaroids (Baumiller et al., 2008), it is plausible that crawling in isocrinids plays an ecological role as an antipredatory adaptation allowing escape from predators (Baumiller and Messing, 2007), similar to the postulated role of locomotion in comatulids (Meyer and Macurda, 1977; Meyer, 1985; Vermeij, 1987).

In the context of this new evidence for more rapid crawling in stalked crinoids (Baumiller and Messing, 2007), a reexamination of the reason for the success of stalkless crinoids seems warranted. In aquarium experiments, Shaw and Fontaine (1990) elicited swimming behavior in the stalkless crinoid *Florometra serratissima* Clark (Order Comatulida) by contact with benthic predator species (asteroids and actinians), while there was no such response with non-carnivorous species. Mladenov (1983) also observed *F. serratissima* swimming when contacted by the predatory asteroid *Pycnopodia helianthoides* Brandt and when under attack from the crab *Oregonia gracilis* Dana. Therefore, swimming behavior is likely an antipredatory behavior allowing rapid escape from benthic predators.

Given that stalked crinoids have been generally assumed to be sessile but have more recently been shown to be capable of relatively rapid crawling (Baumiller and Messing, 2007), it is worth asking whether their locomotory repertoire could have been even greater and included swimming. We approached this problem biomechanically, by formulating an analytical model of swimming in crinoids based on observations of swimming in the extant comatulid crinoid, *F. serratissima*. The model was first tested on *F. serratissima* and then extended to other crinoids of different morphologies in order to explore whether swimming in a stalked crinoid is feasible.

5.3 Model Development

A model of thrust generation was constructed using hydrodynamic principles and observations of the extant comatulid crinoid *F. serratissima* (Shaw and Fontaine,
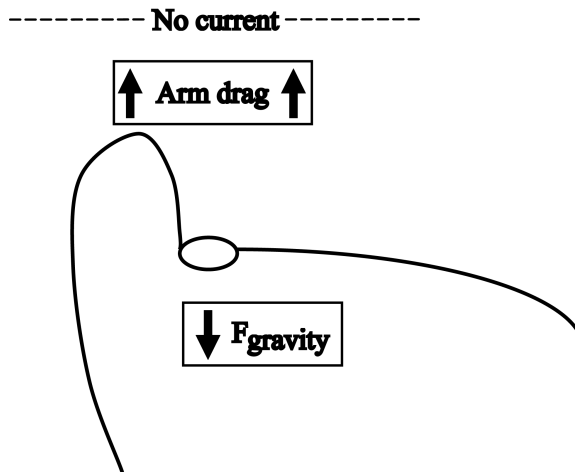
Figure 5.2: Schematic diagram of the drag force exerted by the arms of a swimming crinoid in ambient current with only the vertical component of drag illustrated. The arm on the left is folded close to the calyx in a recovery stroke while the arm on the right is extended in a power stroke.

1990), along with the weight in water (WIW; reported here in grams as a unit of mass, not force) of crinoid specimens from the Smithsonian Institution National Museum of Natural History, Invertebrate Zoology Collections (USNM). For details of comatulid biology see Appendix H.

5.3.1   Swimming, Forces, and Strokes

The definition of swimming adopted here is the capability to generate sufficient thrust to elevate the animal off the seafloor, temporarily transferring it out of the benthic zone. Whereas fluid flow can aid in swimming through contributions to drag or lift (Baumiller, 1992), *F. serratissima* was observed to swim in the absence of currents (Shaw and Fontaine, 1990). Therefore, the animal is capable of producing sufficient upward thrust to allow swimming in the absence of currents and the model ignores any contribution to thrust generation from fluid flow.

Comatulids swim by moving their arms downward in the vertical plane during a power stroke that produces an upward thrust via drag, opposite to the force of gravity (Fig. 5.2). During the power stroke the pinnules extend outward, increase

surface area, and form a paddle oriented perpendicular to the vector of thrust. In the recovery stroke, the pinnules are folded above and onto the arm ambulacra, reducing paddle surface area and minimizing drag by their placement in an apparent hydrodynamically advantageous position. The drag produced during the recovery stroke is thus minimal - recovery strokes for invertebrate paddlers typically are on the order of a few percent of the power stroke under similarly high Reynolds-number (Re) conditions (Vogel, 1994, table 5.2). Further, during the power stroke, the arm is extended out to near its full length, increasing available surface area for thrust generation, while in the recovery stroke it is drawn in close to the calyx, thus reducing surface area. During the recovery stroke a region of curvature of the arm is propagated from the base of the arm to tip (Shaw and Fontaine, 1990, fig. 1). The complexity of the recovery-stroke motion prevents direct use of the model developed here to calculate its negative contribution to thrust. Due to the efficient reduction of surface area by the repositioning of the arms and pinnules and based on observations of other invertebrate paddles, the negative contribution of drag during the recovery stroke to upward thrust is small and is here ignored.

5.3.2 Parameters and Equations

Drag in animal swimmers typically includes two components, pressure drag and skin friction (Vogel, 1994). The ratio of the two forms Re, which can be calculated from the equation:

$$Re = \frac{\rho L U}{\mu} \qquad \text{Reynolds Number} \qquad (5.1)$$

where ρ and μ are the density and dynamic viscosity of the fluid, respectively, and L and U describe the object (L = size of the object, measured as longest linear dimension; U = velocity) moving through the fluid or that the fluid moves past

(Vogel, 1994). Based on the model conditions here, the Re for the arms and pinnules is ~3,000, a situation under which nearly all of the drag is contributed by pressure drag (Vogel, 1994). The Re for the tube feet is ~$1 - 10$ (within the range of previous studies, e.g., LaBarbera, 1984), and calculating the contribution of the tube feet to drag would require describing the skin friction component of drag. The action taken by tube feet during swimming is unknown. They may be extended outward as occurs with the pinnules or they may not be involved in swimming by being retracted and covered by the lappets and thus hidden within the pinnular food groove. Pinnules are known to retract during the feeding process, possibly in order to retain captured food particles and also in response to touch (Byrne and Fontaine, 1983). Because the function of the tube feet during swimming is unknown, their contribution to drag has not been included in the model. In the model all thrust is contributed by pressure drag and can be calculated using the equation:

$$D = \frac{1}{2}C_D \rho S U^2 \qquad \text{Pressure Drag} \qquad (5.2)$$

where C_D is the drag coefficient, ρ and U are as above, and S is the projected surface area of the object perpendicular to motion (Vogel, 1994).

In order to approximate the power stroke, a paddle model moving about a basal attachment was employed (Fig. 5.3). The arm is moderately straight during the power stroke, so while a flat paddle does not precisely reflect the complexity of the movement (e.g., Shaw and Fontaine, 1990, fig.1), it dramatically eases estimation of drag. This simplification likely underestimates drag, resulting in a somewhat conservative model. Though operating at much lower Re ($<< 1$), an analogy is seen in thrust generation by cilia (Fung, 1990). The lower Re for cilia eliminates the applicability of equations derived for ciliary power strokes to the comatulid power stroke. Planar-moving cilia, however, exhibit similar mechanics to the swimming comatulid arm by being moder-
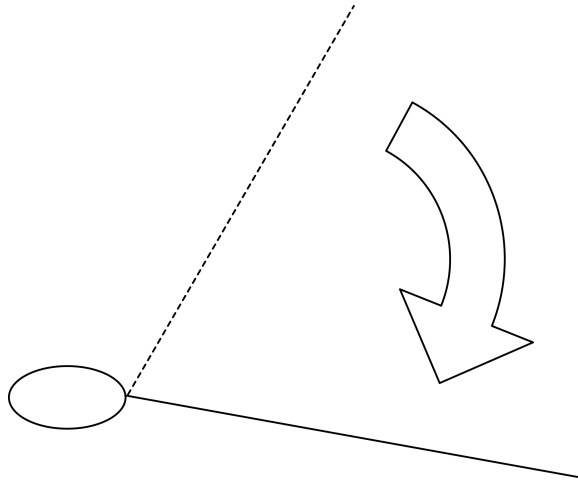
Figure 5.3: Simplified model of crinoid arm movement during a swimming power stroke.

ately straight during the power stroke, while propagating a region of curvature from base to tip during the recovery stroke. They have also been approximated in models as straight and moving about a pivot during the power stroke (Fung, 1990).

To estimate the values of the projected surface area (S), a drawing of the arm of *F. serratissima* in Shaw and Fontaine (1990, fig. 5) was employed (Fig. 5.4A). The shape of the arm was approximated as an isosceles trapezoid and arm dimensions were measured for the top, base, and length of the trapezoid (Fig. 5.4B). Their arm extirpation experiments demonstrated that *F. serratissima* can swim with only the proximal portion of the arm intact. Only the first nine centimeters of the 16 cm arm were employed in the model (Fig. 5.4B) and S was measured as the area of the isosceles trapezoid (Fig. 5.4B). The value of U (velocity of the object) was taken from observations of the time involved in completion of a power stroke (Shaw and Fontaine, 1990) and from the size of the angle through which the arm is inferred to travel (Shaw and Fontaine, 1990, fig. 1), allowing calculation of angular velocity.

The drag coefficient must be measured experimentally. Hoerner (1965, fig. 3-24) provided relationships of the drag coefficient to the solidity of a permeable plate. Solidity was measured by the ratio of area occupied by the arm and pinnules to the
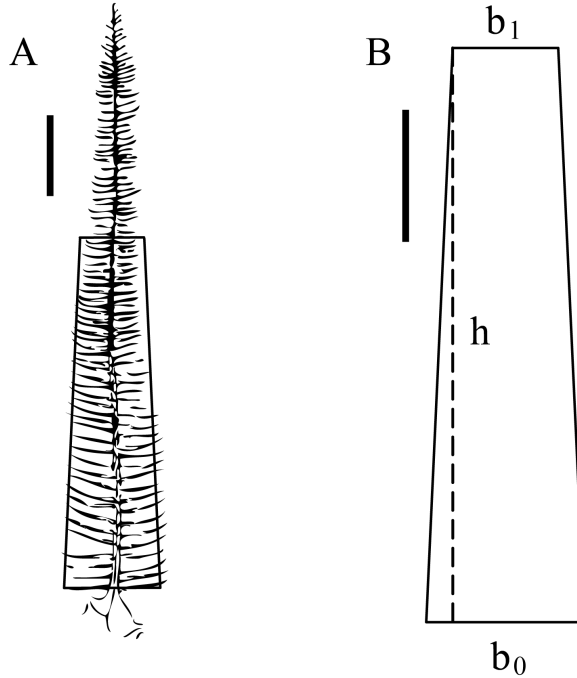
Figure 5.4: Source of model parameters for the analytical calculation of drag. A) Drawing of the arm of *Florometra serratissima* with an overlaid trapezoid to illustrate model dimensions (modified from Shaw and Fontaine 1990, fig. 5). B) Modeled arm area and dimensions. Scale bars = 2 cm.

total area enclosed within the trapezoid in Figure 5.4A, for a result of 0.54. The estimated drag coefficient (C_D) at this value of solidity is 0.73 and is assumed to be constant, which is valid under a case of approximately constant Re. The value of fluid density (ρ) employed is that of seawater, $1.024 \frac{g}{cm^3}$.

Calculating drag perpendicular to a plate traveling at a constant velocity at all points along the plate can be done by inserting the values estimated above into the pressure equation (5.2). Three complications prevent this approach from being used for a swimming crinoid: (1) the arm is hinged at the base so that the linear velocity is not constant at all points (nil at the arm base, maximal at the model arm end); (2) arm width diminishes toward the tip, thus reducing the functional area contributing to drag; and (3) only the vertical component of force contributes to the drag necessary to overcome the downward force of gravity. In order to circumvent these difficulties, an expression was developed, integrating the pressure equation (5.2), that allows drag

perpendicular to the arm (D_T) to be calculated precisely for the model:

$$D_T = C_D \rho V^2 h \left(\frac{b_0}{6} + \frac{b_1 - b_0}{8} \right) \qquad \text{Perpendicular Drag} \qquad (5.3)$$

where b_0, b_1, and h are model parameters measured from the arm (Fig. 5.4B) and V is the linear velocity of the end of the model arm (see Appendix D for details of calculation). From the expression representing the drag perpendicular to the arm (5.3), an expression for the vertical component of drag (D_V) was developed:

$$D_V = D_T \left(\frac{1}{\omega} \right) (\cos(\alpha) - \cos(\alpha + \theta)) \qquad \text{Vertical Drag} \qquad (5.4)$$

where D_T is the total drag calculated perpendicular to the arm (5.3), ω is the angular velocity, α is the starting position of the arm with respect to vertical, and θ is the angle through which the arm rotates (see Appendix E for details of calculation).

The model thus far is of a single arm generating thrust. *F. serratissima*, however, is a ten-armed swimmer; at any moment half of the arms are in a power stroke and half in a recovery stroke. Therefore, the calculated result from the modified drag equation (5.4) is multiplied by five to determine the drag generated by the crinoid.

Lastly, a downward force is exerted by gravity on the mass of the crinoid. This force is counteracted by buoyant forces and the combination of these two forces is most simply measured as the weight in water (WIW) of the crinoid. Specimens from the USNM were weighed using the method described by Baumiller (1992). The weight of water displaced by the specimen was measured to determine the volume of the specimen using an Ohaus triple-beam balance. Specimens were allowed to dry and dry mass was then measured on the balance. Using volume and mass, the density of the animal was calculated, and the WIW was estimated using (5.5):

$$WIW_{crinoid} = V_{crinoid} \times (\rho_{crinoid} - \rho_{seawater}) \qquad \text{Weight in Water} \qquad (5.5)$$

where V is volume and ρ is density. The WIW was calculated for four adult specimens of *F. serratissima* (median value = 0.80 g; Appendix F), each of comparable size to the modeled swimming crinoid.

Analyses were written and figures were created in R version 2.3.1 (R Development Core Team, 2006).

5.4 Results

5.4.1 Model Applied to Extant Crinoids

To test the model, we first applied it to *F. serratissima*. The thrust generated by the model under measured parameters was in close agreement to the WIW of *F. serratissima* (Fig. 5.5), confirming the accuracy of the model.

Given these results the model was extended to test the feasibility of swimming by a stalk-bearing *F. serratissima*. Using a set of maximum estimates of ω and α, a reasonable upper limit to thrust was calculated. WIW of a stalk-bearing *F. serratissima* was approximated as the sum of measured WIW of *F. serratissima* and calculated WIW of the stalk. To get the latter, the stalk was modeled as a cylinder with a density of $1.44 \frac{g}{cm^3}$ and diameter of 0.37 cm. The values for stalk density and diameter represent median values obtained from specimens of extant isocrinids in the collections of the USNM. The results are summarized by Figure 5.5; it is clear that *F. serratissima* would be severely hampered by the weight of a stalk. Whereas the model likely underestimates thrust due to simplification of the mechanics, under a scenario of generous thrust generation, a crinoid with only a minimal stalk length could be lifted off the seafloor; a stalk longer than ~12 cm would most likely ground it.
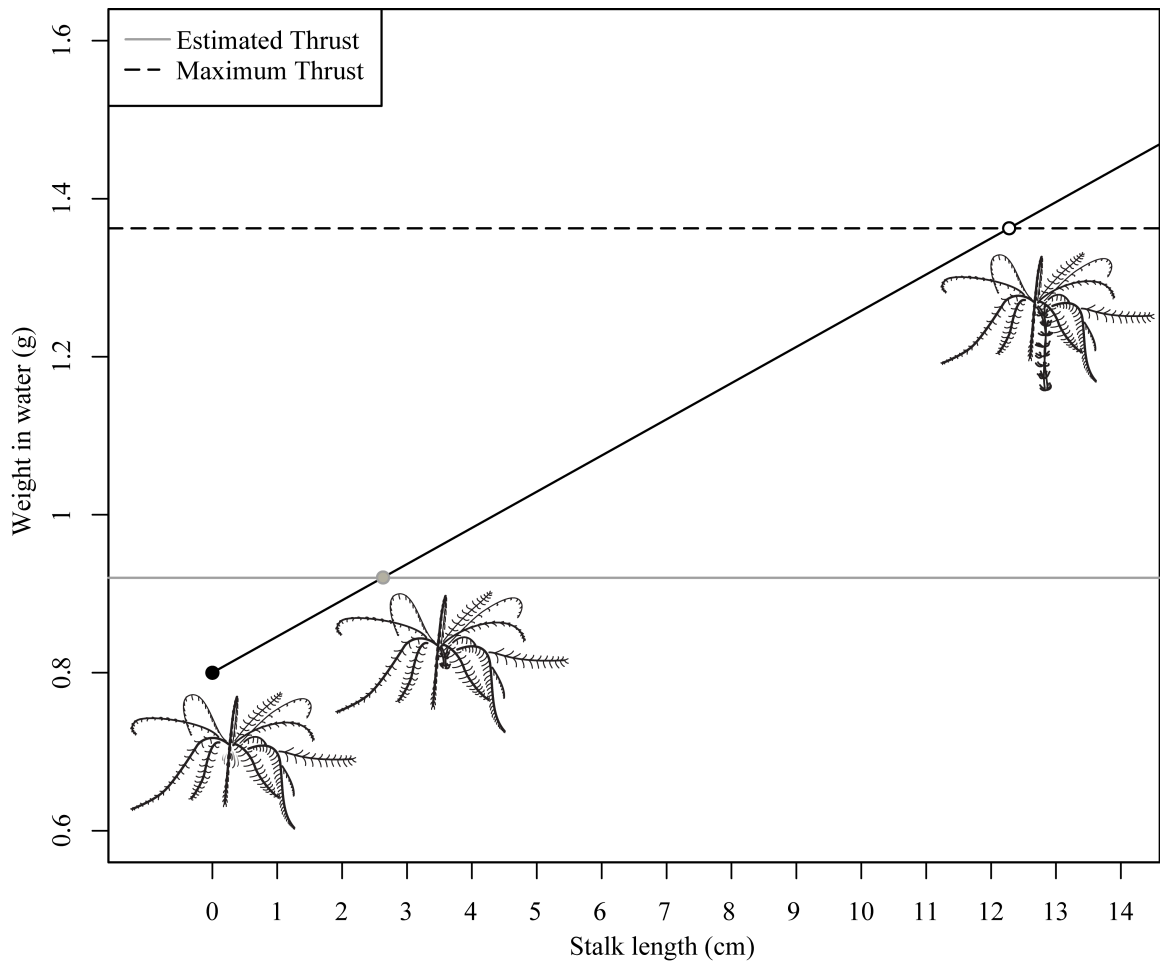
Figure 5.5: Increasing weight in water (WIW) of a crinoid with added stalk. Modeled thrust values generated by the crinoid are indicated for estimated parameters (gray line), as well as maximum thrust using a maximum set of parameters (dashed line). Drawings depict length of stalk capable of being lifted at modeled thrust values.

5.4.2 Effect of Arm Number on Thrust Generation

Given that thrust produced by the model is a function of arm number, it is worth considering the additional thrust that a crinoid might produce with additional arms, even though additional arms add weight. If we assume that the body mass of the animal scales isometrically with the number of arms, we can use the measured WIW of *F. serratissima* with ten arms to predict how much it would weigh with additional arms. The assumption of isometry must be more fully tested but is a reasonable expectation. Adopting a further assumption that the thrust-generating capability of multibrachiate crinoids is comparable to that of the model of *F. serratissima*, we can determine both the additional WIW of added arms and the additional thrust generated by those arms. There are numerous caveats to this assumption, largely concerned with our present ignorance of whether surface area, solidity (e.g., number and spacing of pinnules), and arm velocity are comparable for multibrachiate taxa (or even for other ten-armed taxa). Utilizing this assumption does, however, allow us to consider whether a multibrachiate crinoid could be capable of lifting a significantly greater length of stalk.

Figure 5.6 shows the additional thrust generated by a multibrachiate crinoid model in terms of the additional length of stalk this added thrust could lift after subtracting the WIW of the added arms. The number of arms modeled ranged from 10 (found in *F. serratissima*) to 80; previously, the maximum number of arms reported for a swimming comatulid was 40 (e.g., Clark, 1915). We have recently observed an individual in the 80-armed genus *Pontiometra* swimming vigorously using all of its arms in an aquarium. Modeling a stalk with the smallest diameter and lowest density (dotted line), which is likely unfeasible for a crinoid with a heavy crown, a 40-armed crinoid manages to lift 28 cm greater stalk length. For median stalk diameter and density (solid line), only 10 cm of additional stalk can be lifted. For an 80-armed crinoid these values increase to 55 cm for the narrow width and low density stalk
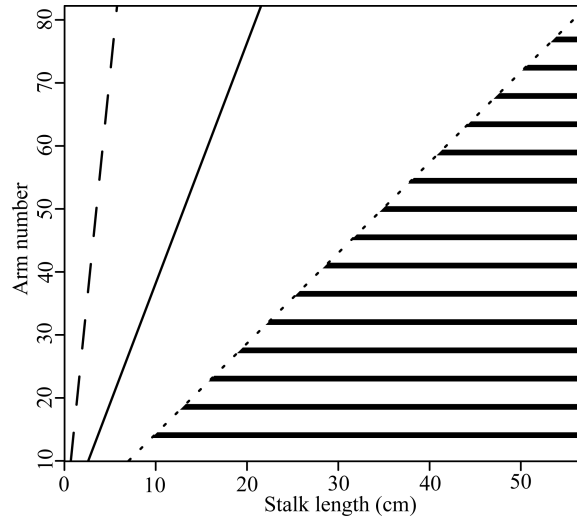
Figure 5.6: Results of model showing additional stalk length capable of being lifted due to added arms in a multibrachiate crinoid. Dashed line = hypothetical stalks with the greatest observed diameter and highest measured density; solid line = median density and diameter; dotted line = smallest diameter and lowest density (Appendix G). Hatched area is biomechanically unfeasible under model parameters of smallest diameter and lowest density stalks.

(dotted line), but only 20 cm at the more reasonable median values (solid line). The highest and lowest density-diameter parameters (dotted and dashed lines) do not actually exist in combination in the observed specimens (Appendix G).

