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The effects of sexual dimorphism on survivorship in fossil ammonoids: A role for sexual selection in extinction

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The effects of sexual dimorphism

on survivorship in fossil ammonoids:

A role for sexual selection in extinction

A thesis submitted in partial fulfillment of the requirements for the degree of
Bachelor of Science in Geology
from the College of William and Mary in Virginia,

by

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Abstract

Recent studies have suggested that sexual dimorphism in modern birds may be tied to increased extinction risk at the species level. If this is the case, it may represent a clear example of species-level selection, i.e., selection occurring at or above the species level. The fossil record provides an ideal opportunity to test this possibility over longer timescales. The goal of this study is to investigate the relationship between sexual dimorphism and extinction and diversification in ammonoid cephalopods.

To do this, I compiled global data on the presence and absence of sexual dimorphism in Mesozoic ammonoids at the genus level from a recent literature compilation. To quantify survivorship across background intervals, I compiled first and last global occurrence data from the Paleobiology Database and the biostratigraphic literature to calculate genus-level durations. With which I found that monomorphic genera had shorter durations than dimorphic genera in the fossil record. This was the same trend seen in a number of other superfamilies. Meaning in at least ammonoids, dimorphism may actually extend one's stratigraphic duration.

To explore this possibility in more detail, I selected a single superfamily on which to focus our diameter measurements, (Acanthocerataceae) to assess the extent to which the magnitude of sexual dimorphism is correlated with survivorship. I found that there was actually a positive correlation between magnitude and duration. I also assessed survivorship across the Cenomanian-Turonian extinction. I found no significant results regarding their extinction or diversification after this extinction.

The general trend among our results could be due to a dietary niche separation between males and females. This would reduce intraspecific competition for resources and could extend their duration.

Introduction

Sexual dimorphism, a state in which the males and females of a species appear physically different, is a sexually or naturally selected trait that can be tracked through the fossil record to present day in many modern organisms. In taxa experiencing sexual selection dimorphism often evolves to help individual's success in attracting a mate and producing offspring. Sexual dimorphism is a form of species selection that through either extinction or speciation it becomes more rare or common throughout time. The reproductive advantages of dimorphism may be counteracted by shorter life spans and therefore natural selection against dimorphism. Modern studies have supported the hypothesis that sexually dimorphic organisms can respond to sexual selection more than natural selection, which would have an impact on the population viability and lead to a higher risk of extinction. Looking in the fossil record for evidence of this trend could extend this hypothesis to a much longer time scale.

The goals of this research are: (1) to determine whether taxa that are sexually dimorphic are more likely to go extinct in the fossil record; (2) to determine if dimorphic taxa are also more likely to be victims of the Cenomanian-Turonian extinction than monomorphic taxa; (3) to determine if dimorphic taxa are also more likely to diversify after the Cenomanian-Turonian extinction than monomorphic taxa; and (4) to identify a possible correlation between the magnitude of sexual dimorphism and taxon survivorship in the Acanthocerataceae superfamily.

Significance

This project is the first to examine potential correlations among extinction rates, origination rates, and dimorphism in the fossil record. It is also the first to study the possible trend of a dimorphic-extinction relation in invertebrates, in a marine organism, and not in birds. This study is also the first to look at the effects of dimorphism in relation to a mass extinction event, by explicitly comparing, survivors, victims, and originators. This is also the first study to examine the effects of the magnitude of dimorphism on durations within any taxa, extinct or extant.

Data collected from this study could provide a further explanation of species selection throughout the history of life. One cannot understand complete evolutionary patterns in species-level selection when it comes to sexual dimorphism without looking at it as a long-term process, meaning applying it to the fossil record, as done with this project.

Background

Sexual Dimorphism

Sexual selection, as one mechanism of evolution, drives evolutionary change and intraspecific competition through mate choice in a system. Sexual selection passes traits of a sexually successful individual through generations. Sexual dimorphism is one of the traits that sexual selection can make more prevalent through time for many populations. This trait exists due to mating pressures regarding sexual reproduction. Sexual

dimorphism can be represented as a difference in body size, coloration, ornamentation, or defensive competitive structures between genders. These morphological traits are exaggerated to give an organism an advantage over its rivals in finding a mate. Sexual dimorphism can also evolve from natural selection. This would occur if the dimorphic trait increases their survivorship (Freeman and Herron, 2004).

Due to the co-dependent nature on the development of sexual dimorphism between the two genders, it is clear that the trait would not evolve without the influence of both sexes. This means that at one point ancestral taxon must have experienced a monomorphic state, after which selection acts on the two sexes to move them in morphologically different directions. Some contemporary examples of sexually dimorphic taxa include peacocks, elk, guppies, a number of primates, and golden toads (Pérez-Barbería et al., 2002).

Body-size dimorphism has been found to develop from pressure of a polygynous mating system. In some taxa, this is due to male-male competition for females. It could also be due to competition for food resources within a social group. It has also been suggested that body size can increase in males due to the increased stress they are responsible for during their mate's pregnancy. Due to the incapacity of the female, the male must have more energy to provide nourishment for his mate (Pérez-Barbería et al., 2002). Body –size dimorphism is prevalent in modern day cephalopods, such as cuttlefish, nautilus, and octopods (Saunders and Spinosa, 1978, Voight, 1995).

Sexual dimorphism is tricky to identify in the fossil record because the fossil record only provides us with the hard parts of organisms. This means that if any of the

organism's soft part displayed a dimorphic trait, it is lost to the effects of time and taphonomy. Therefore much about the species' reproductive habits must be assumed. However, analogies with modern descendants, sex ratios, and assumptions about the same distribution in space and time of the two sexes are three ways to simplify the identification of sexual dimorphism in the fossil record (Davis et al., 1996). Some fossil groups that are thought to be dimorphic include Ammonoidea, Ostracoda, Ranininae, some Artiodactyls, and dinosaurs.

Sexual Dimorphism and Survivorship

With the myriad of advantages of the sexually dimorphic trait, the reproductive success could potentially correlate to a high diversification rate. Sexual selection can improve adaptation and enhance the chance of population persistence. However, sexual selection can also be powerful enough to produce dimorphic traits that are detrimental to the individual's survivorship. This means dimorphism could be seen as a double-edged process, by affecting both radiation and extinction. The extinction aspect was first highlighted by Darwin's discussion of the potential opposition between naturally and sexually selected traits (Darwin, 1859).

Data suggest that sexual dimorphism sometimes puts an organism at a suboptimal fitness state. As seen in Morrow and Pitcher's 2003 study, modern sexually dimorphic bird species have a higher risk of extinction. In this case study, they suggested that this was due to the increasing metabolic cost of producing bright plumage, which made them more attractive to both their mates and predators. The example of the male peacock tail works in a similar way, as the weight and area of the plumage makes it difficult to escape

predators (Figure 1). Beyond impressing females, many of these dimorphic adaptations serve little purpose (Monks and Palmer, 2002). It has been found that these traits often hinder the organism from escaping and camouflaging themselves from predators. Some have called this process evolutionary "suicide" (Kokko and Brooks, 2003).

The opposite trend has been suggested in other studies; in which dimorphism helps extend life due to dietary niche separation between the genders. Since body mass establishes an individual's dietary need, body size dimorphism could significantly cause one species to have a bimodal set of food groups and microhabitat use. Therefore the females and males of one species are not in competition with each other for resources. The evolution of sexual dimorphism can occur solely due to ecological factors to fulfill these niches, eliminating the role of sexual selection (Slatkin, 1984).

Kamilar and Pokempner's 2008 study on 38 different species of primates found that increasing degrees of body mass dimorphism resulted in increasing dietary differentiation between the sexes.   Since the genders feed on separate resources, it lowers intraspecific competition. In this case natural selection is acting in a sex-specific manner by effecting individual sexes with the purpose of making them fit enough to survive (Kamilar and Pokempner, 2008).

The modern cephalopod family Bolitaenidae also displays this niche divergence due to ecological factors. Genders vertically partition themselves within the water column. Due to the difference in depth they have sexually dimorphic glands. Males have larger glands to protect the males from predation as they feed on bioluminescent prey in the deep ocean. Their ecological roles differ which leads to a divergence of niches which can allow resource partitioning among these octopods (Voight, 1995).

Figure 1: Image of the sexually dimorphic male and female peacock side by side. The male is displaying his dimorphic trait, his extravagant tail.
(http://upload.wikimedia.org/wikipedia/commons/a/a9/Peacock_courting_peahen.jpg)
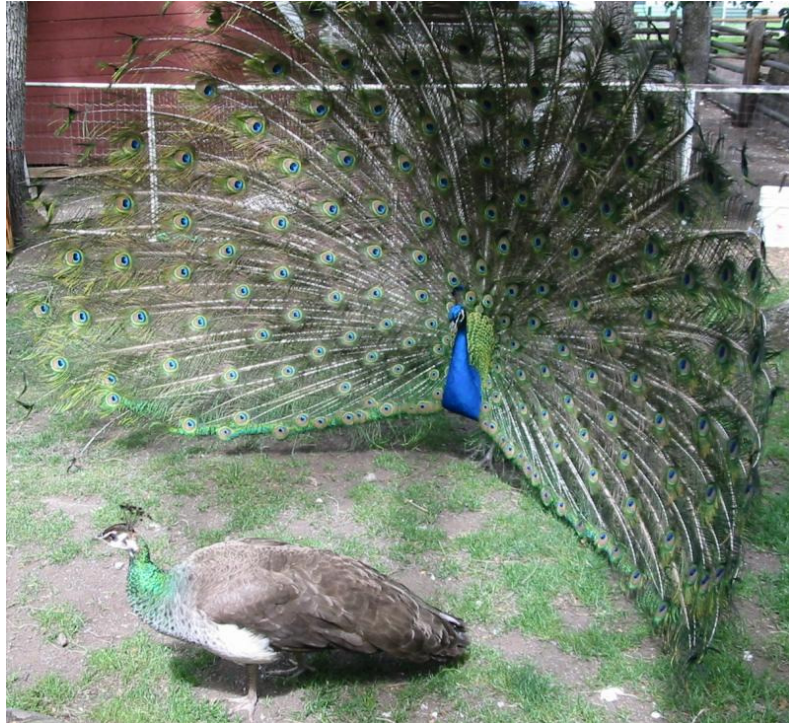
Another reason that body size dimorphism could help extend life duration would be if the female was larger. This trend appeared within the southern flying squirrel *Glaucomys volans*. Larger females produce a larger number of offspring. They also have better access to food resources, which leads to increased health among the plentiful offspring. The increased fecundity of the larger female, paired with a possible higher rate of maturation within a smaller male could produce the opposite trend as well (Fokidis et al., 2007).