In addition to the compromise between WIW and thrust generation with increasing arm number, at some point additional arms would physically obstruct each other, especially as the pinnules are splayed horizontally to create maximum surface area. Also, a multibrachiate crinoid would inefficiently generate thrust due to fluid interference, e.g., if an arm during its power stroke pushed water against other arms that were in their recovery strokes. There would be diminishing returns in adding arms, as the ratio of thrust generated to crown WIW would decrease. Given that many extant swimmers, such as *F. serratissima*, possess ten arms, this number might be optimal for swimming. In a 40-armed swimming crinoid, Clark (1915, p. 111) noted that only a short part of the arm was used and the stroke was shorter, similar to a dog-paddle type of swimming, compared to the usual swimming in ten-armed species.
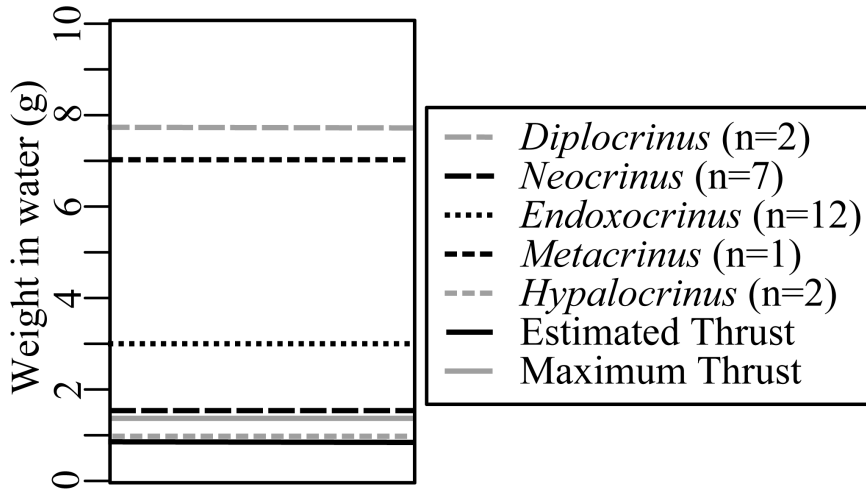
Figure 5.7: Median weight in water (WIW) of stalked crinoid crowns with modeled thrust values from Figure 5.5 demonstrating that the WIW of the crown of most stalked crinoids is much higher than the thrust generated by the model. n = sample size for that genus.

At present, it is not possible to evaluate whether the dog-paddle swimming employed in this multibrachiate taxon is more or less efficient than the style employed by *F. serratissima*. Under a scenario of identical thrust-generating capability for each arm of the model and increased WIW of the arms being the only compromise, it is clear that simply adding more arms is not a guarantee of swimming success in stalked crinoids (Fig. 5.6).

5.4.3   Crowns of Stalked Crinoids

Since the model suggests that loss of nearly the entire stalk is required before a crinoid can swim, it is worth considering whether this is the only prerequisite for crinoid swimming. To estimate the WIW of crowns in stalked crinoids, the WIW of any length of stalk still attached to the crown was estimated by approximating it as a cylinder, and this value was then subtracted from the WIW of the entire animal (Appendix G).

The crowns of stalked crinoids exhibit a range of WIW spanning an order of magnitude (Appendix G). More importantly, the majority of them weigh far more

than the thrust generated by the ten-armed model of *F. serratissima* (Fig. 5.7, Appendix G). This suggests that in order to swim, stalked crinoids would have to either generate much more thrust than *F. serratissima*, a good swimmer among comatulids (Shaw and Fontaine, 1990), or they must significantly reduce crown WIW in addition to losing the stalk. Given that additional arms do not provide drastically greater thrust-generation capability, that stalked crinoids crawling strokes are not faster than swimming strokes in *F. serratissima*, and that only the arms nearest the substrate are used (Baumiller and Messing, 2007, fig.2), WIW reduction seems to be a prerequisite for swimming.

5.4.4   Comatulid WIW

In order to determine how a stalkless crinoid might further reduce its WIW, several features of comatulids were measured (Appendix F). A multivariate linear regression revealed that three measures are significant in predicting WIW: arm length, width of brachials measured in the horizontal plane (i.e., excluding the pinnules) at the midpoint of the arm (brachial width), and number of arms (Fig. 5.8; $R^2 : 0.55, p < 10^{-5}$ for full model).

Whereas arm length is significant in predicting the WIW of comatulids (Fig. 5.8A), its importance in thrust generation guarantees that reducing arm length is unlikely to provide the best method of reducing WIW and still allow a crinoid to swim. In the model of a paddle moving about a pivot (Fig. 5.3), it is the distalmost portion of the arm that has the greatest linear velocity. Furthermore, pressure drag, and thus thrust (5.2), is proportional to the square of the linear velocity. Therefore, a crinoid with shorter arms would have a lower WIW, but it would experience a severe decrease in its ability to generate thrust. In contrast, reduction in brachial width allows for reduction in WIW without drastically affecting surface area of the paddle. This results in a more gracile arm, which likely includes compensations in increased

musculature considered in the discussion (below).

5.4.5 Antedonidae versus Comasteridae

The Comasteridae and Antedonidae are the two most species-rich extant crinoid families (Messing and Hansson, 2010a). Whereas most, if not all, antedonids swim, there are no reports of a comasterid swimming, despite more than a century of study. Clark (1915, p. 120), after attempting to cause numerous comasterid species to swim by various experiments, asserted that the Comasteridae do not swim, but he described the Antedonidae as good swimmers. Therefore, it is possible to compare morphological attributes of swimming antedonids and non-swimming comasterids to see if traits in the two families differ in ways that the swimming model would predict, based on functional morphology.

Table 5.1 summarizes the results of this comparison. WIW and arm number are significantly different between the two families, but arm length and brachial width do not differ significantly. The lower number of arms for the antedonids accords with the result that reduced arm number is a viable way to lower WIW. Arm length for the antedonid specimens was greater than for the comasterids, although not significantly, demonstrating that the former have lower WIW without shortening the arms, which would hamper their ability to generate thrust. Brachial width was lower for the antedonids, but the difference was not significant; however, the antedonids have significantly more gracile arms, measured as the ratio of brachial width to arm length, than the comasterids.

5.5 Discussion

The model employed here includes a number of simplifications, some of which make it conservative in estimating thrust generation. These include the flat-paddle approximation and the omission of tube feet, which might increase solidity and there-
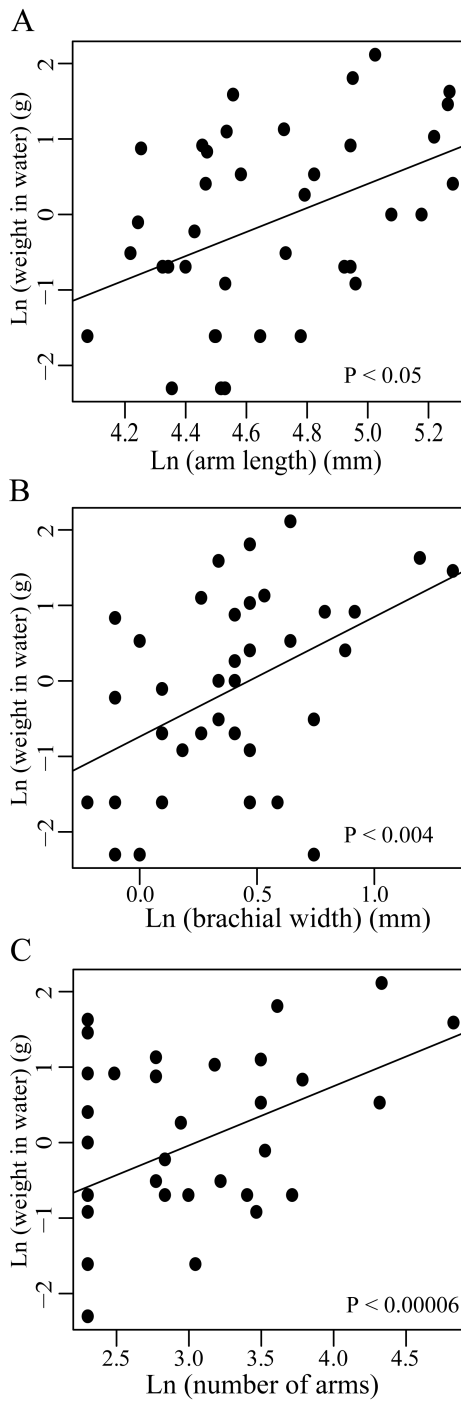
Figure 5.8: Significant predictors of comatulid weight in water (WIW) in a (Ln-Ln) multivariate linear regression model ($R^2 = $ ~0.55, $p < 0.000005$). A) Arm length. B) Brachial width. C) Arm number. Ln = natural log.
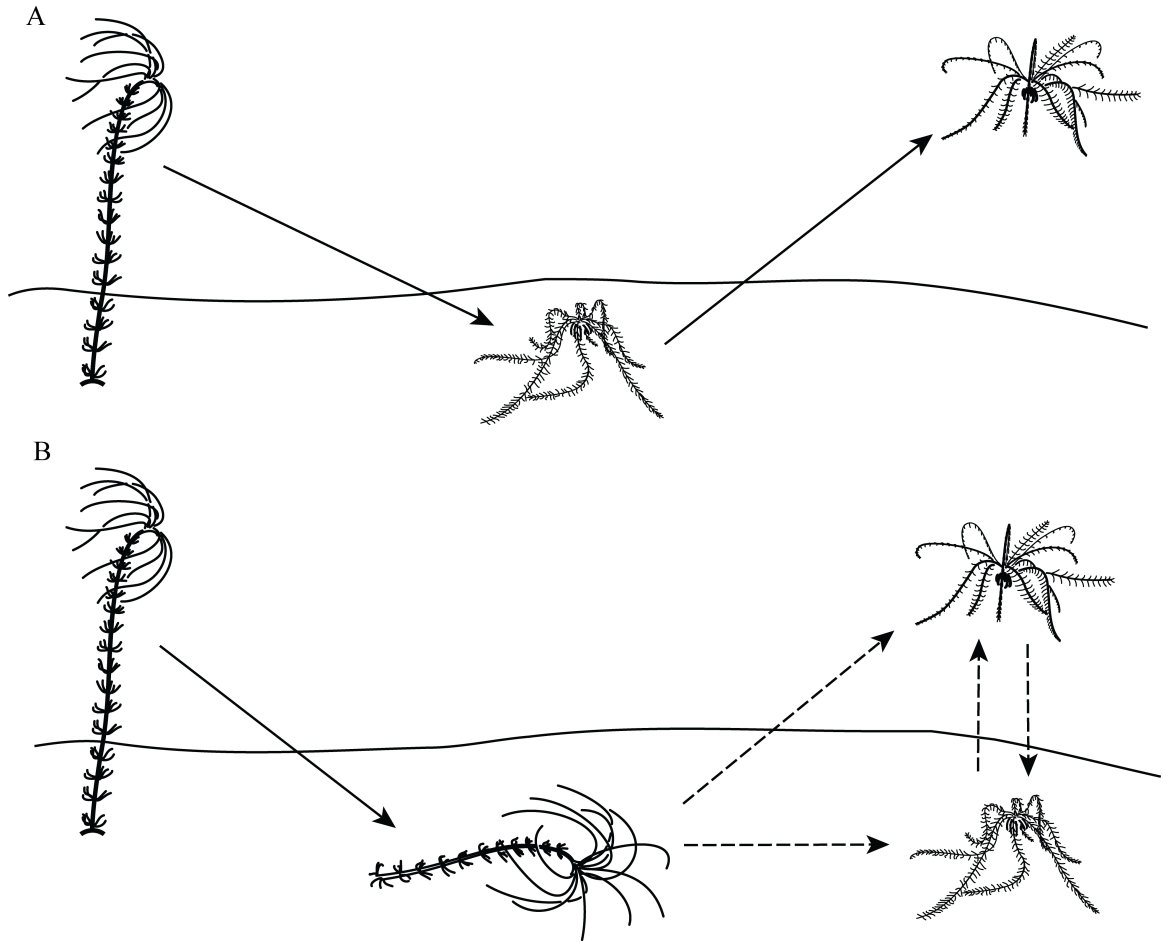
Figure 5.9: Possible scenarios for the evolution of locomotion in crinoids. A) Traditional evolutionary view of a sessile stalked crinoid, evolving into an obligate crawling stalkless crinoid, reaching an 'apex' of crinoid evolution with a free-swimming form. B) More complex scenario considered here in which crawling evolves first in a stalked crinoid and multiple, non-mutually exclusive evolutionary paths are possible (dashed lines). See text for discussion.

fore thrust generation. It is unlikely, however, that including these factors would permit a crinoid with a crown WIW many times greater than that of *F. serratissima* to swim (Fig. 5.7).

Given the low values of thrust that can be generated by a swimming crinoid, WIW reduction must have been the primary prerequisite to allow a crinoid to swim. The obvious way to reduce WIW without affecting the capacity to generate thrust is by reducing stalk length or eliminating it entirely because it cannot contribute to swimming. Given their morphology (Birenheide et al., 2000; Seilacher and Hauff, 2004), it

is unlikely that cirri play a role in swimming. In addition to adding weight, the stalk and hanging cirri would increase frictional drag and would perhaps snag other benthic structures, making swimming more difficult. One mechanism by which the stalk could aid in swimming is if it elevated the crown into a region of higher current velocity above the boundary layer, it contributed to the initial stages of swimming with the crinoid acting as a sail via lift or drag on the crown (Baumiller, 1992). This scenario would provide an evolutionary intermediate between a crawling, stalked crinoid and a swimming form, without a strictly crawling, stalkless intermediate. Whereas this would allow a nascent swimming crinoid to get off the ground and thus represent a stalked crinoid swimming, in the present study this scenario was not considered further because the goal was to determine thrust generation in the absence of current. Stalk loss may have evolved first, producing an obligate crawling taxon, from which swimming then evolved (Fig. 5.9A). Swimming may have evolved directly from a crawling stalked crinoid, with some clades subsequently losing the ability to swim (Fig. 5.9B), or a combination of scenarios may have occurred in crinoids with the loss or gain of swimming occurring multiple times.

Given that stalk loss in isocrinids alone does not reduce WIW enough to allow them to swim (Fig. 5.5), changes to crown WIW are required and this explains the observation that isocrinids with experimentally shortened stalks cannot swim (Nakano et al., 2002). By reducing arm length, brachial width, and arm number, a crinoid may lower its WIW; however, as discussed above, only reductions in brachial width and arm number are possible without greatly affecting thrust-generation capacity. Reducing these two parameters undoubtedly entails many compromises, as the arms of extant crinoids serve purposes other than locomotion (e.g., feeding and reproduction). It can be inferred that WIW reduction to allow efficient swimming must have been under selection pressure to permit these compromises and also that the many crinoids with ten gracile arms are capable of meeting their feeding and reproductive demands.

Crinoid arms are composed of a series of articulations, of which the muscular articulations play a locomotory role. The functional morphology of crinoid arms and articulations is as yet poorly known (Webster and Maples, 2008), and a complete treatment is not possible here; however, some preliminary observations suggest that swimming crinoids bear unique muscular articulations.

Table 5.1: Median values of attributes for the antedonid (swimming) and comasterid (crawling) crinoids (Appendix F) with significance values comparing the two families via the Mann-Whitney U test. Statistically significant correlations are shown in bold. n = sample size (species). Samples from the Smithsonian Institution National Museum of Natural History, Invertebrate Zoology Collections

	WIW (g)	Brachial Width (mm)	Arm Length (mm)	Arm Number	Brachial Width/Arm Length
Comasteridae (n=9)	1.700	1.600	113.200	37	0.013
Antedonidae (n=10)	0.450	1.450	129.000	10	0.010
P-value	**0.041**	0.161	0.447	**0.007**	**0.008**

Table 5.2: Median values of attributes for the antedonid (swimming) and comasterid (crawling) crinoids compiled from Clark (1921) with significance values comparing the two families via the Mann-Whitney U test. Statistically significant correlations are shown in bold. n = sample size (species).

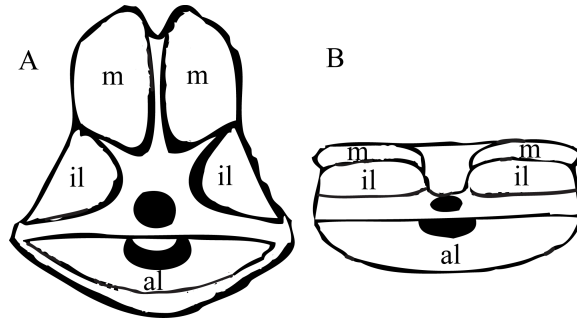|	Radial Width (mm)	Arm Length (mm)	Radial Height (mm)	Width/Length	Width/Height
Comasteridae (n=12)	1.800	125.000	2.300	0.023	0.658
Antedonidae (n=9)	1.400	110.000	2.000	0.016	1.033
P-value	0.915	0.909	0.447	**0.027**	**0.012**

Figure 5.10: Radial articular faces of comatulid crinoids. A) *Florometra asperrima* Clark, swimming crinoid family Antedonidae. B) *Davidaster discoideus* Carpenter, obligate crawling crinoid family Comasteridae. Images not to scale, although relative sizes are accurate. Note the relatively large muscular fossae (m) in A, as well as the greater distance of the muscular fossae from the horizontal transverse ridge between the ligament fossae. Images modified from Rasmussen and Sieverts-Doreck (1978). il = interarticular ligament fossa; al = aboral ligament fossa.

Crinoid muscular articulations are distinguished by the presence of five fossae: two oral muscular, two interarticular ligament, and one aboral ligament fossae (Fig. 5.10). Running transversely between the interarticular and aboral ligament fossae is the transverse ridge, which functions as a fulcrum during locomotion (Ubaghs, 1978). The complete mechanics of the articulation during swimming is poorly understood, although the presence of musculature on only one side of the transverse ridge implies an antagonistic role for the aboral ligament on the other side of the transverse ridge. Muscular articulations in crinoids have a long evolutionary history (Webster and Maples, 2008); well-developed muscular articulations were the character on which the crinoid subclass Articulata was first established (Simms and Sevastopulo, 1993). Relevant to the present discussion is the effect that narrower brachials would have on the muscular articulations and swimming capability of a crinoid.

Clark (1921) collected biometric data on the radial articular faces of many extant comatulids and published measurements of the radial articulations of a number of species. Included are data on the radial heights and widths of 12 specimens of comasterids and nine antedonids. Like the brachial widths reported in Table 5.1, measured at the midpoint of arm length, comasterids generally have wider arms where measured

at the radials, although the differences are not significant (Table 5.2). Additionally, Clark reported radial heights and arm lengths and again these measurements did not differ significantly between the two families. Clark's maximum values of arm length were used in producing Table 5.2, as with the arm lengths for the new data reported here (see Appendix F). Arm gracility, however, as measured by the ratio of radial width to arm length, is significantly different between the two families. An additional measure of arm gracility possible with Clark's data is the height-to-width ratio of the radial, which is also significantly different between the two families. Clark's dataset again points toward the antedonids having more gracile arms than the comasterids, without differing in overall crown size as measured by arm length.

The effect of these relatively more narrow muscular articulations on musculature and ligaments is best illustrated with an example from the radial facets of two crinoids, the antedonid *F. asperrima* Clark and the comasterid *Davidaster discoideus* Carpenter (Fig. 5.10). In the swimming antedonid with its relatively narrow muscular articulation, there is an enlargement of the area of the muscular fossae relative to the overall radial articular facet, but the crawling comasterid possesses comparatively smaller muscular fossae. Precise measurement of the areas of musculature for comparison of the two families is hampered by the sculpted nature of the fossae, which increases surface area for muscle attachment, particularly in the antedonids. Further, measuring only the radial articular facet for comparison purposes is somewhat speculative because it represents only one in a series of muscular articulations extending the length of the arm. Nonetheless, the evidence presented here suggests that swimming crinoids have overcome the demands of lowered WIW with more gracile arms and concomitantly by having larger areas for muscle attachment to compensate for the narrower articular face.

Future directions of research include refinements to the model, such as a closer approximation of the complexity of the arm motion, as well as testing the model by

measuring the force generated by swimming comatulids. Forces might be measurable directly on arms or by swimming experiments that involve added weight to simulate the anchoring burden of a stalk. The model assumed movement without a current, but modeling scenarios could also consider the hydrodynamic lift produced by crinoid filtration fans (Baumiller, 1992), combined with the drag generated by arm paddles, for an evolutionary scenario in which swimming first occurred with the aid of currents in a stalked crinoid with the crown functioning as a sail. Observations on *F. serratissima* reveal that horizontal swimming occurs with the current (Shaw and Fontaine, 1990), greatly increasing distance traveled. Current provides a greater chance for escape from non-swimming predators and may also have helped generate lift in the first swimming crinoids.

Additionally, better understanding of the swimming mechanics of comatulids is needed. This includes the operation of the tube feet during swimming strokes, the contribution to power and recovery strokes provided by the oral muscles and aboral ligaments, and the contributions to thrust for each muscular articulation. Observations on stalked crinoids of the velocity and angular distance of arm movements (e.g., Young and Emson, 1995), coupled with the surface area measurements made here, could allow direct estimation of the thrust generation possible by a stalked crinoid. Most importantly, more observations on swimming in other crinoid species would allow better characterization of whether the assumptions employed here apply for other taxa. Whereas *F. serratissima* is a good swimmer, it is possible that thrust generation is greater for other species, by some combination of increased arm solidity, faster swimming strokes, and longer, more numerous arms. Each of these factors would, however, entail increased WIW and thus limit their effectiveness in producing added thrust.

Lastly, the hypotheses for the gain and loss for the capacity to swim would be more easily understood in the presence of a robust phylogenetic framework for the comat-

ulids. At present, the strong possibility exists that crawling was present in crinoids before comatulids evolved and that swimming may be a plesiomorphic behavior for these stalkless crinoids. Although stalk loss may have negative consequences for feeding or other behaviors typical of stalked crinoids, some comatulids have compensated for this loss by adopting high perches that allow them to live somewhat like stalked crinoids (Meyer and Macurda, 1977). Under a scenario of intense predation pressure from benthic predators, eliminating the stalk would greatly increase the ability of the crinoid to escape, outweighing the possible benefits the stalk provided.

5.6 Conclusion

The analytic model presented here produces sufficient upward thrust to explain the ability of the comatulid crinoid *F. serratissima* to swim. The model suggests that most of the stalk of a crinoid would have to be lost before it would be capable of swimming, assuming that the ability to generate sufficient thrust preceded stalk loss. Reductions in crown weight would also be required and these were provided primarily by narrowing of the arms and reduction in arm number. In order to compensate for these changes or to produce greater thrust, swimming comatulids seem to have undergone increases in the relative proportion of the radial articular facet devoted to muscular attachment.

Meyer (1985) suggested that the success of comatulids today compared to stalked crinoids may be a product of their ability to deal with increased predation pressure during the MMR by their greater capacity for locomotion. The evolutionary scenario considered here assumes that rapid crawling to escape benthic predation evolved in stalked crinoids (Fig. 5.9B) and that swimming evolved later, possibly first in a short-stalked crinoid ancestor. Crawling in comatulids may allow them to avoid predatory fish by being nocturnal or seeking refugia (Meyer and Macurda, 1977; Meyer, 1985); however, swimming is not considered effective in avoiding predation by

fish. Instead, swimming may represent an increased capability in stalkless crinoids for escape from benthic predation, as benthic predators also diversified during the MMR (Vermeij, 1977, 1987). Recent observations of evidence for benthic predation on stalked crinoids suggests that this diversification in response to benthic predators began in the Middle-Late Triassic (Baumiller et al., 2010), pre-dating the MMR. It is thus unsurprising that the oldest known comatulid occurs in Late Triassic strata (Hagdorn and Campbell, 1993).