Ammonoidea

One group in the fossil record that has been described as having sexually dimorphic taxa is the subclass of cephalopods, Ammonoidea. Cephalopods are exclusively marine mollusks with planispiral and often involute shells. Involute shells' last whorl covers the former whorls. Ammonoid shells are divided into chambers that are connected by a siphuncle and form a flat spiral. Ammonoids originated from straight-shelled cephalopods bactritoids in the Devonian.

Ammonoids have a similar body structure to the modern *Nautilus* (Figure 2), but their biological affinities are actually closer to coleoids, including squid and cuttlefish. From examination of fossilized remains and the modern analogue, *Nautilus*, researchers postulate that ammonoids moved by jet propulsion and used their tentacles to forage food from the sea floor. Their diet is assumed to have consisted of slow-moving live animals and carrion. Fossilized remains include fragments of small crustaceans, echinoderms, plankton, and even small ammonoids in the gut contents (Monks and Palmer, 2002).

Figure 2: Extinct cephalopod ammonoid morphology on the left (http://www.connecticutvalleybiological.com/images/es500.jpg) and extant cephalopod *Nautilus* morphology on the right (http://www.gettyimages.com/ detail/82038790/Photographers-Choice-RF).

Note the similar spiral chambered pattern in the shell morphology

Ammonoid Cross Section   Nautilus Cross Section

Ammonoids are also assumed to have lived at a shallower depth and dissolved oxygen level than the *Nautilus*. Ammonoids could most likely withstand very low oxygen levels at some depth. However this would not be as deep as the *Nautilus* due to ammonoids' thinner shells and the risk of imploding with high pressure. Some colonies could have existed at 800 m, but most are suggested to have lived between 30 and 120 m (Clarkson, 1998).

Ammonoids first appeared in the fossil record in the Early Devonian and diversified quickly to reach 30 families by the end of the Devonian. After this, ammonoids went through multiple evolutionary radiations that were punctuated by extinction crises, such as the Cenomanian-Turonian Extinction (C/T). Each of these extinctions left only a few surviving species that later diversified. Origination rates declined after the Permian-Triassic extinction, after which only two genera survived to contribute to the Triassic radiation.   The last of the ammonoids disappeared approximately 65 million years ago at the Cretaceous-Tertiary (K/T) boundary (Clarkson, 1998).

It has been widely accepted that ammonoids are sexually dimorphic since the late 1960's. Dimorphism is believed to exist in many fossil and modern cephalopods. In 1869, Waagen documented the existence of pairs within ammonoid species, but did not recognize that is represented sexual dimorphism. Callomon (1963) and Makowski (1963) later established dimorphism in ammonoids. Further studies of both extinct and extant cephalopods, such as dimorphic cuttlefish, octopods, and nautilus, have supported this theory about ammonoids displaying sexual dimorphism. Cephalopods in general are known to have elaborate courtship rituals, which promote sexual dimorphism among the

individual species. It is also quite possible that many more cephalopods were dimorphic in the past, but in their soft parts which were not preserved in the fossil record.

The two components of a dimorphic pair of ammonoids are called antidimorphs. The two antidimorphs of an ammonoid species are referred to "microconch" and "macroconch" (Figure 3), which are suspected to represent the male and female respectively (Clarkson, 1998).   Differences between the microconch and the macroconch among species range from body size, shell ornamentation, and size of the umbilicus (Davis et al., 1996). Size-related dimorphism is the most common of these differences among ammonoids. There is some ambiguity in determining the sexes; however, the difference is thought to be gender not age.   Dimorphic pairs have identical stratigraphic and geographic ranges. Also, the ability to track development of the ammonoid because they record their entire ontogeny on the interior of their shells supports gender not age (Neige, 1997). As the ammonoid ages, there is a decline in ornamentation, the last septa crowd, the lobe and saddle shorten, and the shell generally becomes more evolute. In order to be considered a dimorphic pair, their ontological stage must be matched; meaning they must be the same age within adulthood. Using these morphometric clues, one can pair microconchs and macroconchs to the same mature age (Kennedy, 1989).

It is suggested that the macroconch may have represented the female given the presence of egg sacs in three separate macroconch specimens. The extra space within the larger macroconch may have been ideal to provide space within which to brood eggs. The sex that was smaller reduced development time and matures earlier. Larger females can be observed in modern cephalopods but does not occur in all taxa, therefore has not been completely accepted.   The extant *Nautilus* displays the opposite gender

Figure 3: *Collignoniceras praecox* macroconch (M) and microconch (m). The macroconch and the microconch are both from Fall River County, South Dakota. They occur in the Carlile Shale (Middle Turonian in age), from limestone concretions about 6 m (20 ft) below base of Turner Sandy Member. Both images are x1. (separate images from Kennedy et al., 2001)
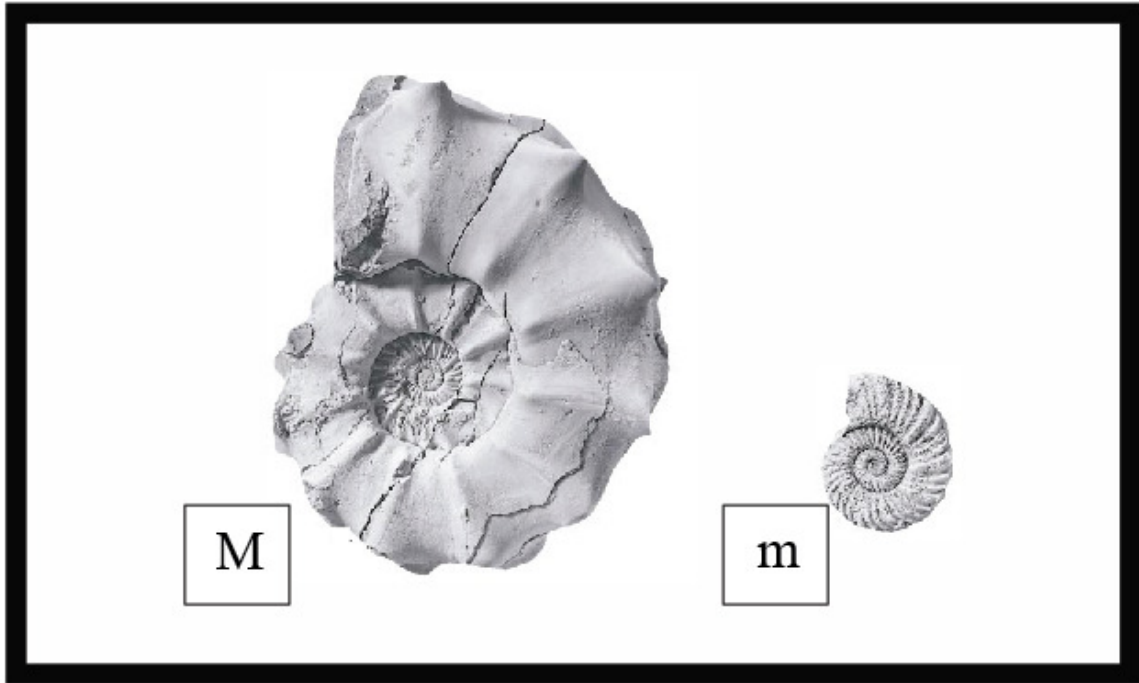
specifications. Males actually have the larger shells, broader aperture, and greater weight

in the *Nautilus*. It is important to note that the *Nautilus* might not be representative of the

ammonoids (Saunders and Spinosa, 1978). Gender specific speculations in ammonoids

also come from the use of sex ratios in both fossil ammonoids and contemporary

cephalopods. The variation in these Jurassic female to male ratios, from 1:100 and 100:1,

has not cleared up the ambiguity (Davis et al., 1996).

I focus specifically on the superfamily Acanthocerataceae to achieve my goal of

comparing the magnitude of dimorphism to stratigraphic duration. This superfamily

existed in the Cretaceous, from the Lower Albian to the Maastrichtian. They are

typically robustly ribbed and develop projections called tubercles. This superfamily is

also known for exhibiting a lot of morphological variety, including dimorphism (Wright

et al., 1996).

Ammonoids are ideal for this study because large numbers of both monomorphic

and dimorphic genera have been documented across multiple lineages. This provides a

large sample size to strengthen statistical tests. They are also perfect due to the lack of

uncertainty regarding their dimorphism in the fossil record. Sexually dimorphic traits are

well-preserved via shell morphology; therefore dimorphism can be physically measured

from their fossilized macroconchs and microconchs.

Methods

Collecting Stratigraphic Duration

I compiled global data on the presence and absence of sexual dimorphism in Mesozoic ammonoids at the genus level from the literature (Appendix I). With the use of the Paleobiology Database (PBDB) and biostratigraphic literature, I gathered first and last global occurrence data. These data were used to quantify stratigraphic duration and survivorship across background intervals.

All genera that recorded a last appearance date at the time of the Cretaceous-Tertiary extinction, 65.5 million years ago, were eliminated from further study. This is to avoid artificially truncating their durations given that the entire clade dies out at this event. After this elimination of genera, I calculated global stratigraphic durations for a total of 100 dimorphic and 112 monomorphic genera from the late Jurassic to the end Cretaceous, with the majority being in the Cretaceous.

To assess the extinction and origination of ammonoids across the Cenomanian-Turonian extinction, I identified the victims, survivors, and originators on the basis of first and last occurrence data. Genera that had last appearance dates at this extinction (93.5 Ma) were labeled victims. Genera that ranged through the extinction were labeled as survivors. Those that had first appearance dates immediately after this extinction were labeled as originators.

Collecting Macro- and Microconch Diameter Measurements

Using an ammonoid phylogenetic tree (Figure 4) and the Ammonoidea taxonomy available on the PBDB, I mapped dimorphic families and genera across the subclass. The majority of the dimorphic families that were not affected by the Cretaceous-Tertiary were

Figure 4: Cretaceous ammonite classification and phylogeny – The superfamily Acanthocerataceae is boxed (Kennedy, 1989)
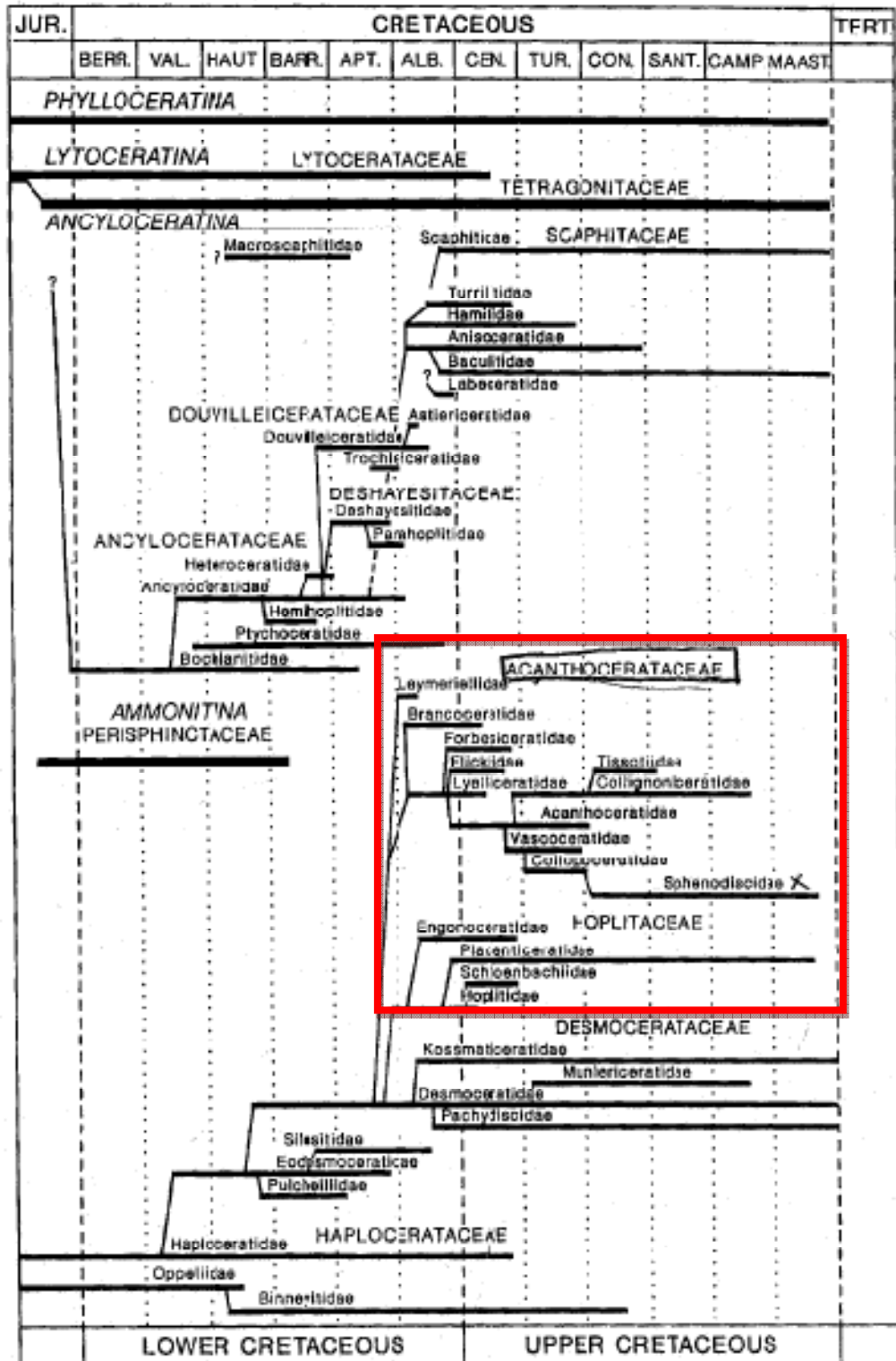
clustered in the Acanthocerataceae superfamily. Focusing on this superfamily allowed me to delve more deeply into the relationship sexual dimorphism and extinction by collection data on the magnitude of dimorphism. This database included 42 dimorphic and 35 monomorphic genera.

I compiled data from literature monographs that included diameter measurements of the macroconchs and microconchs of species within the Acanthocerataceae superfamily that displayed size-related sexual dimorphism. All diameters were measured using the traditional technique of measuring from the opening of the phragmocone, which is the chambered portion of the shell, across the widest part of the ammonoid (Figure 5). All diameters were in millimeters and measured with a ruler.

The resulting database included 65 macroconch and 78 microconch measurements from 31 species within 20 genera of this superfamily (Appendix III). I eliminated any species for which I had only one macroconch or one microconch measurement because there would be no counterpart with which to calculate magnitude. These measurements allow us to assess the extent to which the magnitude of sexual dimorphism is correlated with taxon survivorship within the superfamily Acanthocerataceae. I calculated the average diameter among all macroconchs and the average diameter among all of the microconchs of each species. I then calculated the magnitude for each species represented by subtracting the average microconch measurement from the average macroconch measurement. Then these species' average magnitudes were averaged per genus to produce a single magnitude average per genus within the superfamily. The 16 genera from the superfamily Acanthocerataceae that were represented in the database were *Forresteria, Subprionocyclus, Barroisicera, Collignoniceras, Metoicoceras,*

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Figure 5: How the diameter was measured on both the macroconchs and microconchs from the opening of the phragmocone through the widest part of the shell
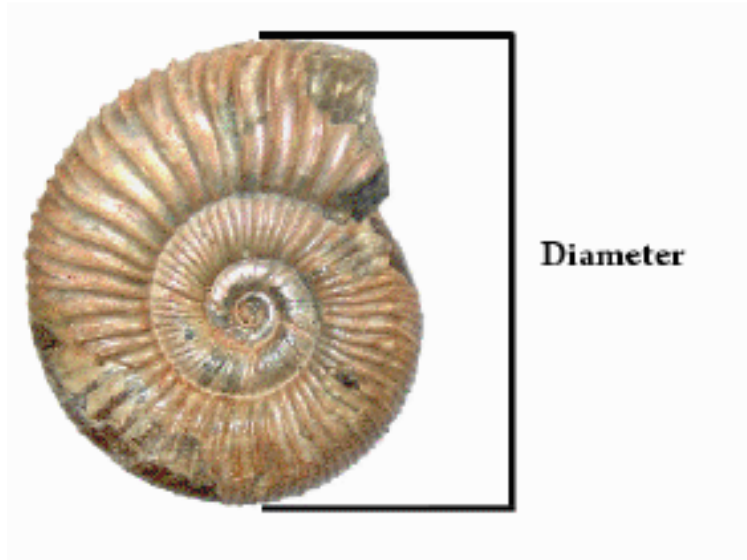
Euomphaloceras, Nannometoicoceras, Acanthoceras, Tarrantoceras, Eucalycoceras,

Calycoceras, Acompoceras, Cunningtoniceras, Thomelites, Fagesia, and Stoliczkaia.

Results and Discussion

All statistical tests were conducted with SPSS Statistics 17.0 Computer Software.

Hypothesis 1: Dimorphic genera will exhibit significantly shorter durations than

monomorphic genera – Table 1

According to Kolmogorov-Smirnov test for normality, the stratigraphic durations

of all ammonoid monomorphic and dimorphic genera were non-normally distributed ($Z_{99, 111}$= 0.167, p = 0.000). Therefore we ran a nonparametric Mann-Whitney U test. For all

ammonoid genera, dimorphic forms actually have significantly longer durations than

monomorphic genera. This result is statistically significant and in the opposite direction

of the hypothesis ($Z_{99, 111}$= -2.436, p = 0.015) (Figure 6).

To control for phylogeny I then tested this hypothesis for seven superfamilies that

contained both monomorphic and dimorphic genera (Figure 7) (Appendix II). The

Acanthocerataceae superfamily also produced the counter-hypothesis result of the

monomorphic genera actually have shorter durations (Figure 8). The data were non-

normally distributed ($Z_{42, 35}$ = 0.198, p=0.000). Attempts to normalize these data through

logging and square rooting durations did not change the normality. I found no significant

difference in duration between monomorphic and dimorphic genera through the Mann-

Whitney U Test ($Z_{42, 35}$ = -0.718, p=0.473)

Next, I analyzed the Ancyloceratoidea superfamily and found that the

monomorphic genera again had shorter durations than the dimorphic genera (Figure 9).