5.7   Acknowledgments

CHAPTER VI

The history of motility in comatulid crinoid evolution

6.1 Abstract

Modern crinoids are dominated in species richness by the stalkless, motile comatulids, notable for their elegant swimming, which may allow escape from predators. This diversity pattern is in contrast to crinoids in the fossil record, which are usually stalked, and traditionally have been thought to be largely sessile. These observations have led to the conclusion that the success of comatulids is due to their greater motility. Recently, rapid crawling has been observed in stalked crinoids, an ability which seems to allow escape from benthic predators. Because of its presence in stalked crinoids, crawling is likely plesiomorphic for comatulids. Based on a previously developed biomechanical model and observations from functional morphology I determined traits that may allow comatulids to swim. These observations allowed inference to whether a fossil comatulid had been a swimmer in life, or whether it had likely only been capable of crawling. I apply these observations to fossil comatulids and suggest that swimming may have been present in the earliest comatulids. The relative diversity of crawling to swimming commatulid species has changed through time, but for most of comatulid history, swimming species have dominated their diversity. Com-

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bined with the phylogenetically widespread presence of swimming in extant comatulid species, the most parsimonious evolutionary scenario is that non-swimming species are members of clades that lost the ability to swim. The origin of comatulids was during the early phase of the Mesozoic marine revolution, and may have been driven by adaptation to benthic predation pressure. The evolutionary dynamics of crawling and swimming comatulid lineages may have been affected by the Mesozoic marine revolution and the expansion of reefs.

6.2   Introduction

Then you better start swimmin'

or you'll sink like a stone

-Bob Dylan

The elegant swimming of some species of extant, stalkless crinoids (Order Comatulida Clark 1908a; henceforth "comatulids") appears to represent a pinnacle in crinoid behavioral capability; yet we should not create a *scala naturae* from sessile to more mobile crinoids with swimming comatulids at the apex without considering the evolutionary history of these animals. Extant crinoids number approximately 600 species of which only 80 or so are stalked sea lilies (Hess and Ausich, 1999). The remaining crinoids are the stalkless comatulids. This diversity pattern is in sharp contrast to the dominance of sea lilies among fossil crinoids: their fossil apogee in the Mississippian resulted in hundreds of species named from a single formation (Ausich, 1999), while the comatulids did not appear until the Late Triassic (Hagdorn and Campbell, 1993).

The diversification of comatulids occurred subsequent to their appearance in the Late Triassic, but the timing of this event is poorly constrained. Because > 80% of extant crinoid species richness is found among the comatulids, Meyer and Macurda

(1977) made a case that modern comatulids are a success story, having undergone an adaptive radiation, while the less species-rich stalked crinoids have declined. It has been claimed that anti-predatory behavioral adaptations in comatulids led to their modern day success, including the evolution of crawling and swimming, as an adaptive response to the Mesozoic marine revolution (MMR) of predators (Vermeij, 1977, 1987; Meyer, 1985). The dominance of comatulids among living crinoids extends beyond species richness; they occupy a wide bathymetric range (intertidal to abyssal), and a variety of habitats (Meyer and Macurda, 1977). These facts of modern comatulid success contrast with those of modern stalked crinoids, which are restricted to > 100 m water depth (Meyer and Macurda, 1977; Oji, 1996; Oji et al., 2009), and thus no longer live in the shallow-water habitats that they occupied in the past. It has long been assumed that comatulid diversification occurred sometime during the Mesozoic or early Cenozoic, that their greater motility was the primary mechanism for that success, and, by implication, that this motility was established early in their evolutionary history. Alternatively, Roux (1987) has argued that it is the ability of comatulids to live in high-energy environments (e.g, reefs) that explains their success, with doubts that stalked crinoids ever occupied these environments. While some comatulid taxa may have adaptations for living in high-energy environments, this does not explain the long shallow-water fossil record for stalked crinoids before the Jurassic, and their subsequent relegation to the great depths observed today.

Meyer and Macurda (1977) provided crucial observations on extant comatulid behavior and functional morphology, but their study did not focus on the timing of the attainment of crawling and swimming ability in comatulids, or the subsequent diversification of comatulids. The evidence for a comatulid radiation and their replacement of stalked crinoids relied on two observations: (1) comatulids first appeared in the early Mesozoic (now known to be by the Late Triassic, Hagdorn and Campbell, 1993), in contrast to stalked crinoids which had diversified considerably by the

Middle Triassic after their rebound from the Permian-Triassic (P-Tr) extinction event (Hagdorn, 1995); and (2) the high diversity of comatulids relative to stalked crinoids today. The relatively poor preservation potential of comatulids compared to stalked crinoids, some aspects of which are discussed here, may affect meaningful comparisons of their diversity history; however, we may still be able to determine the timing of origin of the behavioral adaptations that led to comatulid success, and compare these to the geologic or biologic factors that may have affected comatulid diversification.

Inferring behavior in fossil organisms is challenging, but determining the way of life of extinct species has always been an avenue of paleontological research. Taxonomic studies frequently include inferences on life habits - the organisms and their taxonomy would be less interesting without this aspect of research - and these observations form hypotheses for future study. Research on fossil crinoids, particularly of aberrant taxa, has led to inspired speculation about these crinoids life modes (e.g., Seilacher and MacClintock, 2005), with considerable disagreement over how they may have lived (e.g., Donovan, 2006; Seilacher and MacClintock, 2006). Classic examples of such debates include the life modes of *Uintacrinus* Grinnell 1876 (e.g., benthic, planktonic, or pelagic, see Hess, 1999 for discussion; dredging, Seilacher and Hauff, 2004), and *Pentacrinites* Blumenbach 1804 (e.g., swimming, Hauff, 1984; pseudo-planktonic, active filtrator, Seilacher and Hauff, 2004). These and other fossil crinoids have been claimed to be nektonic or planktonic based on inferences of function from observation of morphology.

Herein, I consider the plausibility of swimming behavior in fossil comatulids by examining the distribution of swimming among extant comatulid families, through a biomechanical paradigm (Plotnick and Baumiller, 2000), by observations of the functional morphology of extant, swimming crinoids (Janevski and Baumiller, 2010), and by applying these observations to the fossil record in order to determine if the species may have been able to swim. My focus here is on when swimming first

appeared in comatulids, and the distribution of swimming among fossil and extant comatulid species through time and in relation to biologic and geologic events. I also discuss the role that swimming could play in anti-predatory defense.

It has been claimed that most extinct crinoids may have been free-living (Kirk, 1911), but acceptance of motility in some stalked crinoids has accelerated with the observation of rapid crawling in stalked crinoids (Baumiller and Messing, 2007). The traits that enable rapid crawling in modern stalked crinoids, muscular articulations with fulcrums in the arms, cirri with fulcrums throughout the stalk, and absence of permanent attachment, have a long fossil history (Baumiller, 2008), suggesting that some stalked crinoids may have been crawling since the Paleozoic. Crawling may primitively characterize all post-Paleozoic crinoids, meaning that non-crawling lineages are derived and have lost the ability to crawl. The P-Tr extinction event may represent a transition between relative dominance of motile taxa over those that are sessile, though it is unclear if this biological transition was due to the dynamics of that extinction event (Baumiller, 2008).

Because crawling was likely present in all Mesozoic crinoids unless secondarily lost, crawling is a plesiomorphic behavior for comatulids (Janevski and Baumiller, 2010). All extant comatulids that have been studied have the ability to crawl, and likely most fossil comatulids could crawl, as well. However, some lineages, like the bourgueticrinids, which may have been derived from comatulids via paedomorphic retention of the attached larval pentacrinoid stage into adulthood (Simms, 1988a), have regained permanent attachment to the substrate and thus no longer crawl.

However, while crawling is almost certainly primitive for comatulids, the same is not necessarily true for swimming. Although swimming may have existed in non-comatulid Mesozoic crinoids, biomechanical analysis suggest that it is unlikely that a long-stalked, heavy-crowned crinoid could swim (Janevski and Baumiller, 2010). This means that swimming could have originated among the earliest comatulid species or

that it evolved only among some subset of comatulids, once or multiple times. I evaluate these ideas by examining the distribution of swimming among extant comatulids, functional morphology of comatulids, from a phylogenetic perspective, and through an assessment of the relative proportion of swimming comatulids in the geologic past.

6.3   Functional morphology of swimming comatulids

Here I describe the functional morphology of swimming comatulid crinoids, considering traits required for swimming, and that can be observed in fossil specimens (Table 6.1). I discuss the importance of stalk loss, changes in arm and brachial morphology, changes to the comatulid calyx, and the formation of the centrodorsal. For details of comatulid biology see Appendix H.

6.3.1   Stalk loss

The most obvious difference between comatulids and other crinoids is the apparent lack of stalks in the former. Stalk loss has occurred many times in separate crinoid lineages, a fact recognized at least 100 years ago (Kirk, 1911). Echinoderms were traditionally divided into two subphyla, Pelmatozoa and Eleutherozoa, whose crown group members are crinoids and all other extant echinoderms, respectively. Modern classifications less frequently use these terms but informal use of the terms pelmatozoan ("stalked") and eleutherozoan ("free-living") remains common (e.g., Clausen and Smith, 2008). For modern crinoid research this usage is ironic because most extant crinoids are comatulids, which as adults are both stalkless and free-living.

A full treatment of stalk loss in crinoids requires determining instances of convergence, a challenging task that requires a phylogenetic framework, particularly for closely related taxa, which could be prone to adopt similar evolutionary solutions to environmental pressures. Convergence and the lack of a robust phylogenetic framework plagues many studies of crinoid evolution. Additionally, comatulids are
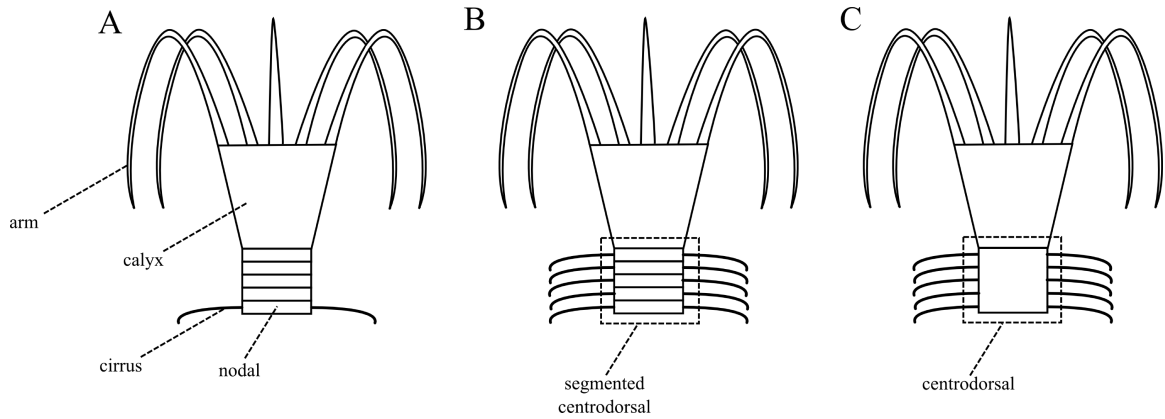
Figure 6.1: Schematic evolution from stalked crinoid to a stalkless comatulid. A) Stalk growth in a stalked crinoid occurs by proximal addition of nodals, with cirri sprouting from distal nodals - intercalation of internodals would occur if stalk development continued (adapted from Nakano et al., 2004, fig. 3D). B) No internodals grow, all nodals have sprouted cirri, additional nodal growth terminates, and this results in a short, cirriferous stalk (segmented centrodorsal), which is the paracomatulid condition. C) Fusion of nodals gives an unsegmented, cirriferous centrodorsal, resulting in a true comatulid.

technically not stalkless. The oldest known comatulids are often described as "paracomatulids" due to the presence of unfused columnals in the nascent centrodorsal; a fused centrodorsal is characteristic of true comatulids. Crinoid stalks contain cirrus-bearing nodal ossicles, and numerous internodal ossicles, which do not bear cirri, between nodals. Fossil specimens of paracomatulid genera *Paracomatula* Hess 1951 and *Eocomatula* Simms 1988b reveal that the comatulid centrodorsal is composed of fused nodal stalk elements, explaining the often high density of cirri on this element, which is sutured to the comatulid calyx. Stalk regrowth in one modern crinoid occurs by proximal nodal development with intercalation of internodals distally (Nakano et al., 2004). This observation suggests that the evolution of the comatulid centrodorsal occurred by loss of internodal development, and subsequent fusion of cirri-bearing nodals (Fig. 6.1).

Though the centrodorsal is technically derived from a stalk, because of its tight suturing it has effectively become part of the comatulid calyx. In extant comatulids, infrabasals are found only in larvae, basals are prominent in larvae but reduced in

most adults, and there are no anal plates beyond the larval stage. Thus the calyx is formed primarily from a prominent circlet of radial plates and from a ring of basal plates that may be reduced, with the centrodorsal tightly sutured to it (Rasmussen and Sieverts-Doreck, 1978).

Despite the origin of the centrodorsal from stalk elements, and the presence of stalks in their larvae, comatulid adults are effectively stalkless. The crinoid stalk functions as an anchor, attaching the crinoid to the substrate via force and friction (Table 6.1; Janevski and Baumiller, 2010). Additionally, the lack of thrust capability of cirri affords little evidence that they play a role in swimming (Baumiller and Janevski, 2011). Thus, stalk loss likely occurred before the evolution of swimming behavior, and stalklessness is a characteristic of most swimming crinoids. The main consequence of stalk loss for swimming is the reduction of crinoid weight - less thrust needs to be generated by the arms to overcome the downward force of gravtiry for a crinoid without a stalk. This effect is discussed in detail by Janevski and Baumiller (2010). The above suggests that the loss of a stalk is an important adaptation for swimming, but stalk absence alone is not sufficient for inferring swimming ability.

Table 6.1: Traits that aid or allow swimming. [1]Janevski and Baumiller, 2010; [2]Meyer and Macurda, 1977

Feature	Form	Function in swimming
Stalk	Absent	Reduced weight and anchoring[1]
Arms	Gracile[1]	Reduced weight[1]
Brachials	Complex musculature[2]	Greater thrust[1], flexibility[2]
Calyx	Small[2]	Reduced weight
Cirri	Many adaptive features[2]	Allows reattachment

6.3.2   Arm and brachial morphology

There is a dearth of understanding on the complete action of musculature and ligaments during the arm stroke of swimming comatulids. The morphology of radial

facet musculature in swimming comatulids may be enlarged and more deeply sculpted compared to comatulids that only crawl (Janevski and Baumiller, 2010, fig. 10). This would provide greater surface area for muscle attachment, which could also be achieved through an increase in the number of muscular articulations. These ideas may represent avenues of future study. There is compelling evidence that swimming comatulids have gracile arms: compared to their overall length they are relatively narrow in the lateral plane (Table 6.1; Janevski and Baumiller, 2010). This gracility results in relatively lower weight of the animal without dramatically hampering thrust generating capability.

Swimming crinoids do not necessarily have overall thinner arms than crawling crinoids. Etnier (2001) found that average arm diameter at the midpoint of the arm of two crinoid species, *Florometra serratissima* Clark 1907 (Family Antedonidae), a good swimmer (Shaw and Fontaine, 1990), and *Comactinia echinoptera* Müller 1841 (Family Comasteridae), an obligate crawler, was thicker in the swimmer. Arm diameter was a significant positive predictor of flexural and torsional stiffness in the arms of those crinoids, with wider arms generally stiffer. These two species are both ten-armed, and of comparable crown size as measured by overall arm length. However, comatulid brachials may be asymmetrical. Though *F. serratissima* has overall thicker arms, the radials are widest in the dorso-ventral direction, while *C. echinoptera* is narrower in the dorso-ventral direction. Functional explanations for these characteristics include that 1) *C. echinoptera*, a nocturnal, semi-cryptic (Schneider, 1988), obligate crawler, may require greater arm flexibility for its life mode, and that 2) *F. serratissima*, as a swimmer, generally benefits from stiffer arms. These observations merit future testing, and should also incorporate the observation that joint number also predicts arm stiffness (Etnier, 2001).

6.3.3 Calyx reduction, formation of a centrodorsal, and expansion of cirri

Unlike many stalked crinoids, comatulids have the visceral mass on top of the proximal rays instead of within the calyx, which results in a reduction of calyx size (Meyer and Macurda, 1977). The density of crinoid stereom, the perforate microstructure unique to echinoderms, is higher than that of soft tissue ($1.2 - 1.7\frac{g}{cm^3}$ [Baumiller, 1992] versus $1.07\frac{g}{cm^3}$ [Brower, 1973]). The loss of plating of the calyx around the viscera lowers the density of the entire crown. This may be one reason why crown densities of extant comatulids are significantly lower than those of stalked crinoids, $1.26\frac{g}{cm^3}$ (N=38) and $1.36\frac{g}{cm^3}$ (N=24), respectively (Appendices F, G). Regardless, it is clear that the lower density of comatulid crowns is compatible with the functional requirements of swimming.

The above suggests that crown density might be a useful character for identifying swimmers - crinoids with high-density crowns do not swim. However, the reverse proves not to be true, not all crinoids with low-density crowns are swimmers. While the average density of the non-swimming comasterids is higher than of swimming comatulids, $1.29\frac{g}{cm^3}$ (N= 9) vs $1.25\frac{g}{cm^3}$ (N= 29), the difference is not significant.

6.4 History of comatulid swimming

6.4.1 Swimming in extant comatulids

The Comasteracea Clark 1908a consists of approximately 100 named species (Messing and Hansson, 2010b), roughly the same species richness that is known for all extant stalked crinoids. Members of the Comasteracea often represent more than half of the crinoid species present in shallow-water environments of the tropical western Pacific Ocean (Messing, 2003). The Comasteracea, therefore, is an important component of extant crinoid and comatulid diversity.

At least one author has claimed that all comatulids except members of the Co-

masteracea can swim (Lawrence, 1987). Although this conclusion may be premature given lack of knowledge of the behaviors of many taxa, it is true that despite over a century of study, there are no published reports of any member of the Comasteracea swimming.

6.4.2 Swimming in extinct comatulids

Given the functional analysis of comatulid swimming Janevski and Baumiller, 2010, and the observations presented here, no single morphological character can be identified as diagnostic for discriminating swimmers from non-swimmers. Therefore, I will begin the analysis of swimming among extinct comatulids by invoking parsimony, assuming that all members of superfamilies of extant swimmers were swimmers, while those of non-swimmers (the Comasteracea) were non-swimmers. I will supplement that with functional morphology for extinct superfamilies.

Figure 6.2 depicts the known stratigraphic ranges of comatulid superfamilies (Ubaghs, 1978), updated to correct a mistake that overextended the range of the Comasteracea (Appendix I), a monotypic taxon containing only the family Comasteridae (Clark, 1908a), which is likely monophyletic (Messing, 1997). Most comatulid superfamilies first appeared in the Mesozoic (Fig. 6.2). All superfamilies also have extant species reported to be swimmers, with the exception of the Comasteracea.

The Solanocrinitacea Jaekel 1918 has no extant species - it is a strictly Mesozoic taxon. Description of the radial articular faces of members of the superfamily shows morphology convergent on that of the comasterids with radials "commonly low and wide" and "muscular fossae generally low" (Ubaghs, 1978, p. T873). In contrast to the gracile arms of typical swimming comatulids, the arms of species in this super-family are often very robust (Fig. 6.3). Interestingly, the family Thiolliericrinidae Clark 1908b, which is taxonomically assigned to the Solanocrinitacae based on cup similarities, actually possesses a stalk with large columnals with synarthrial articu-
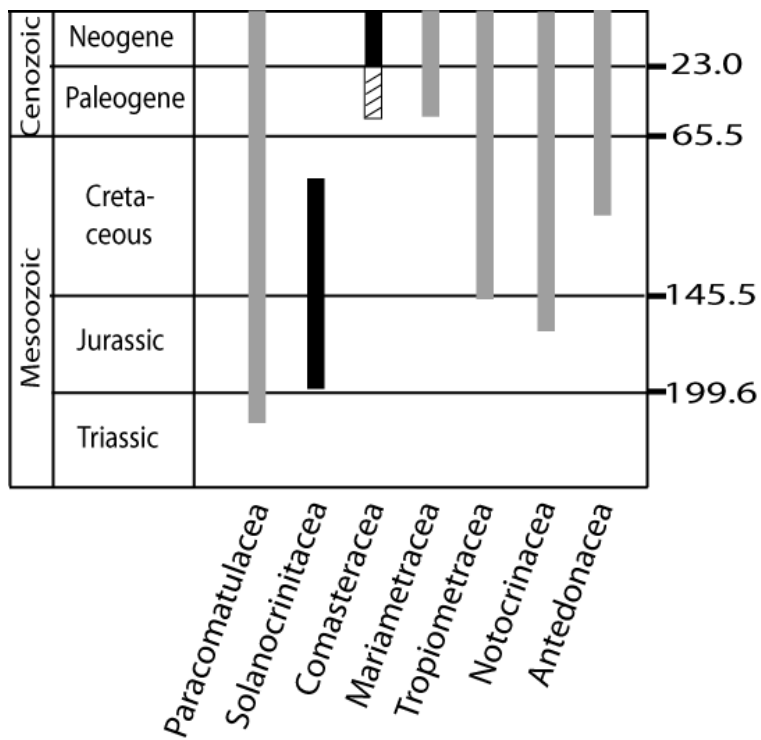
Figure 6.2: Stratigraphic ranges of comatulid superfamilies from Rasmussen and Sieverts-Doreck (1978). The range of the Comasteracea has been revised to exclude an invalid Paleogene occurrence (hatched portion of range; Appendix I). Superfamilies with extant species known to swim are shown in grey. Time scale from Gradstein and Ogg (2004).

lations (Ubaghs, 1978). The stalk is similar to that of extant and fossil members of the Family Bourgueticrinidae de Loriol 1882, which some authors have proposed as descended from a thiolliericrinid (Simms, 1988a). If the placement of Thiollieri-crinidae within the Solanocrinitacea is accurate, it may imply that some members of the superfamily attained a secondarily sessile lifestyle in certain environments (e.g., reefs Ubaghs, 1978). Based on the lines of evidence discussed above, species assigned to the Solanocrinitacea likely were not capable of swimming. If the Comasteracea, Solanocrinitacea, or both are derived from swimming comatulid ancestors it would mean that obligate crawling and/or sessile crinoid clades have evolved from swimming lineages on multiple occasions.

Perhaps most interesting from the perspective of comatulid swimming are the paracomatulids. *Paracomatula* is represented by the Late Triassic *P. triadica* Hagdorn and Campbell 1993 and the Early Jurassic *P. helvetica* Hess 1951. *Eocomatula* is known from the Early Jurassic *E. interbrachiatus* Blake 1876 and fragmentary remains of two articulated columnals in the unfused centrodorsal of the Late Triassic *E. decagonalis* Simms 1994, the latter of which are uninformative in the context of swimming. The relatively complete crowns of the *Paracomatula* specimens reveal morphology that is characteristic of extant swimming taxa: relatively long, gracile arms; relative high radials with very large muscular facets; a very small calyx; a stalk that has been dramatically reduced in length almost to a cirriferous, centrodorsal. These characteristics also seem to apply to the less well-known remains of *E. interbrachiatus*. Based on these observations it is plausible that the earliest fossil comatulids were capable of swimming.

6.4.3   Phylogeny of swimming comatulids

While the fossil record suggests that swimming may have appeared early among the comatulids, examining their phylogeny should prove informative in determining

Figure 6.3: Jurassic specimen of *Solanocrinites costatus* Goldfuss 1829, USNM S2909, showing the very robust arms present in members of the superfamily Solanocrinitacea. The nearly 1 cm wide arms are unparalleled among modern stalkless crinoids (cf. Janevski and Baumiller, 2010, Appendix 3).

whether it is plesiomorphic to the group. Figure 6.4 shows an inferred, family-level comatulid phylogeny based in part on preliminary molecular phylogenetic analyses (Rouse et al., 2010), with the motility of member species added.

At present, the most parsimonious phylogenetic scenario is one in which swimming is plesiomorphic for extant comatulids (Fig. 6.4). Swimming may have evolved directly in concert with initial stalk loss (centrodorsal formation) in the the last common ancestor of comatulids, and has been secondarily lost in obligate-crawling groups like the diverse, extant Comasteracea. If future phylogenetic work can show that the extinct Solanocrinitacea share a common ancestor with crown group comatulids it might imply that swimming was independently lost in that lineage. As swimming is also a common feature of comatulids, if it is not plesiomorphic, it would imply multiple, independent acquisitions of swimming in separate comatulid lineages.

Finally, "comatulids" as currently conceived may be a polyphyletic group as the Atelecrinidae Bather 1899, a swimming family, could represent a non-comatulid lineage that evolved independently from comatulids (Messing, 2003; Fig. 6.4). This
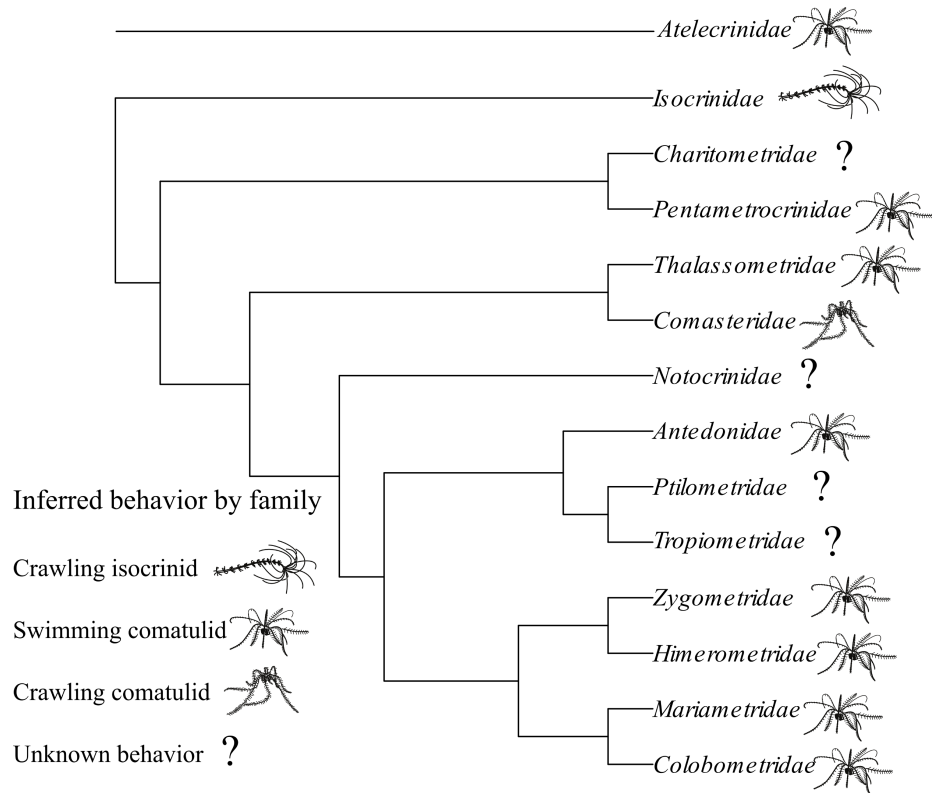
Figure 6.4: A preliminary comatulid phylogeny inferred from molecular phylogenetic analyses (Rouse et al., 2010). Motility habits of member species within clades are shown where known. Likely all comatulids can crawl, which is logical given that crawling is also present in the stalked Isocrinidae. The Atelecrinidae may not be true comatulids (see text for discussion). Swimming may be plesiomorphic. Swimming may also have evolved twice if the Atelecrinidea are found to have indepedent origins. Swimming appears to have been lost in the derived Comasteridae.

would imply that swimming has evolved at least twice in the transition from stalked to stalkless crinoids. These hypotheses merit testing with a more robust reconstruction of the phylogenetic relationships of comatulids, in particular one that includes revised systematics of fossil comatulid specimens.

6.4.4 Comatulid motility through time

Comatulids diversified during the last 220 million years, but the exact timing of diversification is unclear. A direct reading of the comparatively poor comatulid fossil record suggests that before the Recent, stalked crinoids dominated crinoid diversity (Janevski and Baumiller, 2010, fig. 1). The number of fossil species through time shows a peak in diversity during the Late Cretaceous (Fig. 6.5), possibly in concert with expansion of European carbonate platforms. However, this signal may be due in part to biases based on a large amount of marine sedimentary rock available for sampling in the Late Cretaceous (Peters and Foote, 2001; Smith, 2001), and/or to monographic effects (e.g., most Late Cretaceous species come from two works: Gislén 1924; Rasmussen 1961).

The morphological plasticity of modern comatulids makes them a challenging subject for taxonomists (Messing, 1997). This same plasticity and the resultant variability was likely present in the geologic past, and thus some named fossil species may be synonimies. Oversplitting of comatulid species may create a bias toward overestimates of species richness since full population-level variation is so rarely known for fossil specimens, which are described only from the calyx and centrodorsal. A worst-case example was shown by Peck and Watkins (1972) who studied a collection from two closely spaced horizons of 40 comatulid specimens that individually could have been referred to separate genera in separate families; recognizing that these specimens were part of an ontogenetic series allowed their assignment to a single species.

Adding to the difficulties in studying the timing of comatulid diversification are
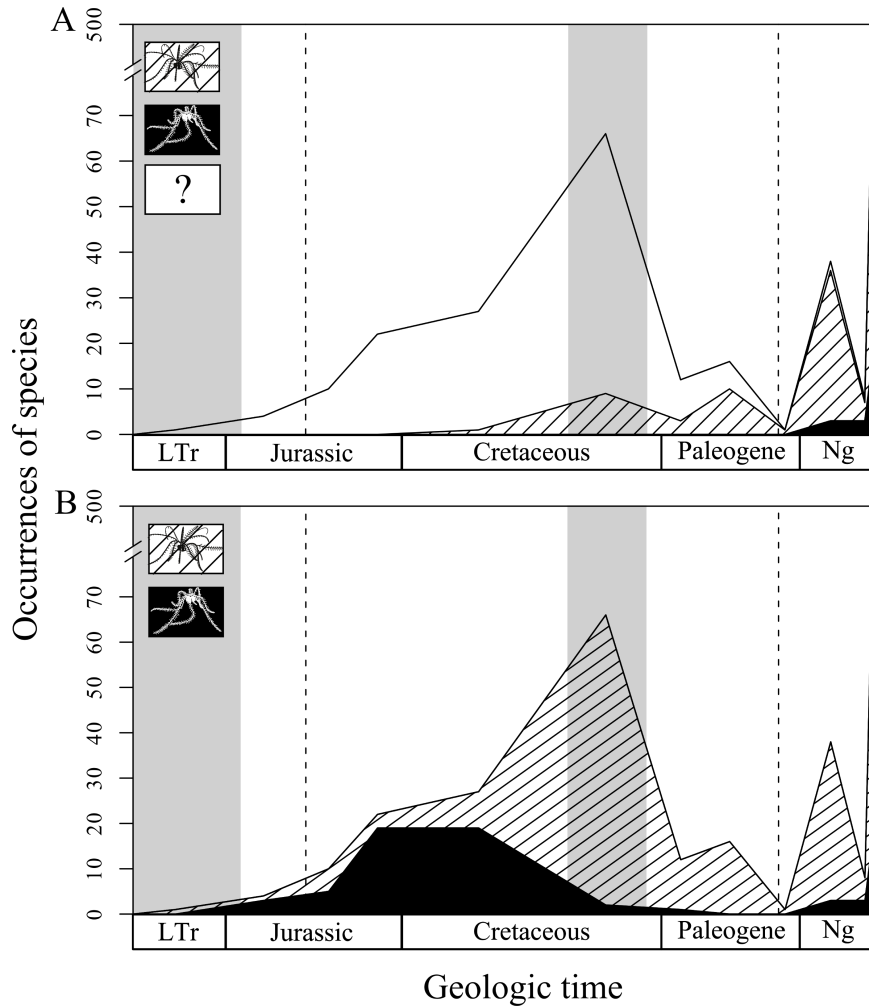
Figure 6.5: Unique occurrences of fossil comatulid species plotted at midpoints of epoch of occurrence (the finest available temporal resolution). Vertical lines (dashed) show onset of expansion in number of reef sites during the Jurassic and Paleogene (see Kiessling, 2009, fig. 3). Shaded areas indicate major times of innovation associated with the Mesozoic marine revolution (Vermeij, 2008). A) Occurrences in which motility behavior is based only on membership in extant families that are known to swim. B) Motility for fossil occurrences also inferred from functional morphology of fossil specimens.

dissimilar approaches to comatulid taxonomy between extant and fossil taxa. The tightly sutured centrodorsal and calyx result in taphonomic bias in the preservation of comatulids, with fossil specimens described primarily from those elements, as the arms, pinnules, and cirri of comatulids rapidly disarticulate after death (Meyer and Meyer, 1986). This bias affects comatulid systematics: most fossil taxa are described from isolated calyxes, but systematic work on extant comatulid morphology is based on elements of the arms, pinnules, and cirrals (cf. Helgen and Rouse, 2006, Table 1), which are rarely preserved as fossils (Jagt, 1999). These differences may allow more species to be identified among extant crinoids than can be done with fossil specimens, which often consist only of the centrodorsal and calyx, and which may be $< 1cm$ wide (Clark, 1921).

Furthermore, the comatulid fossil record is depauperate compared to that of stalked crinoids even in Neogene marine formations where comatulid diversity is much greater among extant taxa and where we might expect them to have a more diverse fossil record (Donovan and Veltkamp, 2001). The lower preservational potential of comatulids compared to stalked crinoids may explain the relative dominance of stalked crinoids in the entire fossil record, and to the appearance that the majority of comatulid diversification occurred geologically recently (Janevski and Baumiller, 2010, fig. 1).

However, a very recent diversification seems unlikely given the 220-million-year fossil record of comatulids. Further, most comatulid higher taxa appeared in the Mesozoic, suggesting an early morphological diversification (Fig. 6.2). Numerous studies have shown an early attainment of high disparity at low taxonomic diversity (reviewed in Erwin, 2007); relevantly, for crinoids (Foote, 1994, 1999). Comatulids clearly diversified to at least some extent by the Late Cretaceous (Fig. 6.5), and had a wide geographic distribution with occurrences in present-day Europe, Asia, North America and South America. Additionally, comatulids occurred in a wide

range of environments, including shallow-water settings, while stalked crinoids were relegated to deeper environments beginning in the Mesozoic (Meyer and Macurda, 1977; though, see Aronson et al. 1997 for an example and discussion of exceptions for stalked crinoids). In light of the evolution and radiation of durophagous predators during the MMR (Vermeij, 1977, 1987; Meyer, 1985), the relative success of comatulids was thought to be due to their ability to locomote, as stalked crinoids were thought to be largely sessile (Meyer and Macurda, 1977; Meyer, 1985).

Measuring comatulid species diversity through time from fossil occurrences is fraught with difficulty; occurrences are generally too few to use occurrence-based diversity measurements (e.g., Alroy, 2010a), range-based diversity methods have flaws (Alroy, 2010b), and would not be useful here as few taxa occur more than once. Figure 6.5 should not be treated as a diversity curve; no sampling standardization nor normalization of any sort has been applied (including for interval duration), and so it is only a depiction of fossil comatulid occurrences in geologic epochs. Despite these qualifications, it is possible to assess the first appearance and relative proportions of motility capability in relation to geologic and biologic events. Figure 6.5A shows all known comatulid species occurrences, shaded to denote fossil and extant species that belong to families that swim (hatched), do not swim (black), or which have uncertain motility habits as members of extinct families (white). Unsurprisingly, the number of species we can assign in this manner decreases into the geologic past, with the clearest signal being that most extant species can swim, and they are members of geologically long-lived higher taxa.

In Figure 6.5, I have overlaid information on the timing of major biologic changes associated with the MMR (Vermeij, 2008), and the beginning of expansion of the number of reef sites during the two largest peaks in reef site number for the post-Paleozoic (Kiessling, 2009). The first appearance of comatulids is during a time of the early phase of the MMR, when major predator-prey innovations occurred across many

marine taxa (see Vermeij, 2008, Table 6.1), but also around the time when evidence for benthic predation in the form of bite marks on stalked crinoids by cidaroid urchins has been observed (Baumiller et al., 2010). The Late Cretaceous peak in comatulid occurrences coincides with the peak in innovation during the MMR, but this could be due to preservational artifacts affecting both patterns. Lastly, the first appearance and diversification of the extant, obligate-crawling species within the Comasteracea appears in concert with the onset of expansion of Neogene reef sites.

In Figure 6.5B, I assigned all fossil species to likely motility habits based on my observations of swimming and crawling comatulid functional morphology. The earliest comatulids were likely capable of swimming, and fossil comatulid occurrences are frequently of taxa that were capable of swimming. Increases in the number of occurrences of likely obligate-crawling comatulids occurred at the onset of the expansion of Jurassic-Cretaceous reef sites. At present it is not possible to determine whether this effect is attributable to greater preservation of crawling species when reef sites are preserved, or if it is a true signal of a relative increase in crawling compared to swimming species. The coincident expansion of extant crawling species during the time of increase in number of Neogene reef sites suggests that obligate-crawling taxa have diversified in reef environments.

6.5   Discussion

By applying observations of extant swimming comatulids and traits that are required for swimming to the fossil record of comatulids I have been able to determine relative proportions of crawling and swimming comatulid species through time, and in relation to the MMR. I strongly caution against blanket application of the observations in Table 6.1 to any fossil crinoid: possession of a few of these traits may not be sufficient to allow swimming, and species with all of these traits may not have been able to swim. For example, while gracile arms may commonly characterize swim-

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mers, there were surely gracile-armed crinoids in the geologic past that did not swim. Nonetheless, the evidence for a swimming life mode presented here are reasonable when carefully applied in consideration of other evidence for a taxon's life mode, and should be most robust when applied to fossil comatulids.

The observations of extant swimming crinoids are the best resource for inferring life habits of extinct species. I do not discount the possibility that some extinct species may have evolved unique solutions to allow swimming. For example, the radial articulation represents the proximal-most articulation of a series of muscular articulations runing the length of the crinoid arm. The thrust-generating capacity of an individual articulation, or multiple in concert, has not been fully considered for extant comatulids. Thus a fossil comatulid with very small radial muscular articulations may have still been able to swim by compensating with their remaining musculature. Some extinct species may have had a greater capacity of thrust generation relative to their weight than do living comatulids. Testing this idea would be most easily accomplished using biomechanical principles, observations of modern analogs, and in a phylogenetic context.

It seems clear that comatulids first evolved during a time of increased predatory behavior in benthic and pelagic realms (Vermeij, 2008; Baumiller et al., 2010). However, the diversification of swimming and crawling species has not proceeded in tandem, and there is no clear evolutionary transition from crawling to swimming comatulids; the reverse may have occurred, possibly on more than one occasion. The putative role of rapid crawling in extant stalked crinoids is to allow escape from benthic predators (Baumiller et al., 2008). Crawling in comatulids may serve a similar function, but this does not explain the role of swimming in their macroevolutionary success.

It has previously been observed that currents greatly increase the distance traveled when a comatulid swims (Shaw and Fontaine, 1990). However, observations

from modern aquaria reveal just how dramatic this effect can be - in the absence of current, the horizontal translation of a swimming comatulid is virtually nonexistent. Additionally, comatulid swimming would do little to aid in escape from nektonic predators, which evolved new predatory innovations during the MMR (Vermeij, 2008). If swimming is an anti-predatory strategy, the clearest role is for it is to aid in escape from benthic predators, an evolutionary next step from the benthic-predator escape crawling in stalked crinoids.

However, numerous lines of evidence suggest that fish do sometimes prey on comatulids: fish-related arm loss and crown damage, crinoid remains inside fish guts, and direct observation of fish attacks (Meyer and Macurda, 1977; Meyer, 1985). Nocturnal and cryptic behavior of comatulids could be adaptations to visual hunters such as diurnal fish (Meyer and Macurda, 1977). Additionally, the possible pattern of apparent increase in crawling comatulid species during times of reef expansion may suggest a greater role for crawling over swimming in reef environments, where nektonic predators may live at high density. In these high-energy environments swimming may sometimes be detrimental, potentially attracting nektonic predators. In these cases the ability to efficiently crawl, to be cryptic or semi-cryptic, and to be nocturnal may be of greater importance than transport out of the benthos. Swimming would be far more beneficial in escape when benthic predators are of greater concern. If obligate crawling represents the loss of swimming ability, it could mean that swimming is unnecessary for success or detrimental in reef environments. For example, obligate-crawling species might benefit from greater arm flexibility in order to seek refugia from predators and more generally to cope with environmental stresses in reef environments. However, while swimming species may be well-adapted to non-reef environments, modern reef environments do include swimming species of comatulid crinoids. Nonetheless, I would predict that relatively young Neogene reefs would overwhelmingly serve as the home to the geologically young Comaster-

acea, while swimming species would be more likely to be found in a wide range of environments. Swimming may be particularly useful on submarine plains where benthic predation is a threat to survival, and where cryptic and nocturnal behaviors are useless.

Lastly, the relative proportions of swimming and crawling comatulid species reported here might be affected by preservational biases. If obligate-crawling species prefer reef environments, it is not surprising that times of preservation of a high number of reef sites will also show greater diversity for these species. Further, if the environments that favor obligate-crawling species are generally poorly preserved, crawling species diversity will appear lower except in those times of good reef site preservation. This would partly explain the possibly recent diversification of the Comasteracea, which have their first fossil appearance at the time of growth of Neogene reef sites, and represent the most species-rich clade of extant comatulids.

6.6   Conclusion

The evolutionary history of comatulids may have been influenced by complex biological and geological phenomena, including evolution of and expansion of reef sites, and the macroevolutionary effects of the MMR. Swimming is only present in some comatulid species, and at present the most parsimonious evolutionary scenario is that obligate-crawling species represent derived lineages that lost the ability to swim. Fossil comatulid species may have had differing relative diversities of swimming and crawling comatulids, the earliest comatulids may have been capable of swimming, and for most of comatulid history, including today, swimming species have dominated their diversity. Thus, a simple view of evolution from a stalked crinoid, to an obligate-crawling stalkless comatulid, and finally a free-swimming comatulid, is not the most likely scenario for comatulid evolution. Instead, the comatulid fossil record appears much more complicated: the ability to swim may have been gained, and lost, multiple

times over the course of comatulid evolutionary history.

6.7 Acknowledgments

CHAPTER VII

Conclusion

Why some species have succeeded while others have failed is one of the most intriguing questions for a paleontologist. The fossil record of marine invertebrates provides a great avenue for determining if and when we can know the cause of causes of extinction and survival. The fossil record of crinoids is particularly strong for investigating these questions because they remain with us today, but were especially diverse in the geologic past.

This dissertation began by investigating the preferential extinction of some taxa, or extinction selectivity, using taxonomic databases. This required development of new methods, and has spurred new advances into our understanding of how extinction selectivity has varied through time. Using data from the Paleobiology Database (PaleoDB) and a method for detecting non-random extinction, I was able to show in Chapter II that the Phanerozoic record of marine invertebrate extinctions was non-random during most intervals of geologic time. This research demonstrates without using a traditional correlated-trait approach that extinction selectivity is the norm in the history of life. These results complement studies that have found correlations between extinction probability and extinction-promoting traits, but also demonstrate extinction selectivity even when traits promoting extinction are unknown or unobservable.

Chapter III followed up on the work of Chapter II by more directly investigating data from the PaleoDB for the Cretaceous-Paleogene (K-Pg) and Permian-Triassic (P-Tr) extinction events, the two best-known mass extinctions. Chapter III showed that extinction selectivity is stronger at these intervals than at any other time in the geologic past, which is surprising given that some claims have been made that mass extinctions may be less selective than background times. This clearly does not appear to be the case at these extinction events. An expansion of the method from Chapter II was further able to show that regional selectivity was not the cause of extinction selecitivity, suggesting that selectivity for one or more traits was important. In combination, these two chapters demonstrate very clearly that not all patterns can be extrapolated across the taxonomic hierarchy: nonrandom extinction of species via selective, clustered species extinctions gave the appearance of random extinction of genera with regard to their species richness. Numerous studies have observed that species richness does not explain survivorship of genera at the K-Pg and P-Tr extinction events, and here, for the first time, that pattern is explained as the simple expectation of very high extinction selectivity affecting species extinctions. When species richness fails to buffer against extinction of genera we may reasonably infer that extinction selectivity ran high.

In order to more carefully test extinction selectivity, a taxonomic study was undertaken for crinoids across the P-Tr extinction event. Given the strong evidence of extinction selectivity at the P-Tr extinction event, Chapter IV presents a test of whether crinoids experienced extinction selectivity. I showed via the first numerical phylogenetic analysis of Paleozoic to post-Paleozoic crinoids that post-Paleozoic crinoids are monophyletic. This means that crinoids were reduced to only one lineage around the time of the P-Tr extinction event. The generally small body size of the earliest post-Paleozoic crinoids, possession of traits conducive to mobility, and adaptation to soft substrates, may indicate that these factors contributed to survivorship at

the P-Tr extinction event. Previous studies that have evaluated extinction selectivity at the P-Tr may have been in error as current taxonomic databases suggest, instead, that crinoids were dramatically reduced in diversity before the P-Tr extinction event.