Figure 6: This displays the mean stratigraphic duration for all genera in the database divided into monomorphic and dimorphic bars. Error Bars are +/- 2.
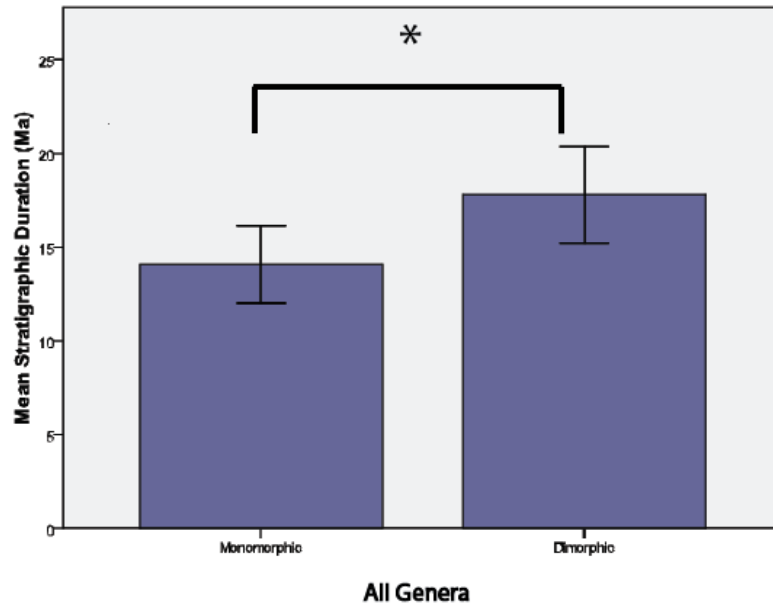
Figure 7: This displays the mean stratigraphic duration of each superfamily. "D" in front of the superfamily's name means it is the dimorphic genera that are included. "M" in front of the superfamily's name means it is the monomorphic genera that are included.
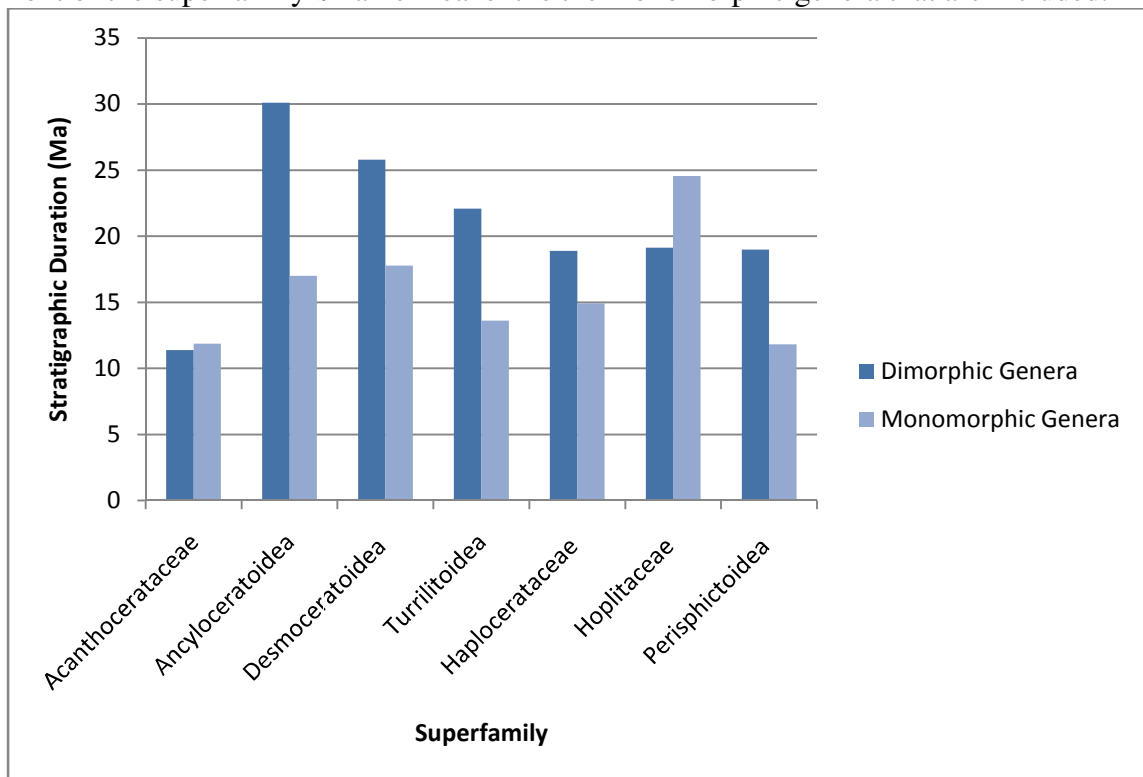
Figure 8: This displays the mean stratigraphic duration for genera within the Acanthocerataceae superfamily in the database divided into monomorphic and dimorphic bars. Error Bars are +/- 2 SE.
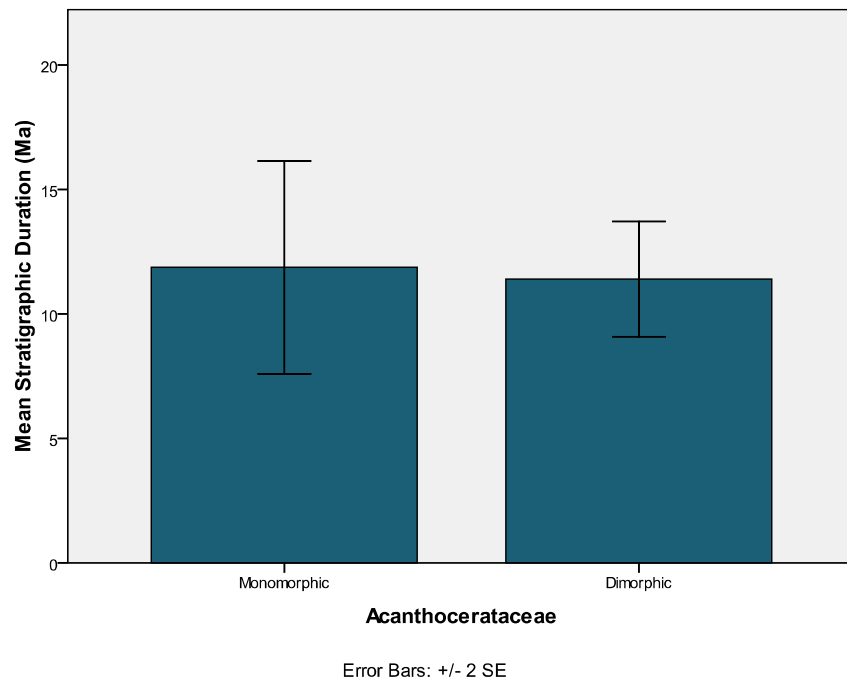
Figure 9: This displays the mean stratigraphic duration for genera within the Ancyloceratoidea superfamily in the database divided into monomorphic and dimorphic bars. Error Bars are +/- 2 SE.
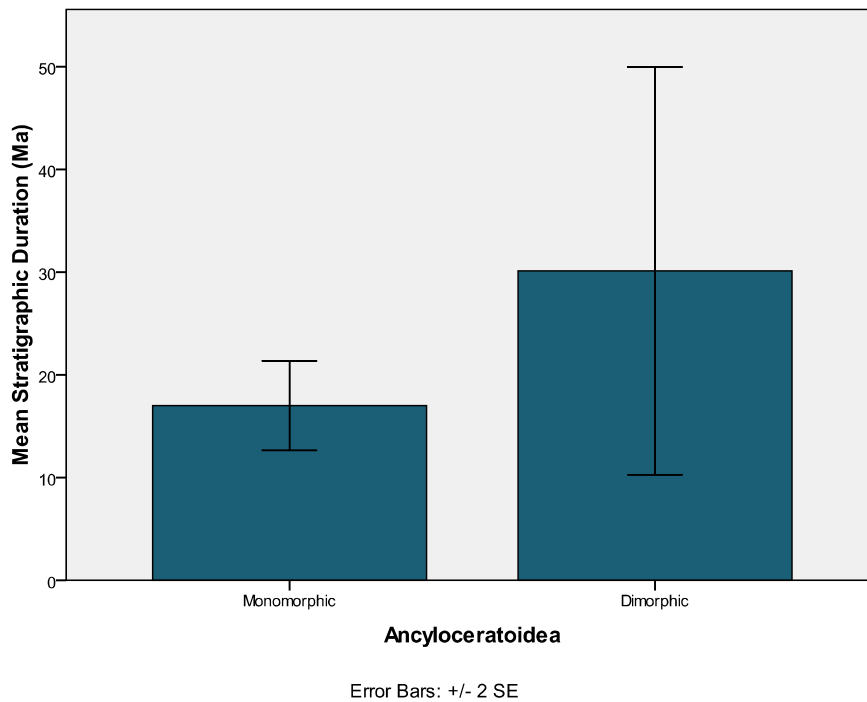
The data were non-normally distributed ($Z_{7,12}$=0.261, p=0.001). However when logged, the durations became normally distributed with a sig value of 0.200 ($Z_{7,12}$=0.145, p=0.200). I then ran a t-test on the logged data which was nonsignificant ($t_{7,12}$=0.864, p=0.400). The durations were also square-rooted, which also produced normally distributed data. The t-test on the square rooted data also was nonsignificant ($t_{7, 12}$=1.278, p=0.218.)

The Desmoceratoidea superfamily yielded a significant difference. The pattern in the data distribution of this superfamily (Figure 10) runs counter to the original hypothesis. This means that the dimorphic genera within the superfamily Desmoceratoidea actually have significantly longer durations in the fossil record. The data were non-normally distributed ($Z_{8, 21}$ = 0.269, p=0.003). This normality did not change with attempts to normalize the data using $\log_{10}$ and square root transformations. The nonparametric Mann-Whitney U test produced significant results ($Z_{8, 21}$ = -.1.960, p=0.050).

I then ran the Haplocerataceae superfamily and found the same pattern of shorter durations among the monomorphic genera (Figure 11). The data were non-normal ($Z_{5, 5}$ = 0.299, p=0.12). Attempts to transform these data did not change this normality (logged data: $Z_{5, 5}$ = 0.270, p=0.037; square rooted data: $Z_{5, 5}$ = 0.286, p=0.020). So I ran a nonparametric Mann-Whitney U test which produced non-significant results ($Z_{5, 5}$ = -.1.485, p=0.138).

Next I tested the Hoplitaceae superfamily and found that monomorphic genera had shorter durations in the fossil record (Figure 12). These data were normally

Figure 10: This displays the mean stratigraphic duration for genera within the Desmoceratoidea superfamily in the database divided into monomorphic and dimorphic bars. Error Bars are +/- 2 SE.

Figure 11: This displays the mean stratigraphic duration for genera within the Haplocerataceae superfamily in the database divided into monomorphic and dimorphic bars. Error Bars are +/- 2 SE.
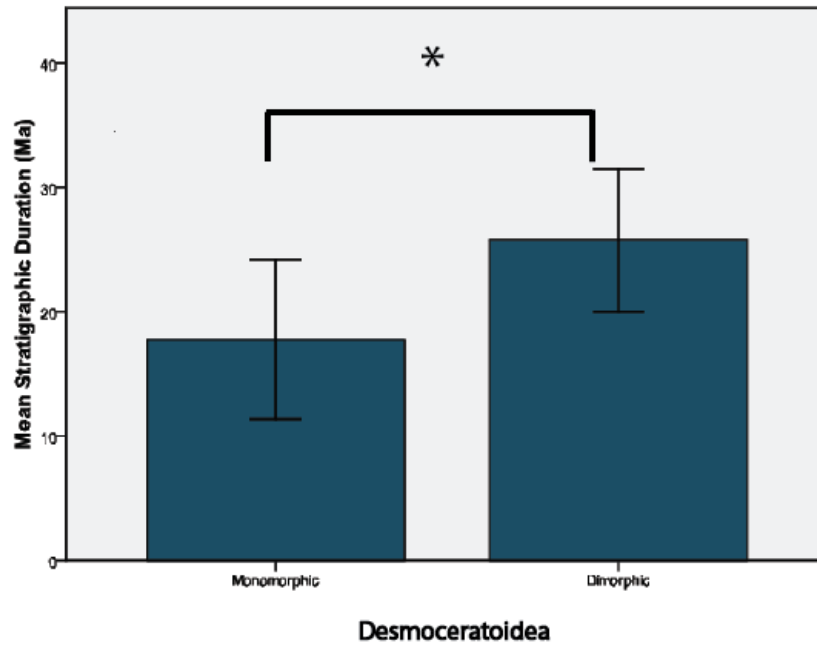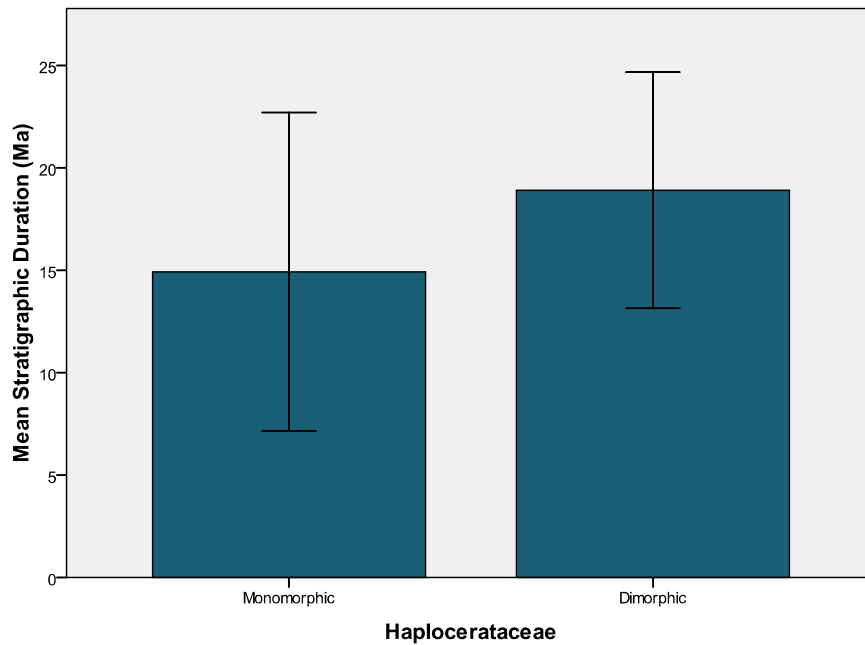
Figure 12: This displays the mean stratigraphic duration for genera within the Hoplitaceae superfamily in the database divided into monomorphic and dimorphic bars.
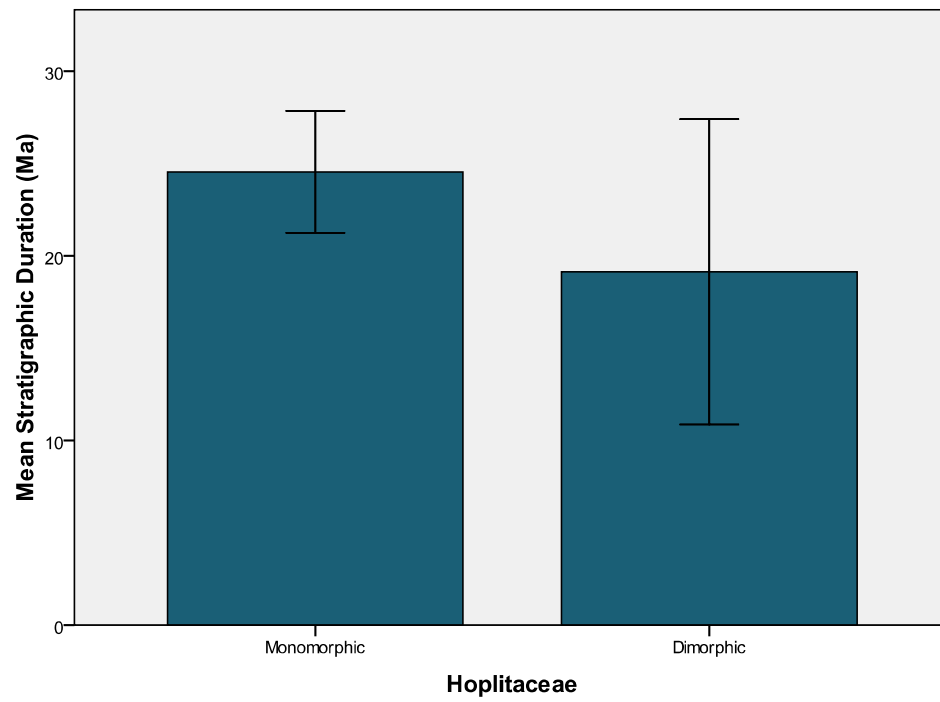
Error Bars: +/- 2 SE

distributed ($Z_{7,\,2}$=0.241, p=0.139). I ran a t-test which resulted a non-significant value ($t_{7,\,2}$=.664, p=0.528).

The Perisphinctoidea superfamily is our second significant superfamily. This superfamily's significance also runs counter to our hypothesis according to their mean duration bar graph (Figure 13). This means that the dimorphic genera within the superfamily Perisphinctoidea actually have significantly longer durations in the fossil record. These data were normally distributed ($t_{5,\,24}$=-0.147, p=0.113). I ran a t-test which resulted in $t_{5,\,24}$=-2.068, p=0.048. This result is statistically significant.

Lastly I tested the Turrilitoidea superfamily, which produced the same pattern of monomorphism leading to shorter durations (Figure 14). These data were normally distributed ($t_{12,\,13}$=0.149, p=0.159). I then ran a t-test which produced $t_{12,\,13}$=-1.701, p=0.102. Therefore, Turriltoidea's data is nonsignificant.

The general trend among the results for hypothesis 1 is that monomorphic genera overall and within separate superfamilies have shorter stratigraphic durations than dimorphic genera. This pattern is very different that that observed in modern bird studies, such as Morrow and Pitcher's 2003 study, where dimorphism leads to a higher risk of extinction.

This pattern may occur due to the advantages of dietary niche separation. Body size dimorphism has been found to create high levels of male-female dietary niche separation. Another possible explanation would be if the females were larger, there could be an increased fecundity among them due to the advantages of size. This separation could increase the survivorship of dimorphic genera. Neither of these can be thoroughly

Figure 13: This displays the mean stratigraphic duration for genera within the Perisphinctoidea superfamily in the database divided into monomorphic and dimorphic bars. Error Bars are +/- 2.
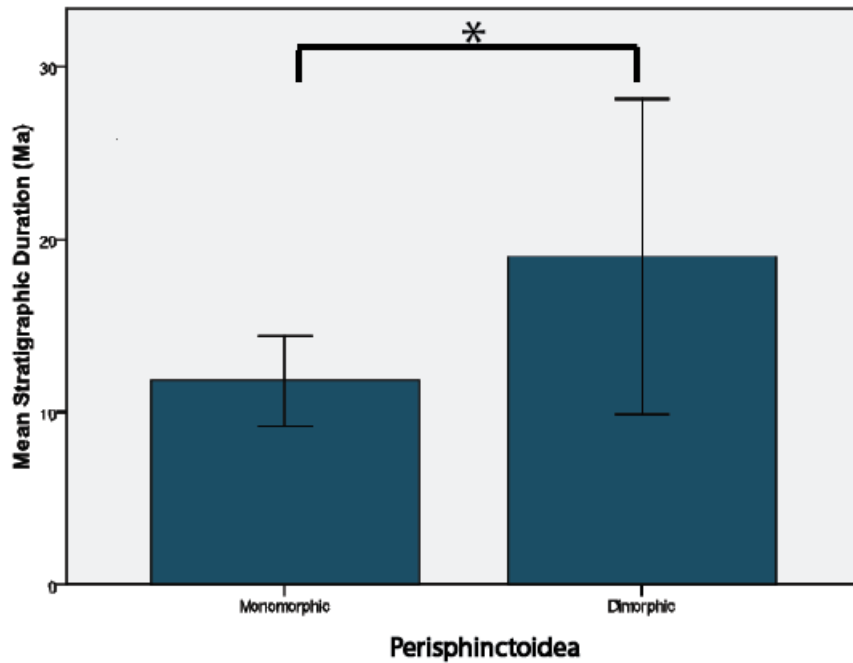
Figure 14: This displays the mean stratigraphic duration for genera within the Turrilitoidea superfamily in the database divided into monomorphic and dimorphic bars. Error Bars are +/- 2 SE.
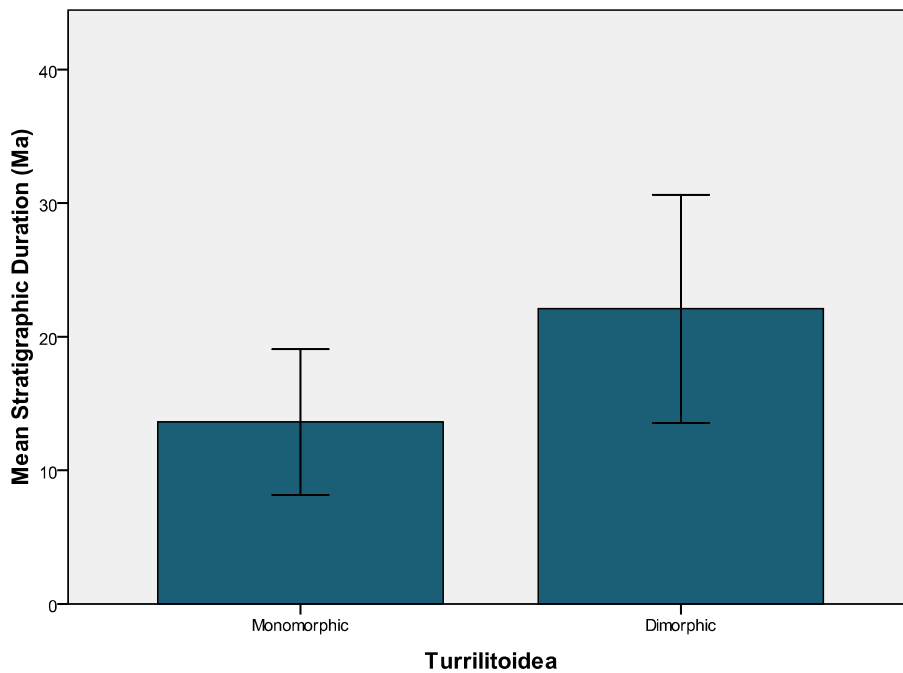
tested in the fossil record, but could offer some kind of explanation for the dimorphic ammonoid genera's longer durations.

Hypothesis 2: For the Cenomanian-Turonian extinction, dimorphic genera are more likely to go extinct than monomorphic genera – Table 2

The database of monomorphic and dimorphic genera consisted of many that were affected by the Cenomanian-Turonian (C/T) extinction at 93.5 Ma. Dimorphic taxa were no more likely to go extinct or survive than monomorphic ones. However, the pattern in the data leads us to believe that monomorphic genera were slightly more likely to go extinct (Figure 15). The observed data included 6 monomorphic victims, 17 dimorphic victims, 9 monomorphic survivors, and 29 dimorphic survivors. The expected data for a chi-square test included 11.5 monomorphic and dimorphic victims, as well as 19 monomorphic and dimorphic survivors. Victims were divided by survivors for both monomorphic and dimorphic. Comparison of observed versus expected yielded a p value of 0.934138. Therefore, this hypothesis was rejected.