Though crinoids rebounded from the P-Tr extinction event, their diversity dynamics have undergone major changes in the ~250 million years since. The most striking change is the diversity and habitat dominance of modern crinoids by the stalkless comatulids (Order Comatulida). Early work on comatulid crinoids, partly at the University of Michigan, suggested that it was the comatulids' increased capacity of mobility that led to their success in the face of the increased predation pressure that attended the Mesozoic marine revolution (MMR) (Meyer and Macurda, 1977). In Chapter V and Chapter VI, I followed up on this University of Michigan tradition by investigating the role of swimming ability in comatulid success.

Chapter V presented an analytic model for thrust generation in swimming crinoids, revealing for the first time some of the prerequisites for crinoid swimming, not the least of which was reduction of the stalk. Further, reductions in crown weight are also required, and these occurred primarily by narrowing of the arms, and possibly by reduction in arm number. Swimming comatulids appear to have enlarged musculature to compensate for these reductions. Based on these observations, an evolutionary scenario was considered in which swimming evolved to allow more efficient escape from benthic predators, as benthic predators also diversified during the MMR. Crawling may allow comatulids to avoid predatory fish, but swimming would not. Instead, swimming likely helps in escape from benthic predators.

In Chapter VI, I took the observations from Chapter V, combined them with observations of modern swimming comatulids, and applied them to the fossil record of comatulid crinoids. By doing so I was able to show that the earliest comatulids had the requisite functional morphology to swim. Lineages that did not swim likely lost the ability. It now seems that comatulid evolutionary history has included the loss of

swimming ability at least twice. The expansion of reef sites may have provided habitats suitable for comatulids that could not swim. Swimming, meanwhile, appears to be both primitive and common among comatulids. Swimming likely appeared in the Late Triassic, during the early stages of the MMR. In the time since, comatulids have dominated crinoid diversity, with obligate-crawling and swimming comatulid clades possibly having very different patterns of diversity through time. The most species-rich extant family of comatulids, the reef-dwelling comasterids, are geologically young and cannot swim.

Using taxonomic databases, new analytical methods, and observation of living and fossil crinoid specimens, this dissertation investigated some of the proposed causes for extinction and survival in marine invertebrates. Extinction selectivity has been frequent in the geologic past, and was especially strong at the P-Tr extinction event, a time during which crinoids were reduced to a single lineage. Whether crinoids were selected against at the P-Tr extinction event is still unknown. The diversity of crinoids since the P-Tr has not been static. The early phase of the MMR and benthic predators may have provided evolutionary pressure that drove comatulid evolution. This set the stage for the wax and wane of clades of swimming and crawling comatulid crinoids, which were may have been affected by the major biologic and geologic changes that the earth has experienced over the last ~250 million years.

APPENDICES

APPENDIX A

Evidence for selectivity for separate (paleo-)continents
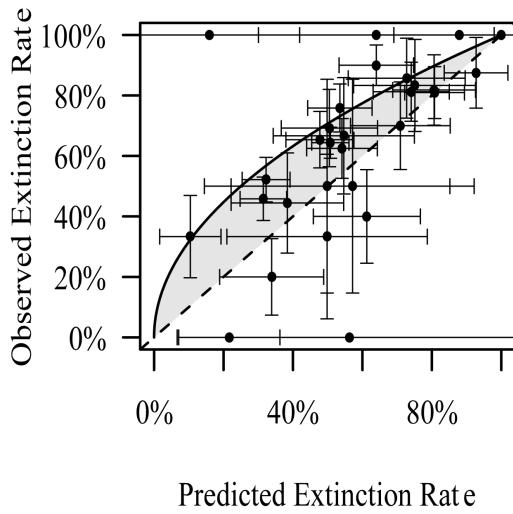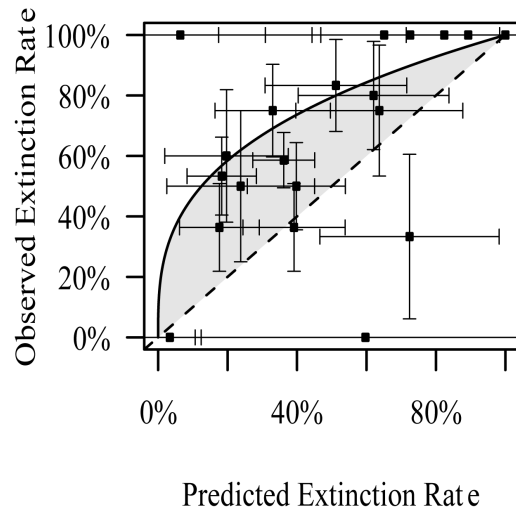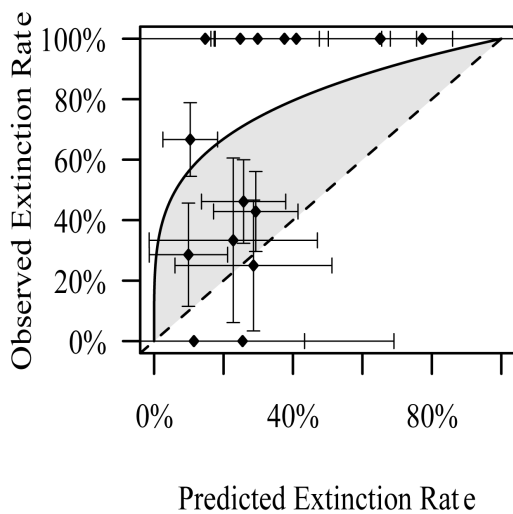
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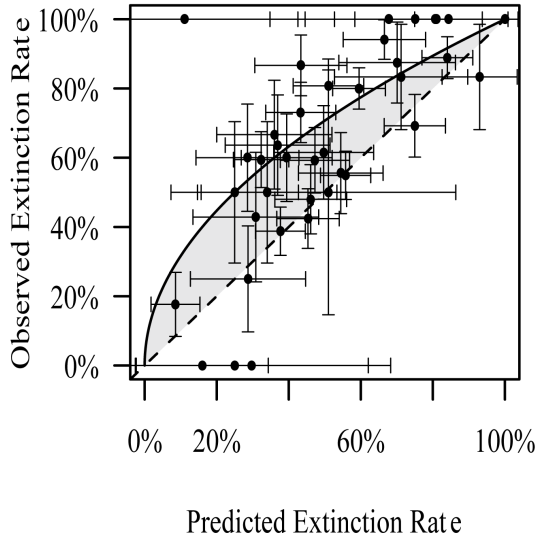
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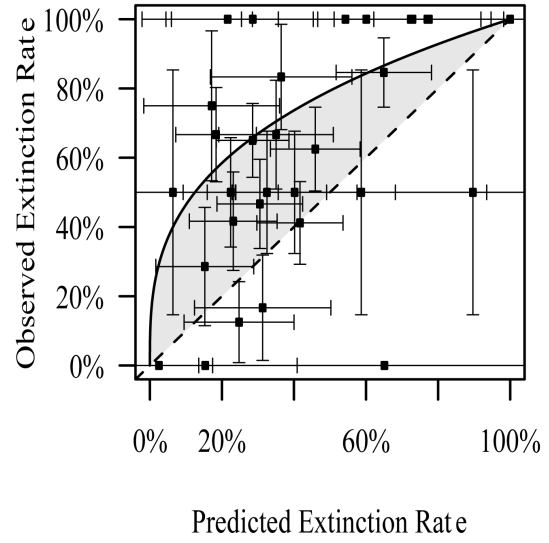
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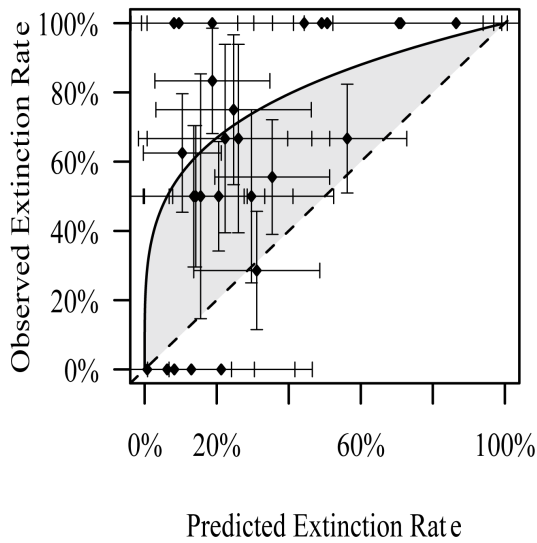
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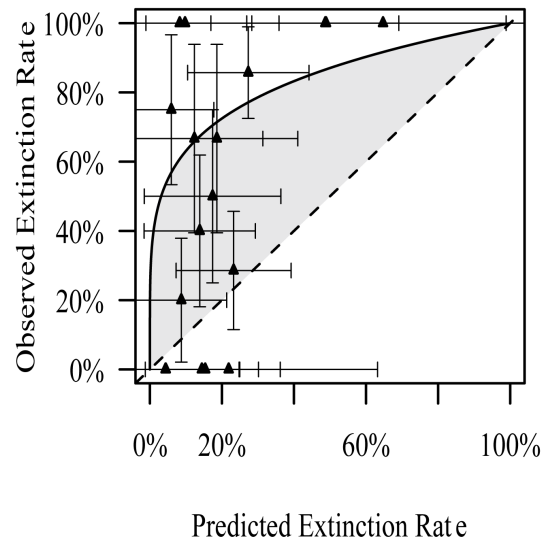
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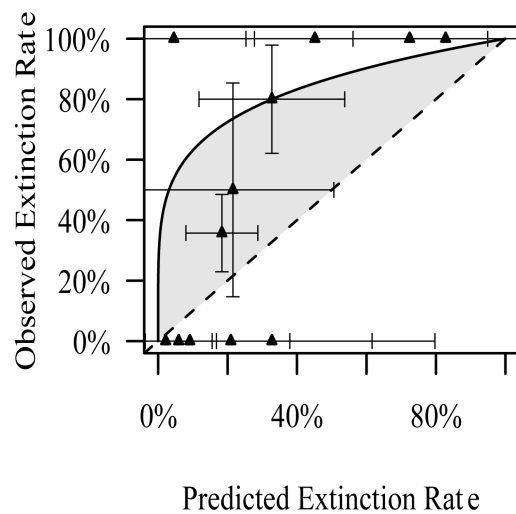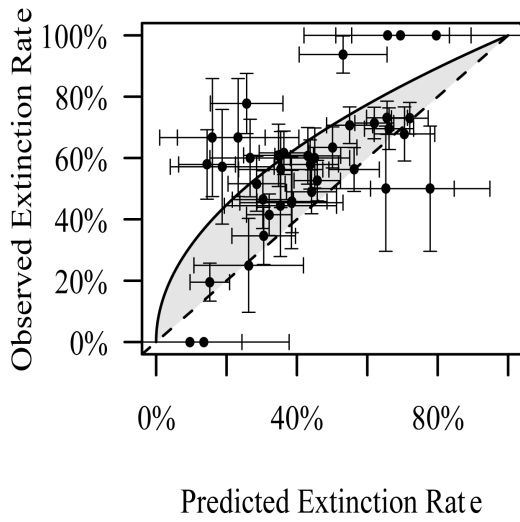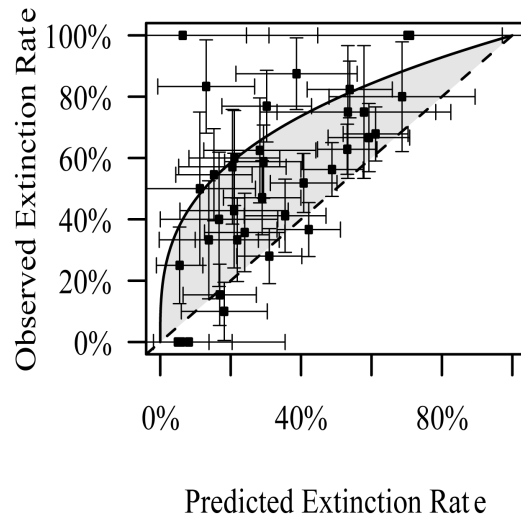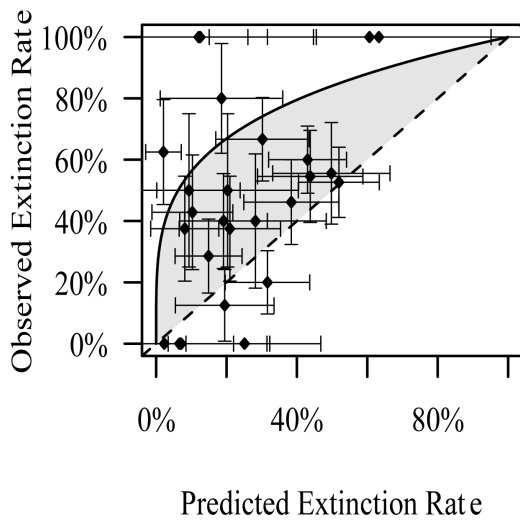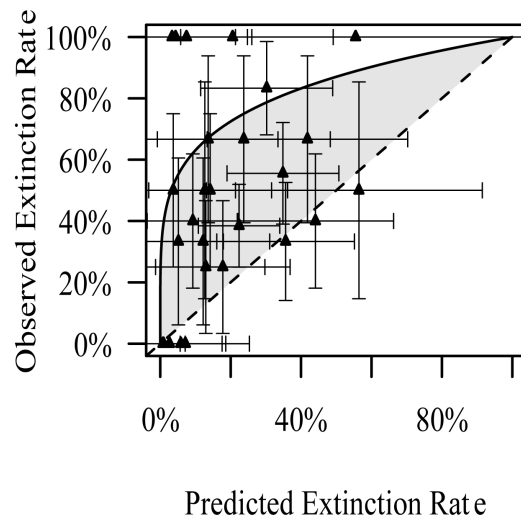## 2 Species Richness Category
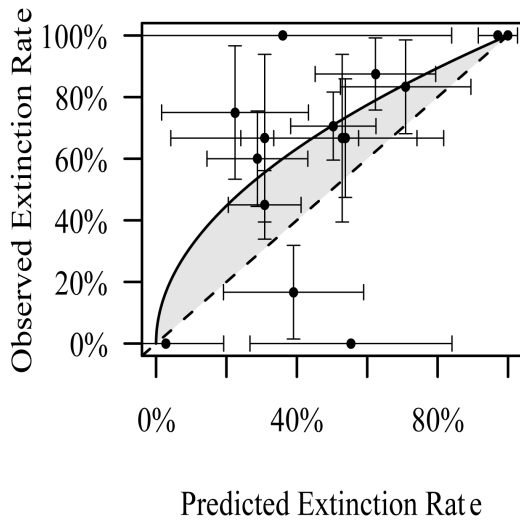
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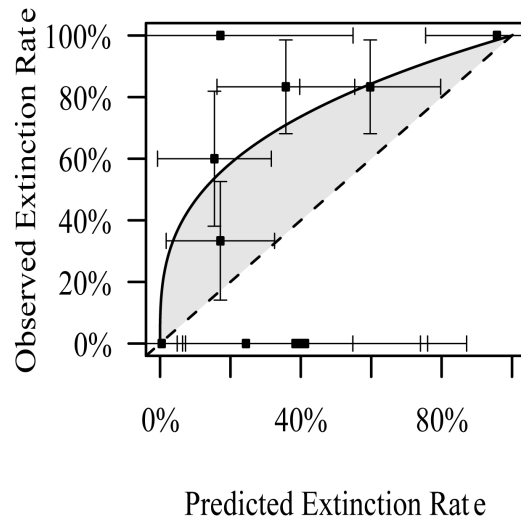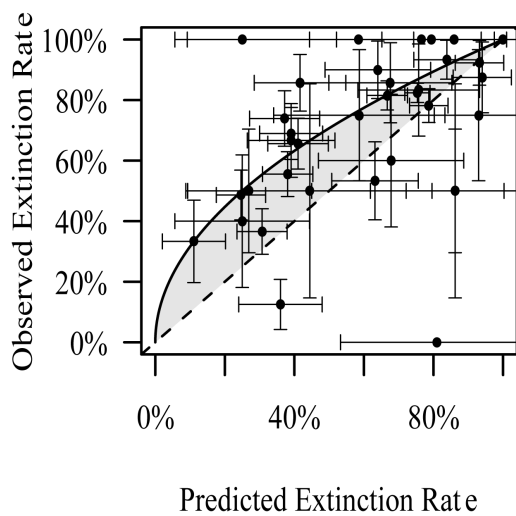

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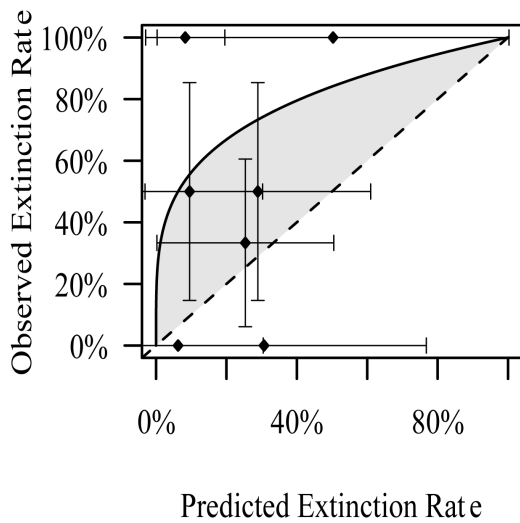
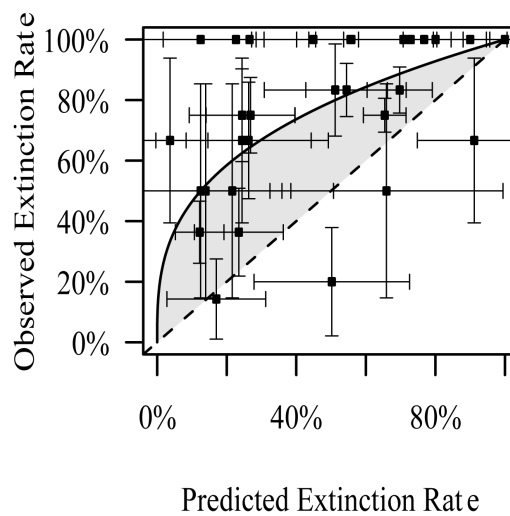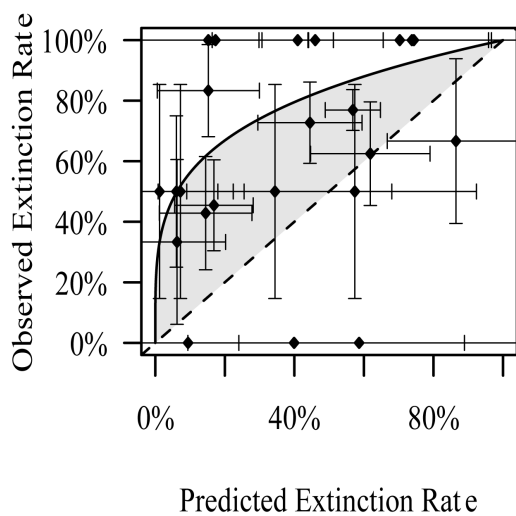## 5 Species Richness Category
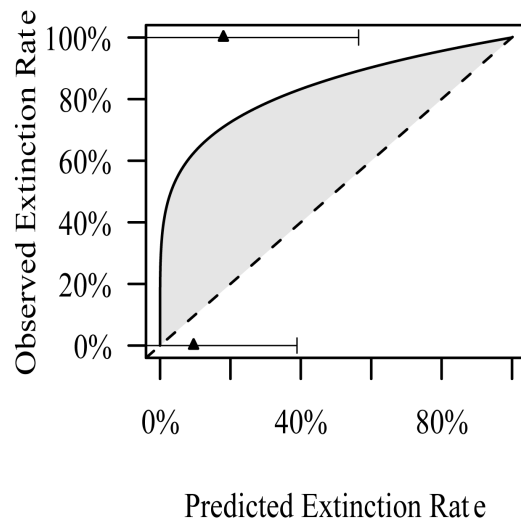
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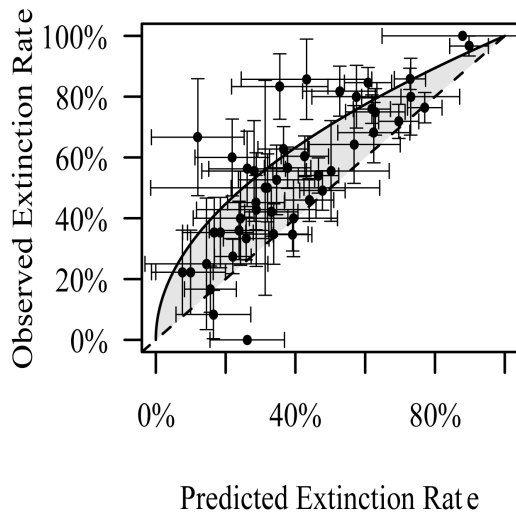
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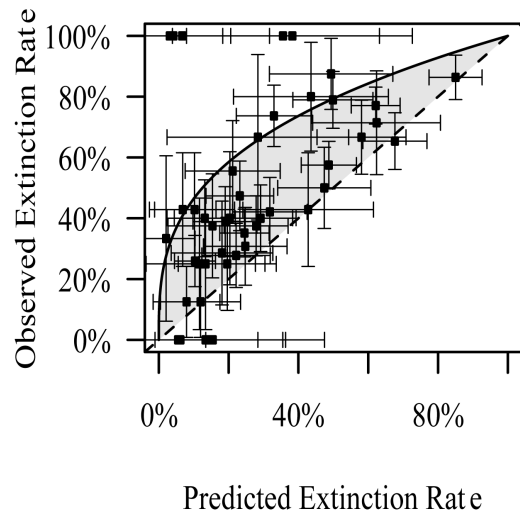
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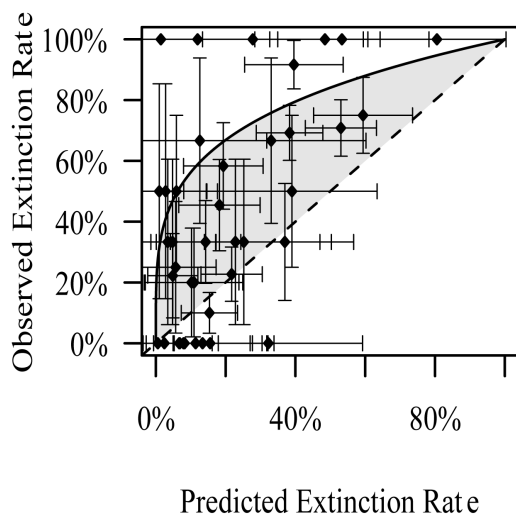
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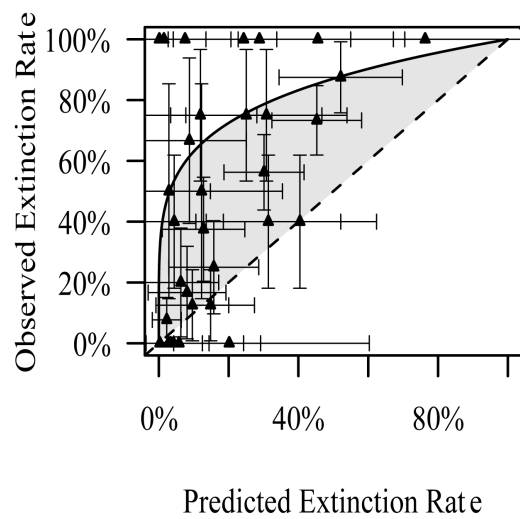
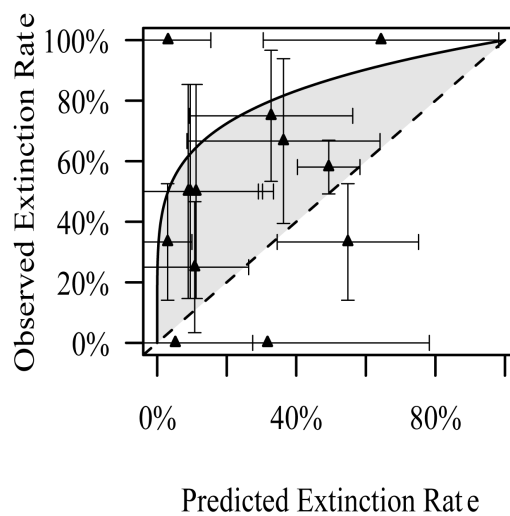# Paleo-Australia

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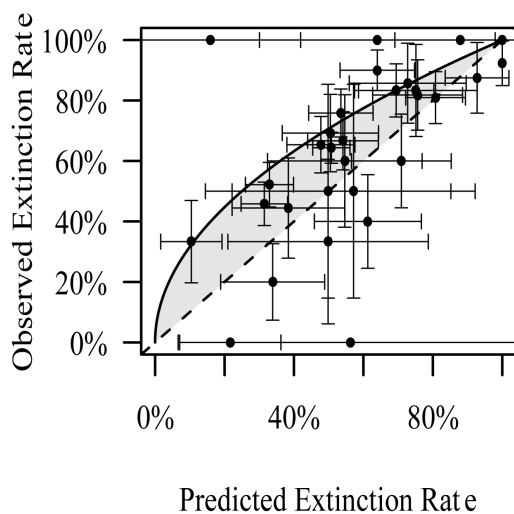
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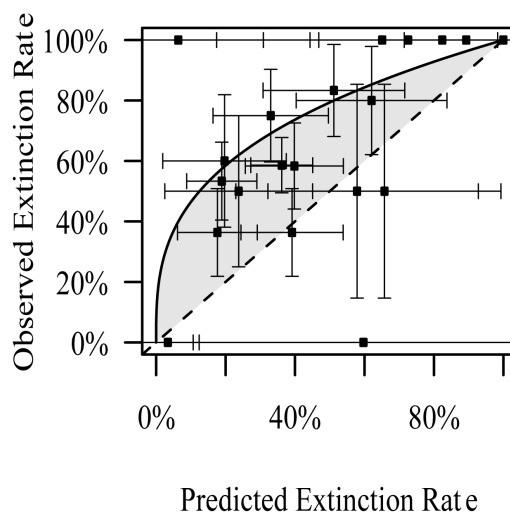
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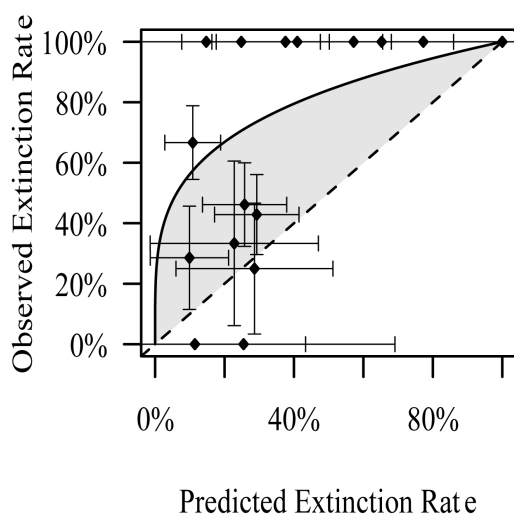
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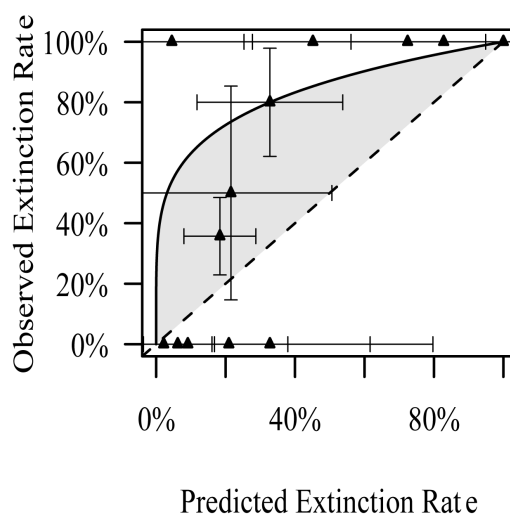
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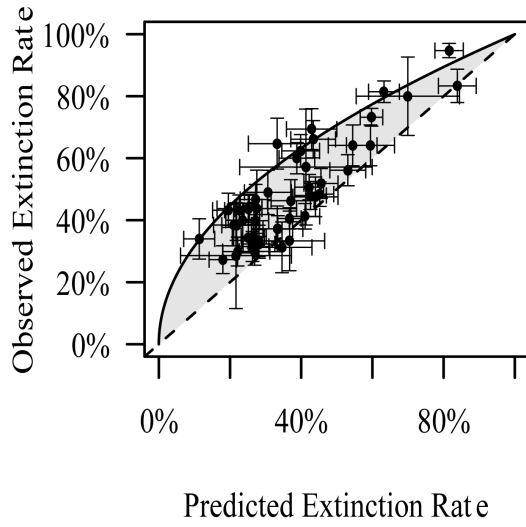## 3 Species Richness Category

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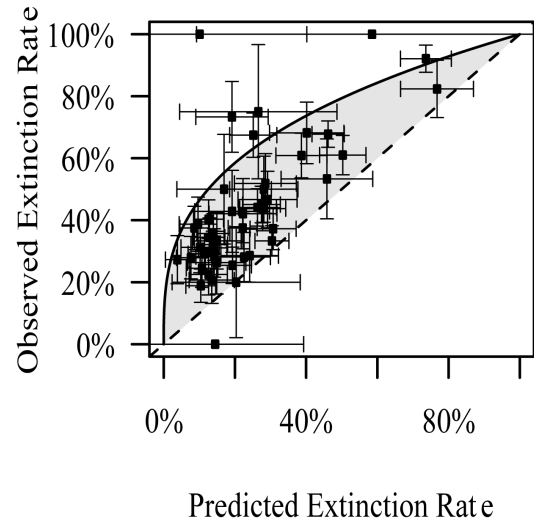

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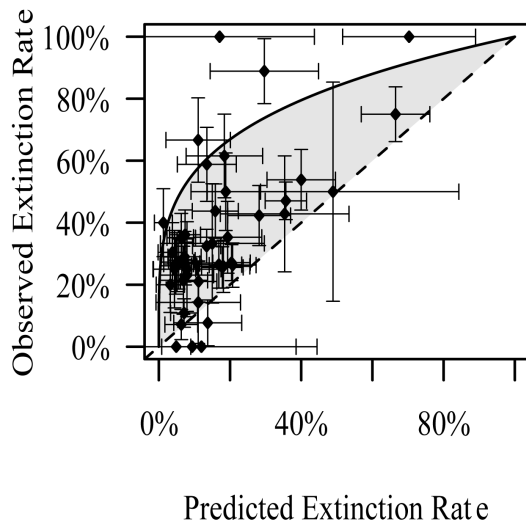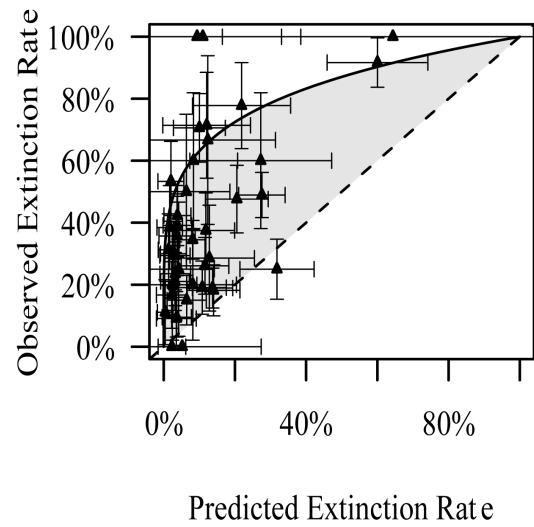## 5 Species Richness Category

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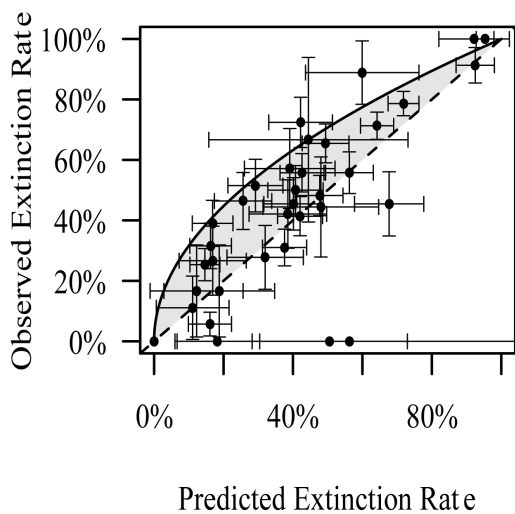
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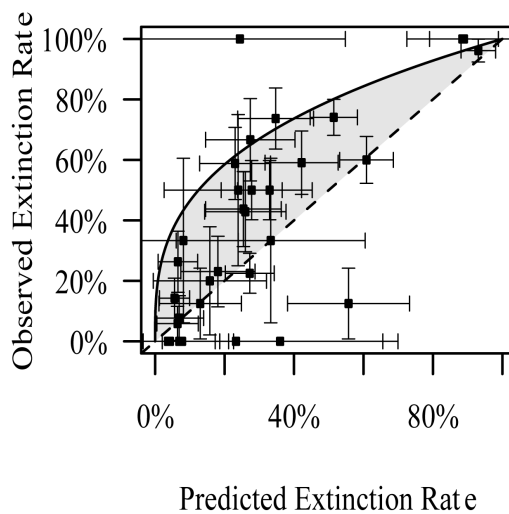
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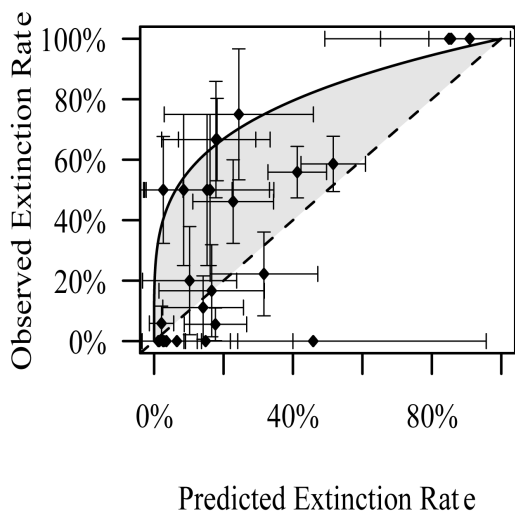
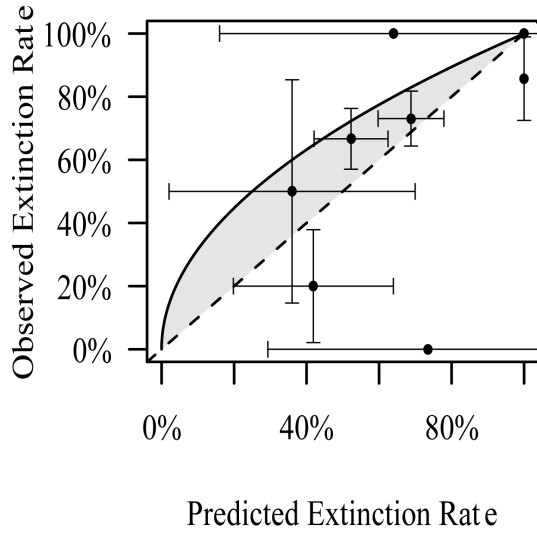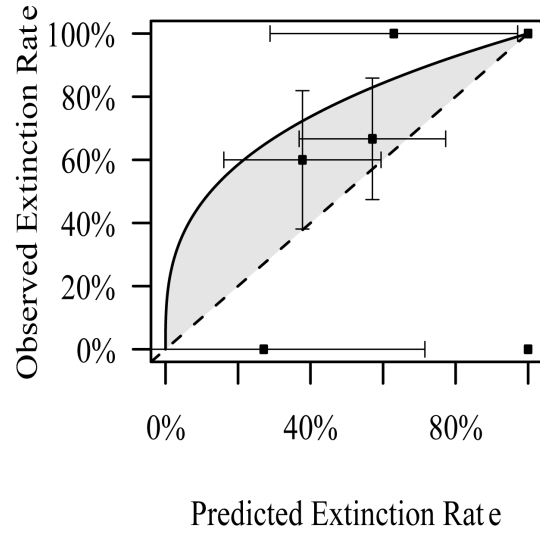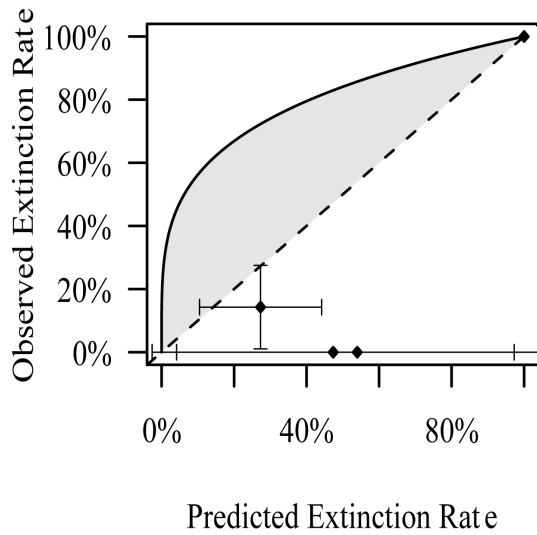5 Species Richness Category
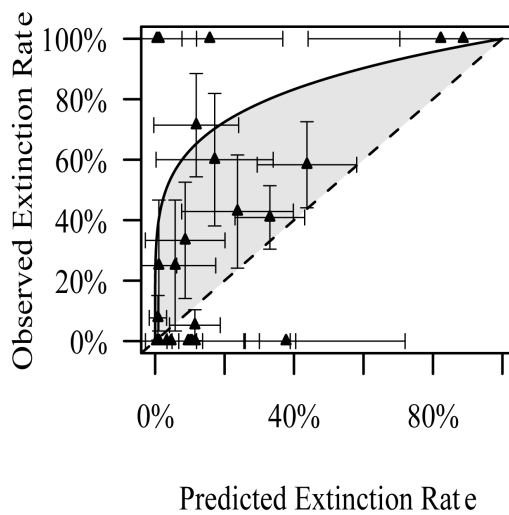
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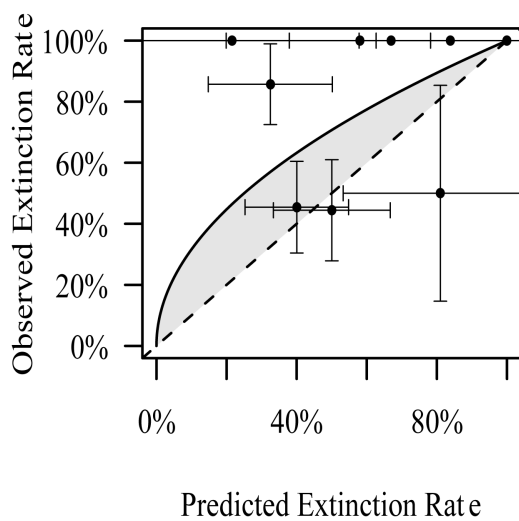
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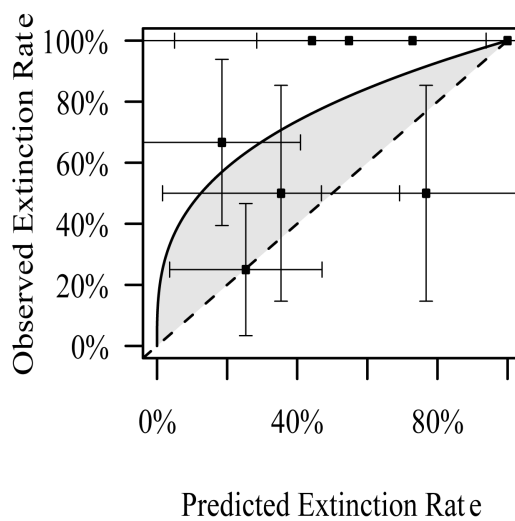
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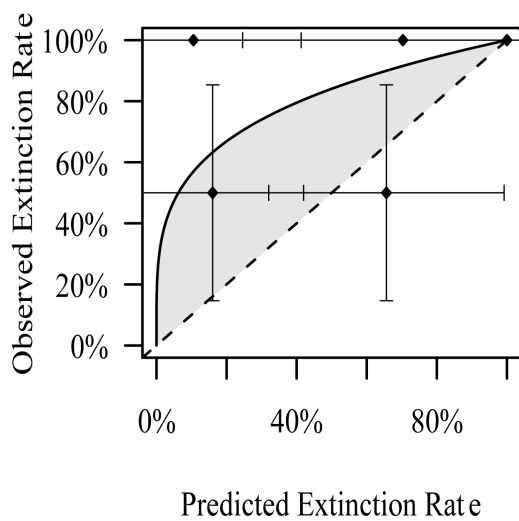
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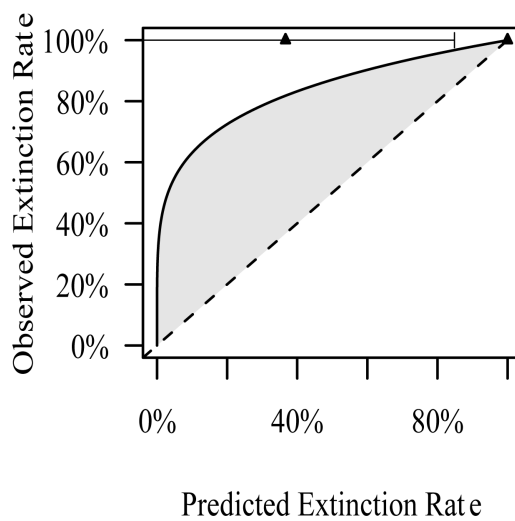
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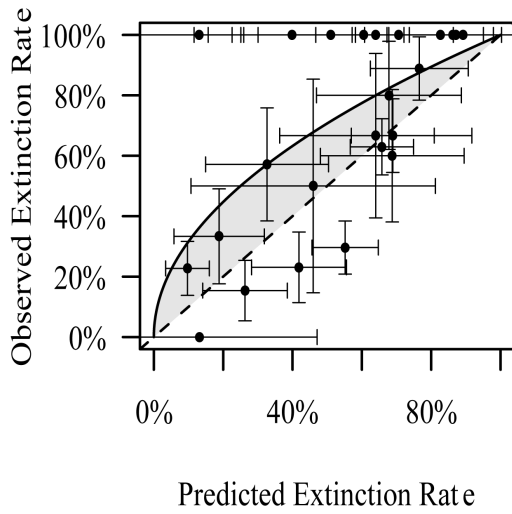
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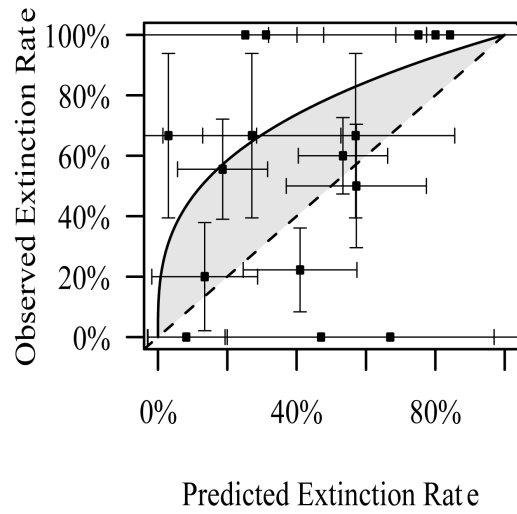
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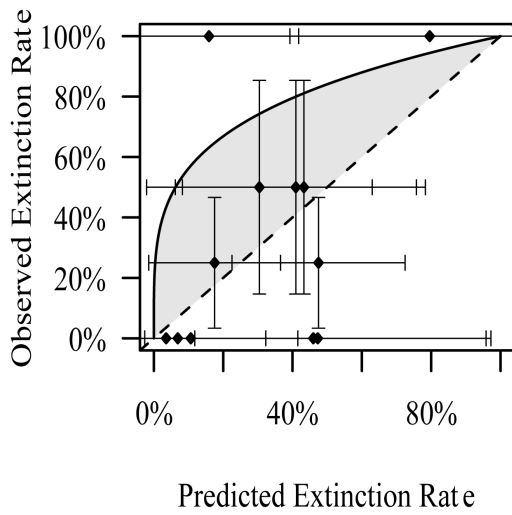
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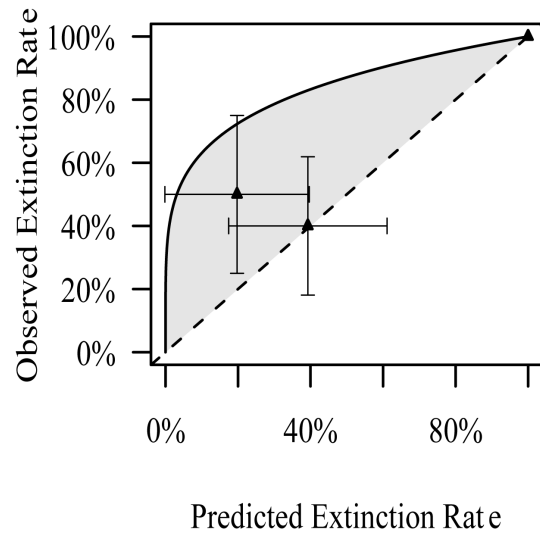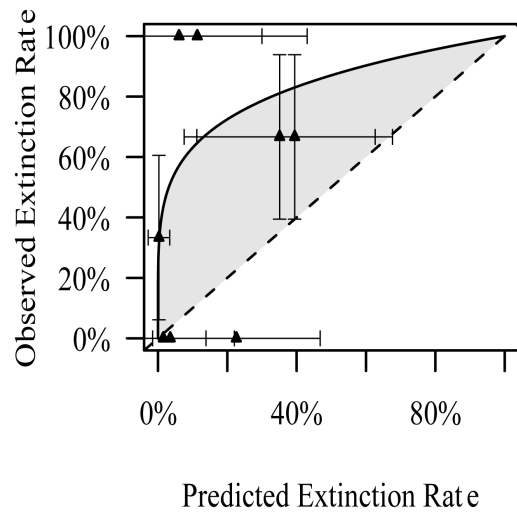
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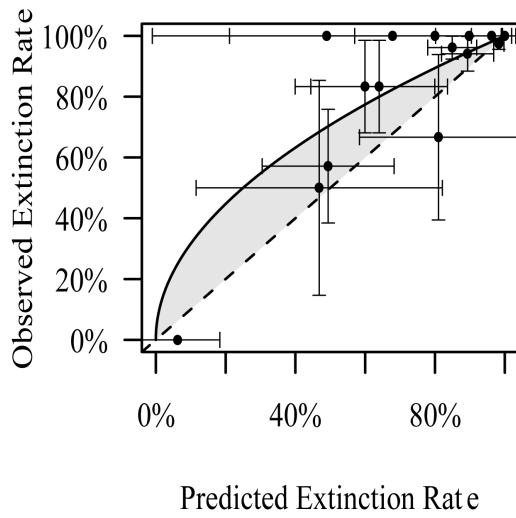
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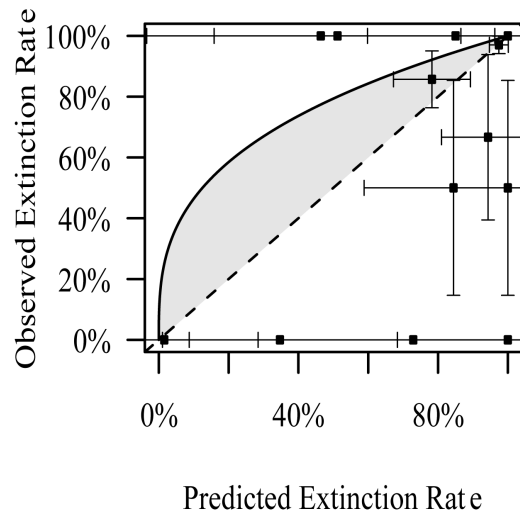
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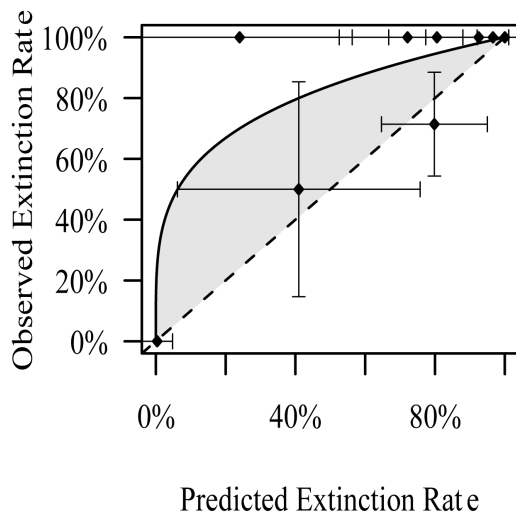
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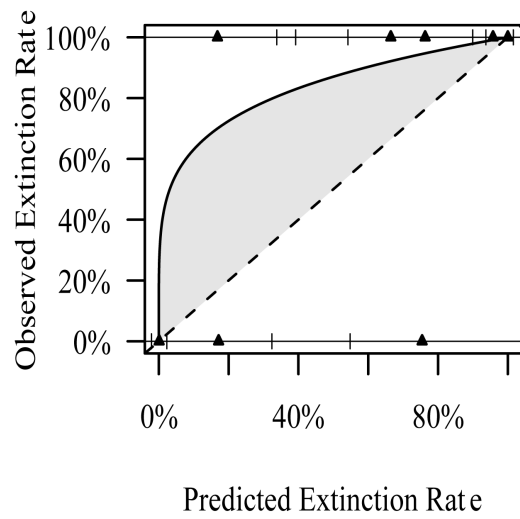
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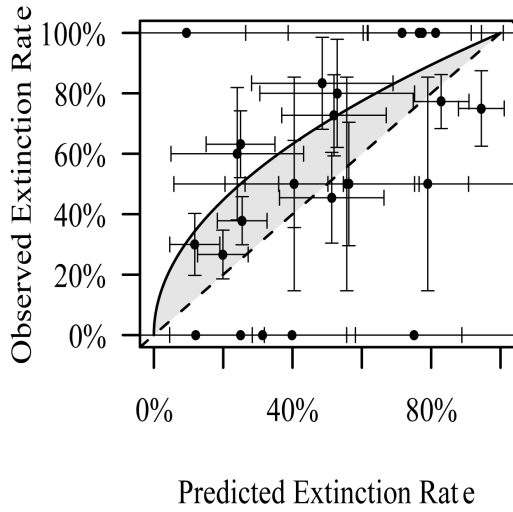
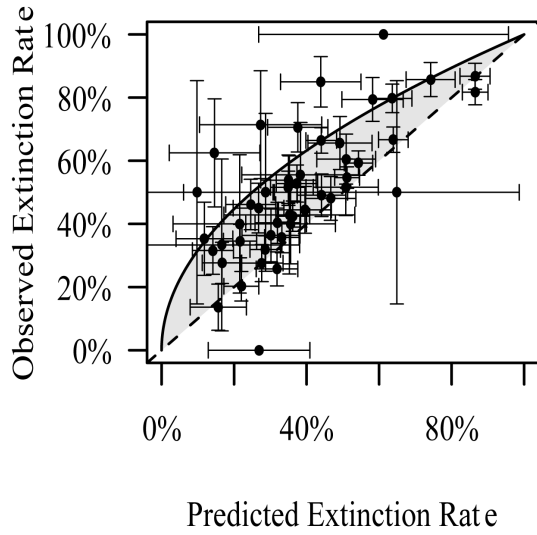## 3 Species Richness Category
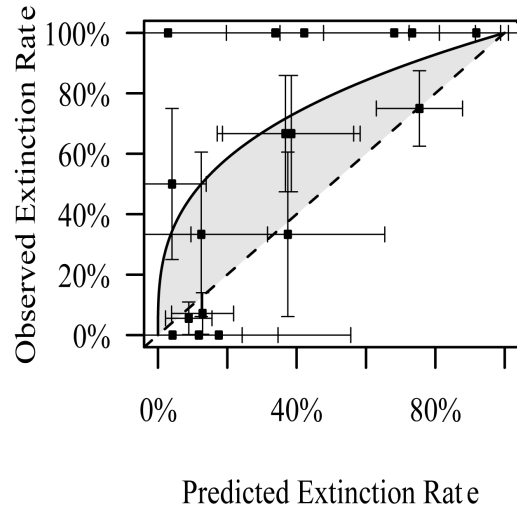
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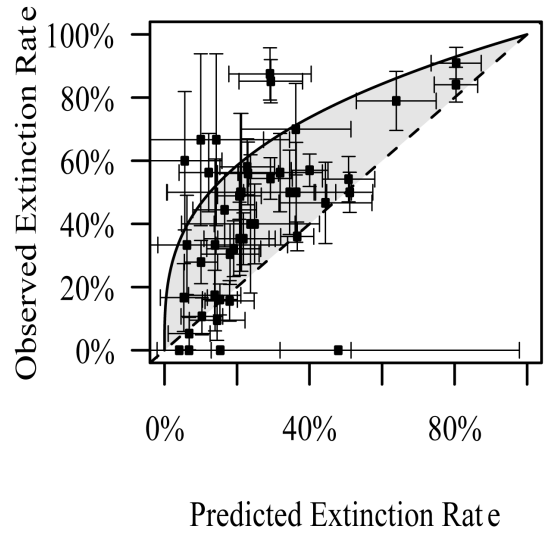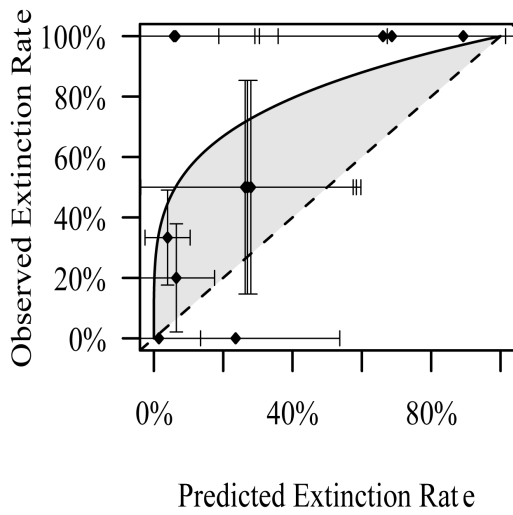