I then applied this hypothesis to specific superfamilies that had a large enough sample size of victims and survivors of the Cenomanian-Turonian extinction. This included the Acanthocerataceae, Desmoceratoidea, Hoplitaceae, and Turrilitoidea superfamilies. The p-values of Acanthocerataceae, Desmoceratoidea, and Turrilitoidea were nonsignificant as 0.69, 0.42, and 0.52 respectively. All three of the patterns within these superfamilies' data run counter to the hypothesis; meaning that monomorphic genera were more likely to go extinct. The Hoplitaceae superfamily produced a p-value of 0.025. The result is in congruence with our hypothesis that the dimorphic genera within this superfamily were more likely to be victims of the Cenomanian-Turonian

Figure 15: This displays the mean percentage of victims in relation to survivors of both monomorphic and dimorphic genera across the Cenomanian-Turonian extinction. Monomorphic genera have a 40% victims and dimorphic genera have 37%.
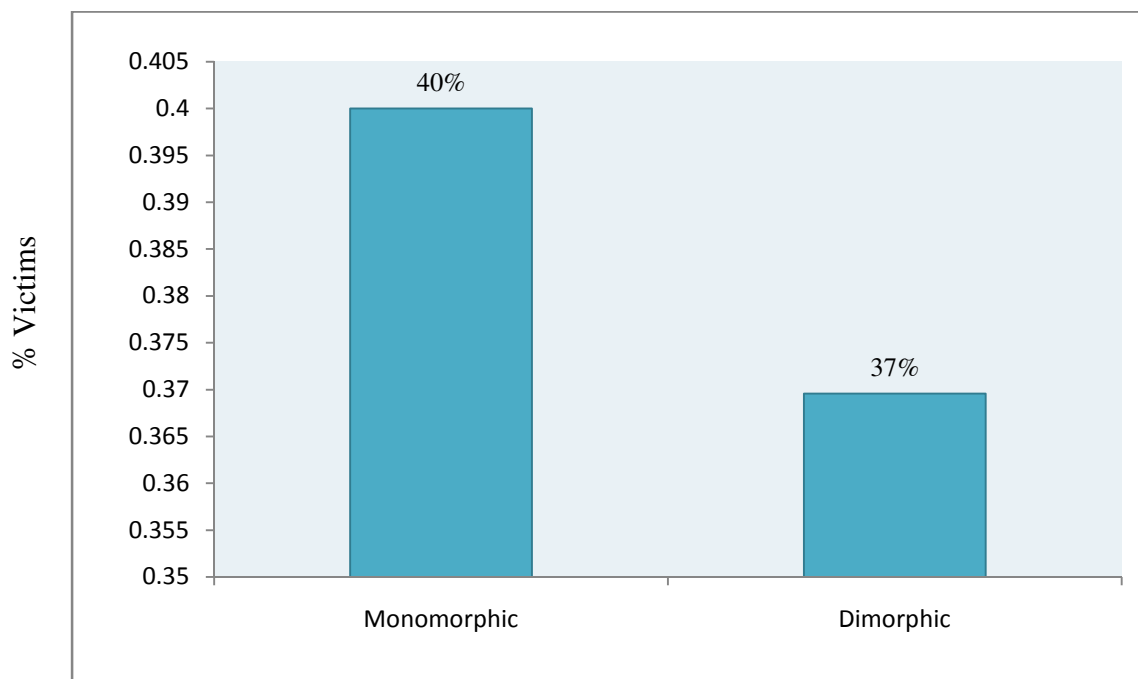
extinction. These are the only data that support the original hypothesis. This may also be due to the small number of genera within the superfamily Hoplitaceae that were involved in the C/T extinction.

The general trend among the results for hypothesis 2 is that monomorphic genera overall and within separate superfamilies are more likely to go extinct at the Cenomanian-Turonian extinction, excluding the Hoplitaceae superfamily. Since this is the first study to examine the effects of dimorphism in relation to a mass extinction event, there is nothing to compare these results to.

Monomorphism leads to a higher risk of extinction within this hypothesis, as with hypothesis 1. This again could be due to the possible advantages of dimorphism for ammonoids. These could include a dietary niche separation or increased female size and therefore fecundity. These are possible options that could lead to increased survivorship among ammonoids.

Hypothesis 3: After the Cenomanian-Turonian extinction, dimorphic genera are more likely to radiate than monomorphic genera - Table 2

It has been suggested that sexual dimorphism may promote radiation of taxa due to the focus on reproduction. Dimorphic and monomorphic genera that originated at the Cenomanian-Turonian extinction were compared to evaluate this hypothesis. The patterns among the data were counter to the hypothesis; meaning monomorphic genera were more likely to radiate than dimorphic genera (Figure 16). These data underwent a chi square test. The observed data included 17 monomorphic originators, 18 dimorphic originators, 9 monomorphic survivors, and 29 dimorphic survivors. This meant the expected data include 17.5 monomorphic and dimorphic victims, as well as 19

Figure 16: This displays the mean percentage of originators in relation to survivors of both monomorphic and dimorphic genera across the Cenomanian-Turonian extinction. Monomorphic genera have a 65% originators and dimorphic genera have 38%.
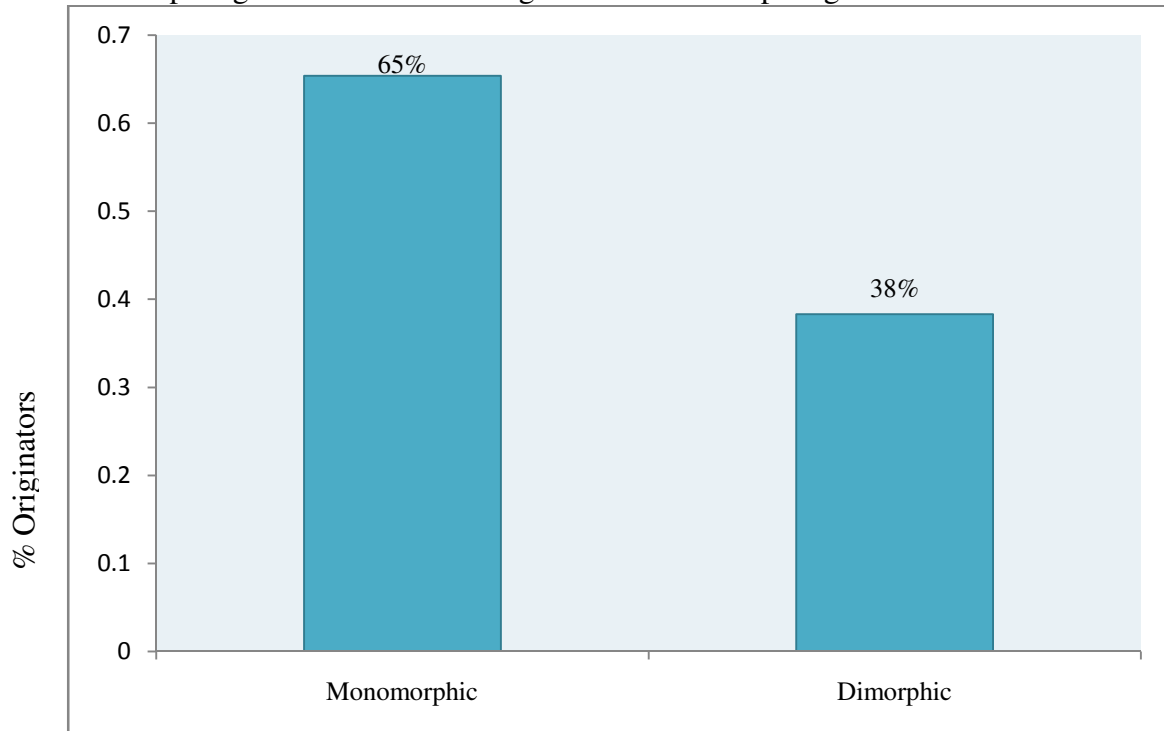
monomorphic and dimorphic survivors. Originators were divided by survivors for both

monomorphic and dimorphic. These numbers produced a non-significant p-value of

0.291.

I then applied this hypothesis to individual superfamilies. First, I ran chi square

tests on the Acanthocerataceae superfamily. This superfamily's p-value of 0.049 was

significant. The observed data that went into this chi square test was 15 monomorphic

and 9 dimorphic genera originating at the Cenomanian-Turonian extinction. Also, there

are 4 monomorphic and 14 dimorphic genera surviving through the C/T. Therefore, after

reviewing the data the significant results seems to also run counter to the hypothesis.

This means that within the Acanthocerataceae superfamily the monomorphic genera are

actually more likely to radiate post-C/T extinction.

The other three superfamilies that had enough data to complete a chi square test

were Desmoceratoidea, Hoplitaceae, and Turrilitoidea. The three p-values were 0.35,

0.32, and 0.68 respectively. Therefore all three were nonsignificant.

The general trend among the results for hypothesis 3 is monomorphic genera were

more likely to radiate than dimorphic genera. Since this is the first study to examine the

effects of dimorphism in relation to the response to a mass extinction event, there is

nothing to compare these results to.