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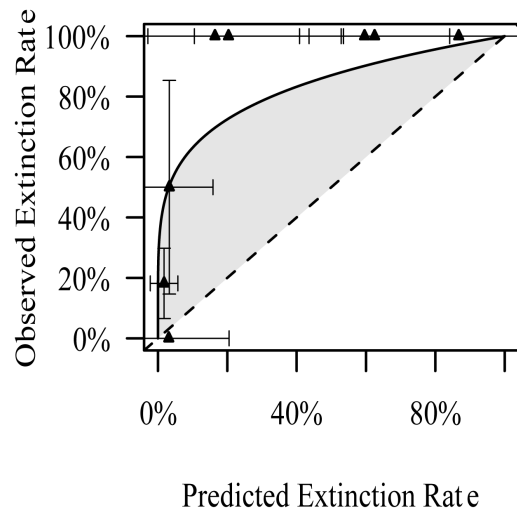
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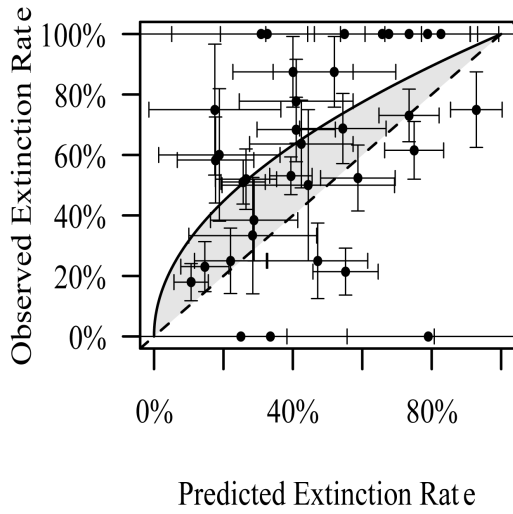
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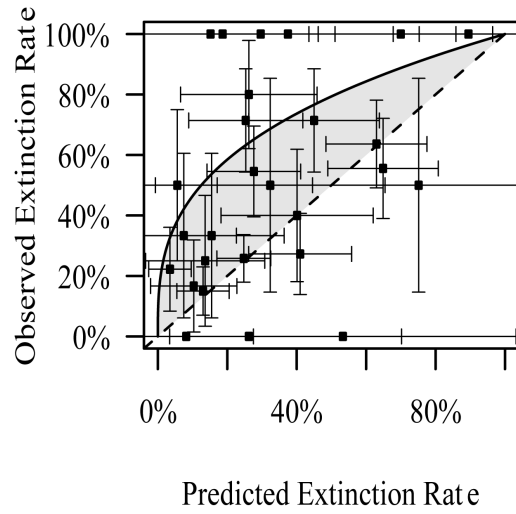
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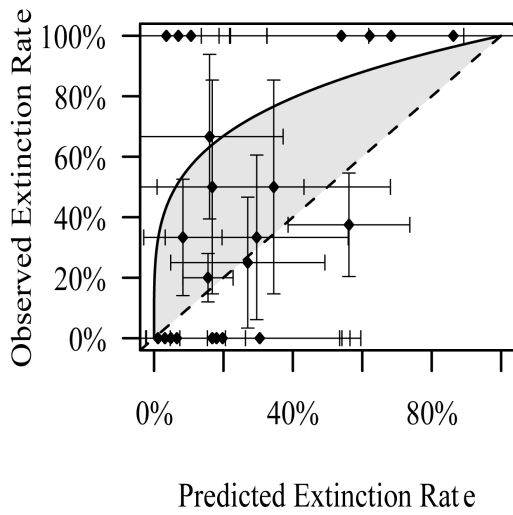
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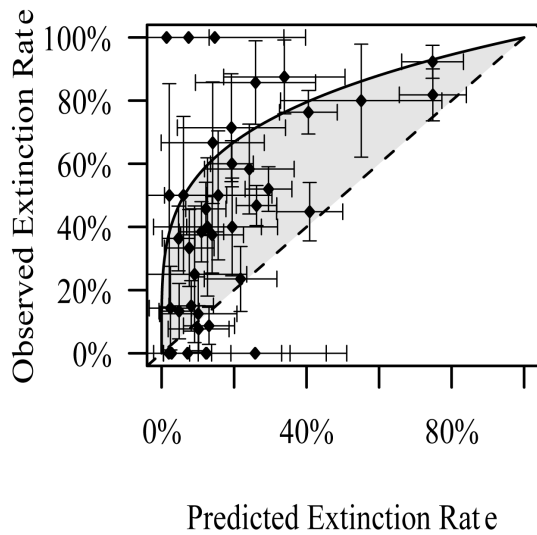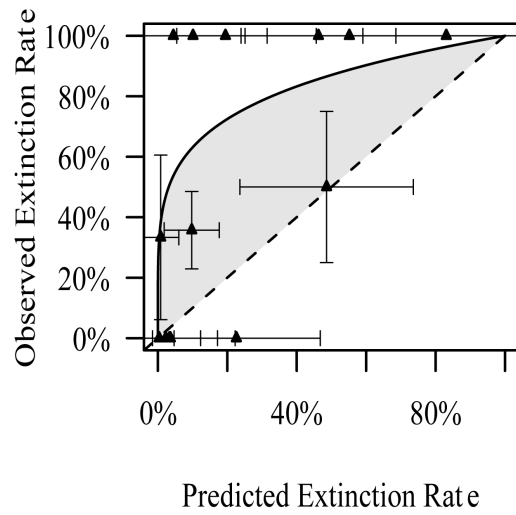
South China

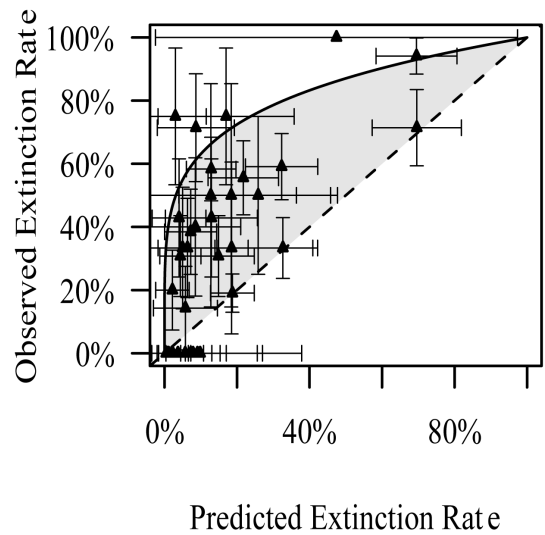## 2 Species Richness Category
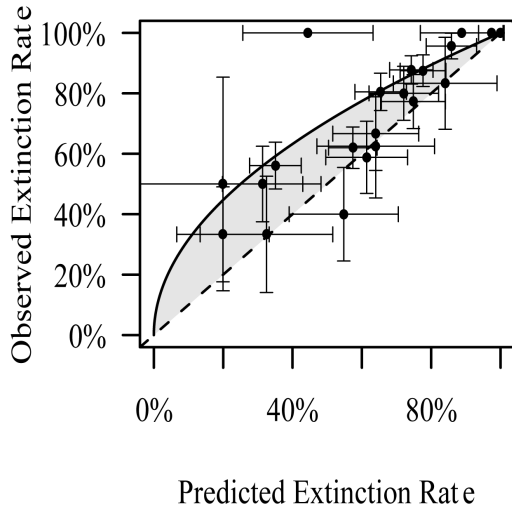
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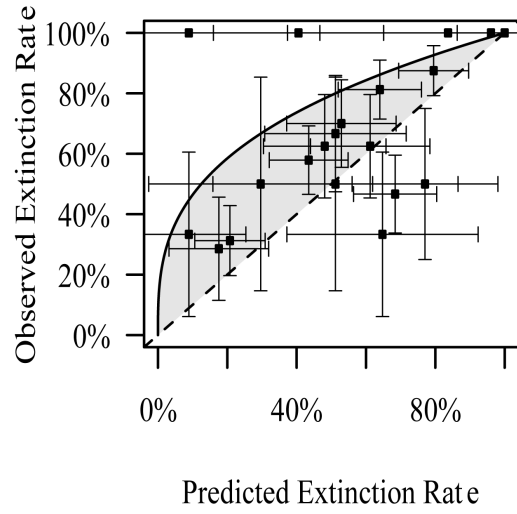
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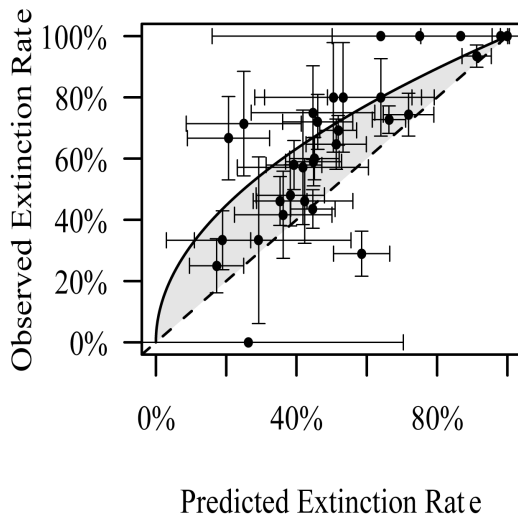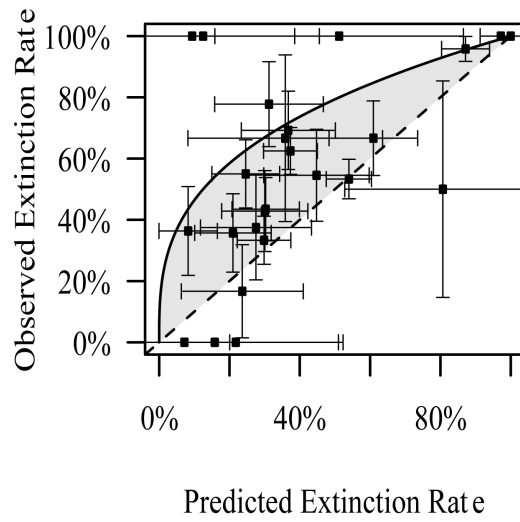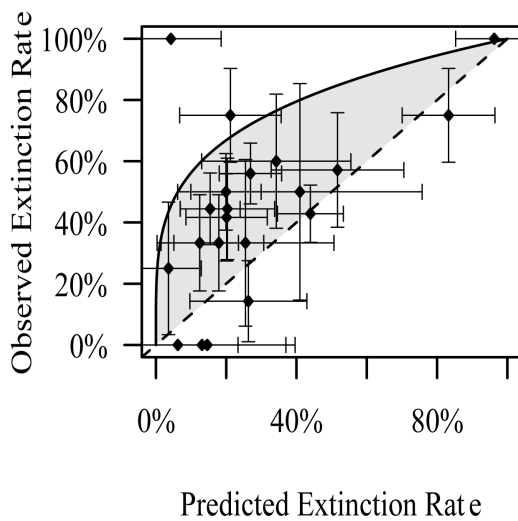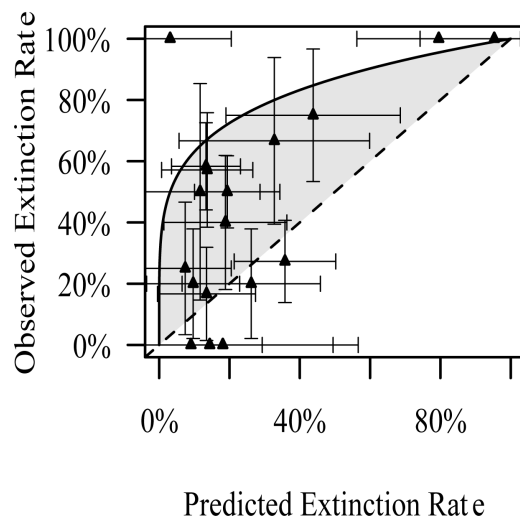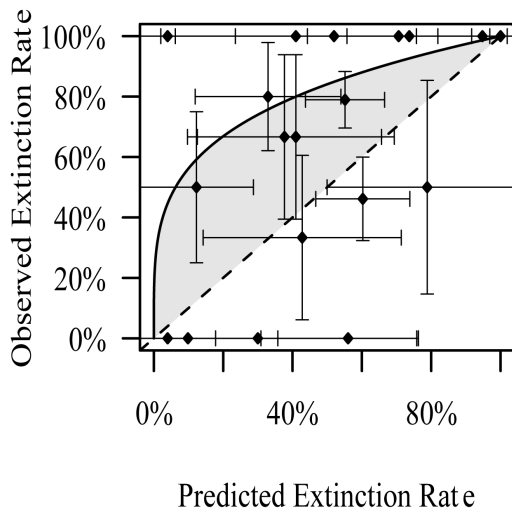

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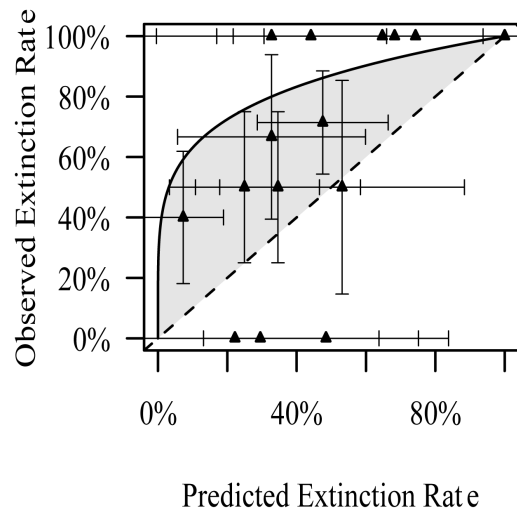
APPENDIX B

Characters and character states used in the phylogenetic analysis of Chapter 4

General calyx features

1. *General profile shape: (0) cone [straight-sided, full and truncated]; (1) bowl [rounded base, vertical sides]; (2) globe/barrel [rounded base, widest below summit of cup]; (ordered).*