Hypothesis 4: For dimorphic genera of the superfamily Acanthocerataceae, the

magnitude of dimorphism will be negatively correlated to stratigraphic duration

After graphing these data and logging the magnitude of dimorphism (Figure 17) it

became apparent that there was a positive trend.   This means that as the magnitude of

dimorphism increases, so does the stratigraphic duration. I then ran a linear regression

Figure 16: This graph displays the positive correlation between magnitude of dimorphism and mean stratigraphic duration within the Acanthocerataceae superfamily's dimorphic genera.
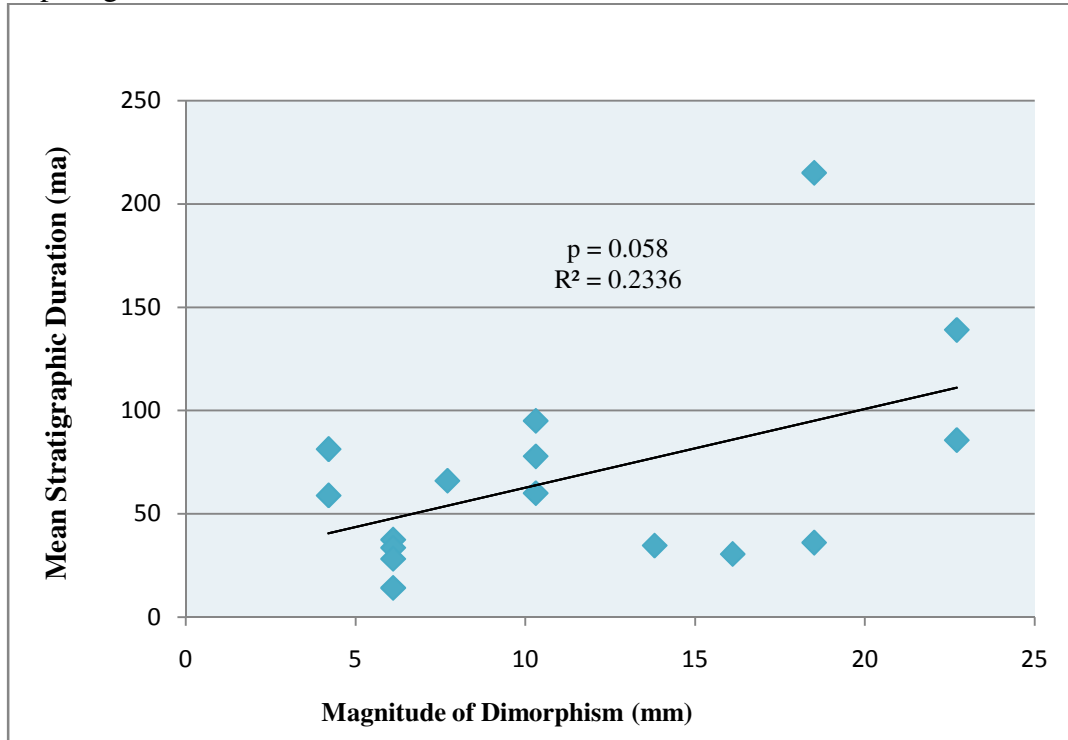
which produced a sig value of 0.058. This is very close to a significant value of 0.05 or below. The results of this regression was R=0.234, p = 0.058. The nearly significant result along with the graph show that it actually is running counter to the hypothesis.

The general trend among the results for hypothesis 4 is as the magnitude of dimorphism increases within the superfamily Acanthocerataceae, so does the stratigraphic duration. Since this is the first study to examine the effects of the magnitude of dimorphism on durations there is no previous work to compare this result to.

This pattern could be directly due to a dietary niche separation within this superfamily. As the difference between the gender increase, as does the resources they require for surviving. Therefore, as magnitude increases their niches become more separate which leads to a decrease in intraspecific competition. This separation could be linked to their increased survivorship within the superfamily.

Conclusions

The data provides significant results about species selection in the fossil record. Nearly all of the significant results ran counter to our original hypotheses. The general trend among the hypotheses is that dimorphic genera would have shorter durations than monomorphic genera. The trend that the actual data produced is that dimorphic genera actually tend to have longer stratigraphic durations than monomorphic genera. This could mean that dimorphism, a species-level trait, is linked to increased survivorship, at least in ammonoids.

This could be due to either a dimorphic niche separation between the genders or increased fecundity within the larger females. Due to a body size difference, the genders might not be competing for resources. The reduction of intraspecific competition could

increase survivorship. Also, if indeed the females are larger among ammonoids, they

might have greater access to resources and produce a larger number of offspring. Both of

these processes would be difficult to test within the fossil record.

Future projects could include more phylogenetic control than the superfamily

analyses. This could be done with explicit phylogenetic framework and the use

independent contrasts, which is currently unavailable for ammonoids. This control would

eliminate the influence of the closeness of their relationships on the results. Other studies

could include investigating more extinction events. It could be that the C/T extinction

was not representative of dimorphic responses to extinction crises in either victims or

originators.

It would also be interesting to look into more taxa in the fossil record that have

both monomorphism and dimorphism to see if they have any significant connections to

their survivorship. Two examples of this are ostracodes and artiodactyls.   Even looking

at another aspect of dimorphism within ammonoids, such as ornamentation, ornament

size, and umbilici size, could possibly lead to different results.

Table 1: Statistical Results from Mann Whitney U and T-Tests for Hypothesis 1

Significant Values are **bolded** with an asterisk

Superfamily	Sample Size (Dimorphic, Monomorphic Genera)	P-Value for Hypothesis 1 (Dimorphism & Stratigraphic Duration)
All	99, 111	**0.015 ***
Acanthocerataceae	42, 35	0.473
Ancyloceratoidea	7, 12	0.218
Desmoceratoidea	8, 21	**0.050 ***
Haplocerataceae	5, 5	0.138
Hoplitaceae	7, 2	0.528
Perisphinctoidea	5, 24	**0.048 ***
Turrilitoidea	12, 13	0.102

Table 2: Statistical Results from Chi-Square Tests for Hypotheses 2 and 3

Superfamily	P-Value for Hypothesis 2 (Dimorphism & Extinction)	P-Value for Hypothesis 3 (Dimorphism & Recovery)
All	0.934	0.291
Acanthocerataceae	0.692	**0.049 ***
Desmoceratoidea	0.420	0.352
Hoplitaceae	**0.025 ***	0.317
Turrilitoidea	0.519	0.683

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The Paleobiology Database:
The data were downloaded from the Paleobiology Database on 30 November, 2009 and 1 December, 2009, using the following parameters: Taxa to include: All listed in Appendix I. Basic fields: collection name, collection aka, reference number, publication year, authorizer, enterer, modifier, research group. Geography fields: country, state, county, geographic scale, tectonic plate id, latitude/longitude in decimal, paleolatitude/longitude in decimal. Time fields: period, epoch, Cenozoic subepoch, stage, 10 m.y. bin, maximum interval, minimum interval, maximum age (Ma), minimum age (Ma), midpoint age (Ma). Stratigraphy fields: formation, member, stratigraphic scale, stratigraphic comments. Lithology fields: lithification 1, lithification 2, lithological description, minor lithology 1, minor lithology 2, environment, lithology 1, lithology 2, geology comments.

Appendix I: Ammonoid Genera and their Minimum and Maximum Date and Stratigraphic Duration (in Ma)

Genus Name	Maximum Date (Ma)	Minimum Date (Ma)	Duration (Ma)
Abrytasites	136.4	125	11.4
Acanthoceras	112	89.3	22.7
Acanthodiscus	145.5	125	20.5
Acompoceras	112	93.5	18.5
Aconeceras	130	99.6	30.4
Acrioceras	136.4	125	11.4
Aleteceras	112	99.6	12.4
Allocrioceras	99.6	85.8	13.8
Anahoplites	112	93.5	18.5
Ancyloceras	140.2	70.6	69.6
Ankinatsytes	89.3	85.8	3.5
Astiericeras	112	99.6	12.4
Australiceras	125	99.6	25.4
Baculites	112	58.1	53.9
Barremites	136.4	125	11.4
Barroisiceras	99.6	83.5	16.1
Beaudanticeras	112	99.6	12.4
Benueites	93.5	89.3	4.2
Berriasella	150.8	136.4	14.4
Blanfordiceras	150.8	140.2	10.6
Boehmoceras	85.8	83.5	2.3
Boliteceras	112	99.6	12.4
Buchiceras	93.5	85.8	7.7
Budaiceras	112	93.5	18.5
Burckhardtites	125	112	13
Callihoplites	112	93.5	18.5
Calycoceras	99.6	89.3	10.3
Chesapeakella	83.5	70.6	12.9
Cibolaites	93.5	89.3	4.2
Cirroceras	83.5	70.6	12.9
Clioscaphites	89.3	83.5	5.8
Coilopoceras	112	85.8	26.2
Colchidites	130	125	5
Collignoniceras	93.5	89.3	4.2
Cophinoceras	112	99.6	12.4
Crioceratites	140.2	99.6	40.6
Cryptotexanites	83.5	70.6	12.9
Cunningtoniceras	99.6	89.3	10.3

Cyrtosiceras	150.8	140.2	10.6
Delphinella	161.2	140.2	21
Desmoceras	130	83.5	46.5
Didymoceras	93.5	58.1	35.4
Distoloceras	140.2	130	10.2
Douvilleiceras	125	93.5	31.5
Dunveganoceras	99.6	93.5	6.1
Elenaella	145.5	140.2	5.3
Eleniceras	140.2	130	10.2
Eomarshallites	112	99.6	12.4
Eubostrychoceras	93.5	70.6	22.9
Eucalycoceras	99.6	93.5	6.1
Euhomaloceras	85.8	70.6	15.2
Euhoplites	112	93.5	18.5
Euhystrichoceras	99.6	93.5	6.1
Eulophoceras	93.5	70.6	22.9
Euomphaloceras	99.6	85.8	13.8
Fagesia	99.6	89.3	10.3
Favrella	140.2	112	28.2
Forbesiceras	112	99.6	12.4
Forresteria	93.5	85.8	7.7
Gauthiericeras	89.3	83.5	5.8
Graysonites	112	93.5	18.5
Groebericeras	145.5	140.2	5.3
Gyaloceras	125	99.6	25.4
Hamiticeras	130	112	18
Haploceras	155.7	130	25.7
Helicancylus	125	99.6	25.4
Herrickiceras	93.5	89.3	4.2
Heteroceras	130	70.6	59.4
Hoplitoides	93.5	89.3	4.2
Hoploscaphites	85.8	65.2	20.6
Hypacanthohoplites	125	112	13
Hypacanthoplites	125	89.3	35.7
Hypengonoceras	112	99.6	12.4
Hyphantoceras	93.5	70.6	22.9
Hyphoplites	112	93.5	18.5
Hysteroceras	112	93.5	18.5
Idanoceras	125	99.6	25.4
Jabronella	145.5	140.2	5.3
Jimboiceras	93.5	70.6	22.9
Jouaniceras	85.8	83.5	2.3
Kamerunoceras	99.6	89.3	10.3