2. *Height to width ratio: (0) very high [>1.5:1]; (1) high [1.5-1:1]); (2) low [1:1-1:2] ; (3) very low [~1:2-1:4];(4) extremely low [>1:4]; (ordered).*

3. *Transverse (oral) shape: (0) round; (1) subpentagonal; (2) pentagonal; (ordered).*

4. *Triple junction dimples: (0) absent; (1) present.*

5. *Ornament: (0) none; (1) fine [granular]; (2) coarse [nodes]; (ordered).*

6. *Basal invagination: (0) present; (1) absent.*

7. *Basal plane plates: (0) IBb; (1) Bb; (2) Rr.*

8. *Sutures: (0) smooth; (1) impressed.*

9. *Plate thicknesses: (0) thin; (1) medium; (2) thick; (ordered).*

Infrabasal plate features

10. *Number of plates: (0) multiple; (1) fused*

11. *Attitude: (0) upward-flared; (1) flat; (2) downward-flared; (ordered).*

12. *Character: (0) straight; (1) curved.*

13. *Relative size: (0) dominant; (1) equitable; (2) diminutive; (ordered).*

Basal plate features

14. *Attitude: (0) upward-flared; (1) flat; (2) downward-flared; (ordered).*

15. *Character: (0) straight; (1) curved; (2) inflated/bulbous; (ordered).*

16. *Relative size: (0) dominant; (1) equitable; (2) diminutive; (ordered).*

Radial plate features

17. *Character: (0) straight; (1) curved; (2) inflated/bulbous; (ordered).*

18. *Muscular articulation facet slope: (0) inward/horizontal; (1) distinctly outward.*

Anal plate features

19. *Number of plates at or below Rr: (0) 0; (1) 1.*

20. *Position of proximal suture: (0) IBb; (1) Bb; (2) Rr; (ordered).*

21. *First tube plate: (0) 2; (1) 1.*

Brachial plate features

22. *Ornament: (0) none; (1) textured; (2) spines.*

23. *Primaxil [branching]: (0) present; (1) absent.*

24. *Secundaxil [branching]: (0) present; (1) variable; (2) absent.*

25. *Tertaxil [branching]: (0) present; (1) variable; (2) absent.*

26. *Number of IBr: (0) Armenocrinus; (1) 3; (2) 2; (3) all IBr.*

27. *Number of IIBr: (0) >20 arms; (1) 10-20 arms; (2) all IIBr; (3) all IBr.*

28. *Proximal IBr and IIBr articulations: (0) ligament/muscle pairs; (1) not paired; (2) Fused.*

29. *Distal IBr and IIBr articulations: (0) ligament/muscle pairs; (1) not paired; (2) fused; (3) all muscular.*

30. *Proximal Br articulation shape: (0) rectangular; (1) cuneate.*

31. *Distal Br articulation shape: (0) rectangular; (1) cuneate.*

32, *Pinnulation style: (0) alternating; (1) mixed; (2) successive; (3) hyperpinnulated; (ordered).*

33. *Pinnulation type: (0) simple; (1) bifurcating*

Stalk

34. *Stalk: (0) present; (1) absent*

35. *Proximal shape: (0) round; (1) subround; (2) pentagonal; (3) pentastellate; (4) no stalk; (ordered).*

36. *Distal shape: (0) round; (1) other; (2) no stalk.*

37. *Cirri: (0) absent; (1) present; (2) no stalk.*

38. *Cirri per nodal: (0) 0, none; (1) <5; (2) 5; (3) no stalk.*

39. *Cirri/nodal articulation: (0) none; (1) round symplexial; (2) elliptical transverse ridge; (3) no stalk.*

APPENDIX C

Character and taxon matrix used in the

phylogenetic analysis of Chapter 4

Table C.1: Characters are in groups of five. See Appendix B for characters and states.
* = outgroup, ** = alternative outgroups

Encrinus liliiformis	11100 02120 10222 1111- -1022 22010 00002 000-
Pentacrinites briareus	02200 ?2110 10202 0211- -0000 22000 02003 1022
Millericrinus milleri	11101 0112? ???02 0011- -1000 20001 00001 00--
Dadocrinus gracilis sp. 1	01100 01110 10200 0011- -0022 22001 10002 000-
Dadocrinus kunischi	01100 01010 10200 0011- -0022 22001 10002 000-
Encrinus aculeatus	12100 02120 00210 0211- -2022 22010 00000 000-
Encrinus robustus	11100 11120 10200 0111- -0022 22010 ?0001 000-
Chelocrinus schlotheimi	11100 02120 10210 0111- -1002 21010 10002 000-
Holocrinus acutangulus	20000 10120 01101 0111- -0022 22001 10002 0122
Holocrinus dubius	01100 00120 00100 0011- -0022 22001 10003 1122
Traumatocrinus caudex	11100 02120 10220 1011- -0000 20010 00000 000-
Dadocrinus gracilis sp. 2	01100 01110 10200 0011- -0022 22001 10001 000-
Encrinus brahli	12100 02120 10220 1211- -2022 22010 00001 0111
Somphocrinus mexicanus	00100 1102- --200 0011- -2022 220?1 ???0- ----
Carnallicrinus carnalli	11100 01120 10200 0011- -0002 21010 00001 000-
Apiocrinites rotundus	21000 1102- --201 0111- -0022 210?1 10100 000-
*Corythocrinus insculptus**	00011 00000 00000 00?00 01001 10000 00000 0000
*Armenocrinus tenuidactylus***	00001 00000 00000 00000 0000? 00110 00000 0000
Aesiocrinus deliculatus	23?12 11000 10101 00?01 02022 22??0 02002 11?2
Aesiocrinus francisensis	22101 11110 21102 00001 10022 22131 12001 0111
Aesiocrinus harii	23000 11010 10001 00001 00022 22021 12003 1122
Aesiocrinus magnificus	22000 11020 10001 00001 00022 22021 12003 1122
Allosocrinus bronaughi	22001 11010 21001 00001 11122 33000 01001 0111
Allosocrinus ivanovi	22001 11010 21001 00001 1?122 330?0 ??002 ?11?
Ampelocrinus mundus	01000 00000 00100 00001 00022 22111 01001 0122

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Ampelocrinus kaskaskiensis	01000	00000	00100	00001	00001	20110	01001 0122
*Armenocrinus watersi**	00001	00010	00000	00?00	00022	22111	1?000 0000
Belashovicrinus ghzelensis	11000	00020	11001	01001	00122	331?1	1?002 0111
Calceolispongia sp.	11101	00120	11002	00001	02122	33000	00000 0111
Cambellicrinus compactus	00000	00010	00000	00?01	00012	11001	02000 ????
Chlidonocrinus echinatus	02112	00000	00000	00001	02001	20010	01003 1122
Chlidonocrinus ornatus	22012	00000	11000	00001	02001	20010	01003 1122
Cymbiocrinus cherribunensis	22000	11110	21001	00?01	0?022	220?0	02002 ????
Cymbiocrinus grandis sp. 1	23100	11010	21101	01001	00022	22010	02000 0111
Cymbiocrinus grandis sp. 2	33100	11110	21112	01001	00022	22010	02000 0111
Cymbiocrinus gravis	33200	11120	21111	11001	00022	222?1	13002 0112
Jimbacrinus bostocki	11101	00120	01002	00001	00122	33000	00000 0000
Moundocrinus luxuris	22100	11020	21001	00001	10022	22111	12002 0111
Moundocrinus osagensis	22101	11010	21001	00001	10022	22111	12002 0111
Moundocrinus patens	22101	11020	21001	00001	11022	221?1	12003 ?12?
Nowracrinus ornatus	22?11	01000	10001	00001	02000	20000	00100 0111
Oklahomacrinus loebelichi	34201	12010	21111	11001	00022	22031	12001 0122
Oklahomacrinus spicatulus	24200	12120	21121	11001	10022	22001	02002 0122
Oklahomacrinus supinus	34200	12120	21111	12002	10022	220?0	12001 ?122
Paracymbiocrinus ormandi	21000	11110	21101	00001	10022	22231	13002 ????
Paragassizocrinus caliculus	12000	00121	01000	00001	00022	22021	12014 2233
Paragassizocrinus tarri	01000	00021	01000	00001	00022	22021	12014 2233
Polusocrinus amplus	12000	00110	01000	01001	00012	22021	12003 1112
Polusocrinus avanti	12000	00010	01000	01001	00012	22021	12003 1112
Polusocrinus ochelataensis	12000	00010	01000	01001	00022	21021	12003 1112
Proallosocrinus glenisteri	22001	11110	21001	00001	11022	22??1	12001 ????

APPENDIX D

An expression for the total drag, D_T, produced by the biomechanical model in Chapter 5

An expression for the total drag, D_T, produced by the model is found by integrating (5.2) over the length of the arm, from 0, to h where y is the variable of integration:

$$D = \int_0^h \frac{1}{2} C_D \rho S U^2 \tag{D.1}$$

$$S = \left(b_0 + \frac{b_1 - b_0}{h} \right) y \tag{D.2}$$

$$U = \left(\frac{V}{h} \right) y \tag{D.3}$$

$$D_T = \frac{1}{2} C_D \rho \int_0^h \left(\left(b_0 + \frac{b_1 - b_0}{h} \right) y \right) \left(\left(\frac{V}{h} \right) y \right)^2 \tag{D.4}$$

$$D_T = \frac{1}{2} C_D \rho \left(\frac{b_0 V^2 h}{3} + \frac{b_1 - b_0 V^2 h}{4} \right) \tag{D.5}$$

where variables are as stated in the text. A simplified form of the equation (D.5) is provided in the text as the drag perpendicular to the arm (5.3). To determine the total drag produced by multiple arms in a power stroke the result in (D.5) must be multiplied by the number of arms.

APPENDIX E

An expression for the vertical component of drag, D_v, produced by the biomechanical model in Chapter 5

In order to calculate the vertical component of drag, D_v, a modified version of the perpedicular drag equation (5.3) was developed that accounts for the starting position of the arm relative to vertical, α, and the angle through with the arm rotates, θ, the latter of which affects the angular velocity of the arm, ω. The instantaneous vertical component of thrust is found via trigonometry as:

$$D_{Vinst} = D_{Tinst} \sin(\alpha) \tag{E.1}$$

To get total vertical thrust, the equation (E.1) is integrated with respect to time during the translation of the arm from the start of the power stroke to its completion,

from $t = 0$ to $t = t$:

$$D_V = \int_0^t D_T \sin(\alpha)\mathrm{d}t \qquad\qquad (\text{E.2})$$

$$D_V = D_T \int_0^t \sin(\omega t) \qquad\qquad (\text{E.3})$$

$$D_V = D_T \left(\frac{\cos(\alpha)}{\omega} + \frac{\cos(\alpha + \theta)}{\omega} \right) \qquad\qquad (\text{E.4})$$

(E.4) is slightly rewritten in the text to form the vertical drag equation (5.4), and is the model's analytical solution.

APPENDIX F

Measurements of comatulid specimens from the USNM collections used in Chapter 5

Mostly complete, adult specimens were chosen from the USNM collections. Measurements were made with Mitutoyo Digimatic calipers. WIW was calculated as described in the text. Arm length was measured on complete arms, and brachial width was measured at the midpoint of that arm. ANT, Antedonidae; ATE, Atelecrinidae; CHA, Charitometridae; NOT, Notocrinidae; COM, Comasteridae; THA, Thallasometridae; AST, Asterometridae; PTI, Ptilometridae; TRO, Tropiometridae; COL, Colobometridae; ZYG, Zygometridae; HIM, Himerometridae; MAR, Mariametridae. WIW is in g, arm measurements are in mm.

Table F.1: Comatulid specimens from the USNM collections

USNM.No	Species	Family	WIW	Arm Number	Brachial Width	Arm Length
E7976	*Promachocrinus kerguelensis*	ANT	0.46	20	1.53	137.4
E42689	*Atelecrinus sp.*	ATE	0.15	10	1.78	89.91
35812	*Florometra serratissima*	ANT	0.97	10	1.5	160.34
35829	*Florometra serratissima*	ANT	0.4	10	1.59	142.59
35713	*Florometra asperrima*	ANT	1.45	10	2.35	196.51
35794	*Florometra serratissima*	ANT	1.02	10	1.37	177.07
E42582	*Crinometra brevipinna*	CHA	2.84	24	1.6	184.7
35704	*Monachometra patula*	CHA	3.14	16	1.65	112.6
35638	*Glyptometra lateralis*	CHA	2.46	10	2.47	140.22
E43384	*Notocrinus virilis*	NOT	0.13	10	2.1	77.75
E34770	*Ctenantedon kinziei*	ANT	0.18	10	0.81	89.71
E28084	*Antedon mediterranea*	ANT	0.18	10	0.93	104.14
E34740	*Taxometra paupera*	ANT	0.07	10	1.02	91.45
E42713	*Coccometra guttata*	ANT	0.08	10	0.85	92.7
E17944	*Crinometra brevipinna*	ANT	1.34	19	1.45	120.61
1093338	*Comanthus suavia*	COM	6.07	37	1.63	141.28
35597	*Cosmiometra philippinens*	THA	0.85	17	0.86	83.77
E5282	*Asterometra cristata*	AST	1.51	10	1.6	86.99
35547	*Pterometra trichopoda*	AST	0.24	21	1.1	58.87
35503	*Ptilometra australis*	PTI	2.37	16	1.5	70.25
E19190	*Tropiometra carinata*	TRO	0.51	10	1.46	75.54
E48097	*Tropiometra afra*	TRO	5.09	10	3.31	194.28
35222	*Pontiometra andersoni*	COL	8.32	76	1.87	152.04
35305	*Cenometra delicata*	COL	3.05	33	1.26	93.21
1010993	*Stylometra spirifera*	THA	1.74	33	0.98	124.3
35174	*Zygometra elegans*	ZYG	0.91	34	1.14	69.64
E3205	*Amphimetra tesselata*	HIM	2.54	12	2.22	86.04
E34703	*Lamprometra palmata*	MAR	0.5	30	1.31	81.35
E48114	*Stephanometra indica*	MAR	0.47	17	1.09	76.88

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USNM.No	Species	Family	WIW	Arm Number	Brachial Width	Arm Length
E34586	*Cenometra bella*	COL	0.37	32	1.23	92.76
E34545	*Comanthus parvicirrus*	COM	0.52	41	1.47	140.17
E34578	*Comanthina shlegeli*	COM	1.68	75	1.94	97.67
34962	*Comaster multibrachiatus*	COM	4.86	125	1.38	95.15
34927	*Comatula purpurea*	COM	0.19	10	1.59	118.95
E26113	*Comactinia meridionalis*	COM	4.31	10	3.84	193.18
349002	*Capillaster multiradiata*	COM	0.63	16	2.1	67.9
E25890	*Nemaster grandis*	COM	0.57	25	1.41	113.24
E19779	*Neocomatella alata*	COM	2.32	44	0.94	87.4

APPENDIX G

Measurements of stalked crinoid specimens from the USNM collections used in Chapter 5

See Appendix F for details on specimen housing and measurement. Stalked specimens were chosen that had mostly complete crowns, but little stalk. Crown WIW for stalked crinoids was measured by subtracting the WIW of the stalk, which was estimated by modeling the stalk as a cylinder of bulk density as the whole animal. Dashed entries indicate missing data for the specimen, due to incompleteness or taxon characteristics (e.g., no stalk in *Holopus rangii*). Isolated stalks were used to measure stalk density and are noted by their lack of arm length and crown WIW. HYO, Hyocrinidae; HOL, Holopidae; BOU, Bourgeuticrinidae; ISO, Isocrinidae. Density is in $\frac{g}{cm^3}$, WIW is in g, other measurements are in mm.

Table G.1: Stalked crinoid specimens from the USNM collections

USNM.No	Species	Family	Density	WIW	Arm Length	Stalk Width	Stalk Length	Crown WIW
E47881	*Calamocrinus Diomedae*	HYO	1.24	0.63	65.06	3.31	6.31	0.62
E47881	*Calamocrinus Diomedae*	HYO	1.62	0.77	-	2.7	221.68	-
E33383	*Holopus rangii*	HOL	1.27	1.91	-	-	-	1.91
E33380	*Holopus rangii*	HOL	1.37	1.68	-	-	-	1.68
E42724	*Phrynocrinus nudus*	BOU	1.07	0.81	-	-	-	0.81
35993	*Diplocrinus alternicirrus*	ISO	1.43	4.81	91.92	4.43	3.74	4.79
E21120	*Diplocrinus maclearanus*	ISO	1.52	9.73	91.78	4.23	8.17	9.67
5811	*Diplocrinus maclearanus*	ISO	1.52	9.53	91.25	4.69	57.2	9.04
E21094	*Diplocrinus maclearanus*	ISO	1.57	6.7	89.09	3.65	34.42	6.5
E17521	*Neocrinus decorus*	ISO	1.44	1.7	-	4.34	254.41	-
E18007	*Neocrinus decorus*	ISO	1.28	2.46	123.79	3.84	24.16	2.39
E47575	*Endoxocrinus parrae*	ISO	1.36	2.24	83.91	3.42	12.54	2.2
E1021237	*Endoxocrinus parrae*	ISO	1.3	6.99	135.66	4.84	5.25	6.96
36057	*Neocrinus blakei*	ISO	1.28	1.37	110.55	2.76	5.6	1.36
E18021	*Neocrinus blakei*	ISO	1.1	0.46	105.31	2.98	15.26	0.45
12355A	*Neocrinus blakei*	ISO	1.59	1.63	80.48	2.68	8.56	1.6
12355B	*Neocrinus blakei*	ISO	1.38	2.25	90.84	3.31	8.96	2.22
E26001	*Endoxocrinus parrae*	ISO	1.1	1.52	98.81	5.04	20.66	1.49
E32657	*Endoxocrinus parrae*	ISO	1.35	5.68	119.84	4.21	16.77	5.6
E42618	*Endoxocrinus parrae*	ISO	1.28	3.47	115.65	3.51	5.64	3.46
E45846	*Endoxocrinus parrae*	ISO	1.17	0.86	89.74	4.22	51.35	0.76
E17950	*Endoxocrinus parrae*	ISO	1.54	3.63	76.15	2.99	41.07	3.48
E17990	*Endoxocrinus parrae*	ISO	1.23	2.69	111.55	3.95	14.2	2.65
E17994	*Endoxocrinus parrae*	ISO	1.36	5.41	105.88	4.59	21.36	5.29
E18033	*Endoxocrinus parrae*	ISO	1.51	14.3	126.24	6.05	28.08	13.91
E19969	*Endoxocrinus parrae*	ISO	1.53	1.81	73.85	3.42	45.89	1.6
12549	*Endoxocrinus parrae*	ISO	1.25	2.63	93.11	3.61	54.47	2.5
E36338	*Metacrinus rotundus*	ISO	1.44	1.32	-	5.96	130.85	-
E36338	*Metacrinus rotundus*	ISO	1.41	7.06	113.27	4.94	13.55	6.96

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USNM.No	Species	Family	Density	WIW	Arm Length	Stalk Width	Stalk Length	Crown WIW
17531	*Hypalocrinus naresianus*	ISO	1.33	0.56	-	3.18	19.05	-
17531	*Hypalocrinus naresianus*	ISO	1.23	1.44	113.94	3.23	8.28	1.43

APPENDIX H

Features of comatulid skeletal morphology

Pinnule

Brachial

Radial

Basal

Centrodorsal
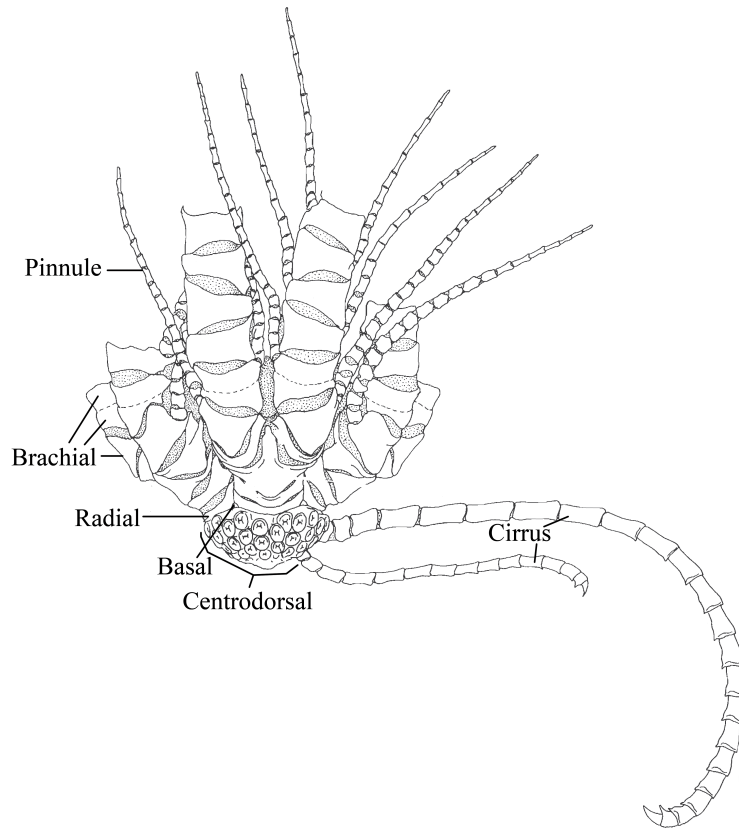
Cirrus

Important features of the comatulid skeleton used in text of Chapters V-VI. Proximal portion of three rays are shown, and most cirri have been removed to reveal the centrodorsal, which is covered with cirrus sockets. The radial and basal plates form the calyx of the comatulid, which is tightly fused to the cirriferous centrodorsal. Arms are made of brachial plates and have smaller, extensions, the pinnules, which are important in comatulid swimming. Modified from Messing and Dearborn (1990, fig.3).

APPENDIX I

Revised stratigraphic range of the comatulid superfamily Comasteracea Clark 1908a

The Treatise on Invertebrate Paleontology reports a single Eocene occurrence of the genus *Nemaster* Clark 1909, citing Howe (1942). The reference in a question was an address by the president of the Society of Economic Paleontologists and Mineralogists (SEPM) at a joint meeting of the American Association of Petroleum Geologists & SEPM in which Howe encouraged micropaleontologists to focus also on sometimes fragmentary fossil remains of larger organisms, including comatulid crinoids. However, Howe (1942) does not contain a taxonomic diagnosis, but rather cites Springer (1924, mistakenly cited as 1925), who in describing what was then known about Tertiary American crinoids, mentioned a single fragmentary Eocene specimen from South Carolina as belonging to genus Nemaster, but without a citation and again without a taxonomic diagnosis. With the exception of this single questionable occurrence, the earliest definitive reports of the Comasteracea are in the Miocene (e.g., Jagt et al., 2002) and at or close to the Oligocene-Miocene boundary (Eagle, 2008).

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BIBLIOGRAPHY

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