Karakaschiceras	140.2	130	10.2
Kennicottia	112	99.6	12.4
Kilianella	145.5	130	15.5
Koloceras	112	99.6	12.4
Labeceras	112	99.6	12.4
Lechites	112	93.5	18.5
Leopoldia	140.2	130	10.2
Lewyites	83.5	70.6	12.9
Luppovella	140.2	136.4	3.8
Lyelliceras	112	93.5	18.5
Lyticoceras	140.2	130	10.2
Lytocrioceras	130	125	5
Macroscaphites	130	99.6	30.4
Mammites	145.5	136.4	9.1
Manambolites	83.5	70.6	12.9
Mantelliceras	112	83.5	28.5
Mariella	112	89.3	22.7
Marshallites	112	99.6	12.4
Melchiorites	136.4	99.6	36.8
Menuites	85.8	58.1	27.7
Mesopuzosia	99.6	70.6	29
Metaplacenticeras	93.5	70.6	22.9
Metaptychoceras	99.6	93.5	6.1
Metoicoceras	112	89.3	22.7
Mitonia	93.5	89.3	4.2
Moremanoceras	99.6	93.5	6.1
Morrowites	93.5	89.3	4.2
Mortoniceras	112	83.5	28.5
Myloceras	112	99.6	12.4
Nannometoicoceras	99.6	93.5	6.1
Naramoceras	112	99.6	12.4
Neocardioceras	99.6	93.5	6.1
Neocomites	145.5	112	33.5
Neocrioceras	99.6	83.5	16.1
Neoglyptoxoceras	85.8	70.6	15.2
Neohoploceras	140.2	136.4	3.8
Neophlycticeras	112	99.6	12.4
Neoptychites	112	89.3	22.7
Neopuzosia	89.3	83.5	5.8
Nigericeras	99.6	89.3	10.3
Nostoceras	93.5	58.1	35.4
Nowakites	89.3	83.5	5.8
Olcostephanus	145.5	125	20.5

Onitshoceras	89.3	85.8	3.5
Pachydesmoceras	112	85.8	26.2
Pachydiscus	93.5	61.7	31.8
Paracrioceras	130	125	5
Paramammites	93.5	89.3	4.2
Parandiceras	125	112	13
Parapuzosia	99.6	70.6	29
Paraspiticeras	136.4	125	11.4
Paratexanites	89.3	83.5	5.8
Patagiosites	83.5	70.6	12.9
Pedioceras	130	112	18
Peroniceras	93.5	83.5	10
Placenticeras	99.6	58.1	41.5
Plesiotexanites	89.3	70.6	18.7
Polyptychoceras	89.3	70.6	18.7
Prionocycloceras	93.5	85.8	7.7
Prionocyclus	93.5	89.3	4.2
Prionotropis	93.5	89.3	4.2
Prolyelliceras	125	99.6	25.4
Proplacenticeras	112	85.8	26.2
Protexanites	89.3	83.5	5.8
Pseudaspidoceras	99.6	89.3	10.3
Pseudoaustraliceras	125	112	13
Pseudobaculites	89.3	85.8	3.5
Pseudocalycoceras	99.6	93.5	6.1
Pseudocrioceras	130	125	5
Pseudohaploceras	136.4	112	24.4
Pseudoneocomites	140.2	136.4	3.8
Pseudoneoptychites	93.5	89.3	4.2
Pseudosilesites	125	112	13
Pseudotissotia	93.5	89.3	4.2
Puzosia	130	70.6	59.4
Quitmaniceras	93.5	89.3	4.2
Reesidites	93.5	89.3	4.2
Reginaites	85.8	83.5	2.3
Rhaeboceras	83.5	70.6	12.9
Rhamphidoceras	93.5	89.3	4.2
Roemeroceras	89.3	85.8	3.5
Romaniceras	155.7	83.5	72.2
Rubroceras	99.6	93.5	6.1
Salaziceras	112	99.6	12.4
Sanmartinoceras	130	112	18
Sarasinella	145.5	130	15.5

Saynoceras	140.2	125	15.2
Scalarites	93.5	83.5	10
Scaphites	199.6	61.7	137.9
Sciponoceras	112	85.8	26.2
Sharpeiceras	112	83.5	28.5
Shuparoceras	93.5	89.3	4.2
Silesites	136.4	99.6	36.8
Sinzovia	125	112	13
Solgerites	89.3	83.5	5.8
Spathites	93.5	89.3	4.2
Spathites	93.5	89.3	4.2
Spiroxybeloceras	112	70.6	41.4
Stoliczkaia	112	93.5	18.5
Subalpinites	145.5	136.4	9.1
Subastieria	145.5	125	20.5
Submortoniceras	85.8	70.6	15.2
Subprionocyclus	93.5	89.3	4.2
Subprionotropis	93.5	85.8	7.7
Subsaynella	135.4	130	5.4
Substeueroceras	150.8	136.4	14.4
Substreblites	150.8	140.2	10.6
Sumitomoceras	99.6	93.5	6.1
Taraisites	140.2	136.4	3.8
Tarrantoceras	99.6	93.5	6.1
Texanites	89.3	70.6	18.7
Thomasites	93.5	89.3	4.2
Thomelites	99.6	93.5	6.1
Thurmanniceras	145.5	125	20.5
Tirnovella	145.5	136.4	9.1
Tlahualiloceras	112	99.6	12.4
Tonohamites	125	112	13
Toxoceratoides	130	112	18
Trachyscaphites	83.5	58.1	25.4
Tropaeum	125	99.6	25.4
Tuberosciponoceras	112	99.6	12.4
Uhligites	150.8	140.2	10.6
Umsinenoceras	112	99.6	12.4
Valanginites	140.2	125	15.2
Valdedorsella	136.4	99.6	36.8
Vascoceras	99.6	89.3	10.3
Watinoceras	112	89.3	22.7
Worthoceras	112	89.3	22.7
Yabeiceras	89.3	85.8	3.5

Yezoites	112	70.6	41.4
Yokoyamaoceras	93.5	70.6	22.9

Appendix II: Average Monomorphic and Dimorphic Stratigraphic Durations for each Superfamily

Superfamily	**Dimorphic Average (Ma)**	**Monomorphic Average (Ma)**
Acanthocerataceae	11.39	11.8685
Ancyloceratoidea	30.11	17
Desmoceratoidea	25.789	17.7714
Turrilitoidea	22.091	13.615
Haplocerataceae	18.9	14.92
Hoplitaceae	19.142	24.55
Perisphictoidea	19	11.825

Appendix III: Macroconch (M) and microconch (m) measurements within the
superfamily Acanthocerataceae

- Superfamily = <u>underlined</u>, Genus = **bolded**, species = *italicized*
- References listed in Appendix IV

<u>Collignoniceratidae</u>
    Forresteria
        Forresteria petrocoriensis
            M: 110 mm
            m: 44 mm
    Subprionocyclus
        Subprionocyclus minimus
            M: 109.3 mm
            m: 50.4 mm, 63 mm
    Barroisiceras
        Barroisiceras onilahyense
            M: 101.9 mm, 93.36 mm, 107 mm, 84.68 mm, 115 mm
            m: 75.25 mm, 64.58 mm, 67.05 mm, 74.6 mm, 72 mm, 65 mm
    Collignoniceras
        Collignoniceras woollgari
            M: 79 mm
            m: 30 mm, 54 mm, 38 mm, 36 mm, 35 mm, 41 mm
        Collignoniceras praecox
            M: 240 mm, 140 mm, 144 mm
            m: 48 mm, 49 mm, 54 mm, 50 mm, 45 mm, 50 mm
<u>Acanthoceratidae</u>
    Metoicoceras
        Metoicoceras mosbyense
            M: 125 mm, 255 mm, 231 mm
            m: 89 mm, 30 mm, 17 mm
        Metoicoceras geslinianum
            M: 250 mm, 185 mm
            m: 200 mm, 215 mm
    Euomphaloceras
        Euomphaloceras septemseriatum
            M: 80 mm, 76 mm, 98 mm
            m: 50 mm
    Nannometoicoceras
        Nannometoicoceras acceleratum
            M: 32.8 mm, 33 mm, 33.5 mm, 37.5 mm,
            m: 17 mm, 17.5 mm, 20.5 mm, 20.8 mm, 21.5 mm, 22.8 mm
    Acanthoceras
        Acanthoceras amphibolum
            M: 330 mm
            m: 133 mm

Acanthoceras rhotomagensis
    M: 300 mm
    m: 150 mm
Acanthoceras jukesbrownei
    M: 320 mm, 300 mm, 157 mm
    m: 159 mm, 170 mm

Plesiacanthoceratoides
Plesiacanthoceratoides vetula
    M: 19.3 mm, 19 mm, 20.3 mm
    m: 13.8 mm

Tarrantoceras
Tarrantoceras sellardsi
    M: 90 mm, 100 mm
    m: 57.5 mm

Eucalycoceras
Eucalycoceras pentagonum
    M: 140 mm, 130 mm
    m: 110 mm
Eucalycoceras rowei
    M: 120 mm
    m: 70 mm, 90 mm, 69.9 mm, 74.9 mm, 84.6 mm

Calycoceras
Calycoceras asiaticum asiaticum
    M: 163.5 mm, 210 mm, 130 mm, 87 mm
    m: 45 mm, 48.3 mm
Calycoceras gentoni
    M: 70 mm, 85 mm
    m: 45 mm, 60 mm, 39.5 mm, 73.2 mm
Calycoceras sarthacense
    M: 70 mm, 101 mm, 150 mm
    m: 50 mm, 55 mm, 53.9 mm
Calycoceras naviculare
    M: 200 mm
    m: 100 mm
Calycoceras guerangeri
    M: 200 mm, 250 mm
    m: 100 mm, 120 mm

Acompoceras
Acompoceras renevieri
    M: 350 mm
    m: 135 mm

Cunningtoniceras
Cunningtoniceras cunningtoni
    M: 240 mm
    m: 180 mm, 180 mm

Protacanthoceras

Protacanthoceras bunburianum

M: 32.8 mm, 32 mm, 29.2 mm, 24.8 mm, 23 mm, 33 mm

m: 18.3 mm, 21.7 mm, 22.4 mm, 22.5 mm, 17 mm, 22 mm,

Protacanthoceras proteus

M: 20 mm, 27 mm,

m: 15 mm

Protacanthoceras proteus vascoceratoides

M: 26.8 mm

m: 19.6 mm

Kastanoceras

Kastanoceras spiniger

M: 10 mm

m: 8 mm

Thomelites

Thomelites sornayi

M: 130 mm

m: 85 mm, 100 mm, 93.5 mm, 123 mm, 107.3 mm

Vascoceratidae

Fagesia

Fagesia catinus

M: 200 mm

m: 100 mm, 110 mm

Lyelliceratidae

Zuluscaphites/Huescaries

Huescaries companyi

M: 55 mm

m: 38.5 mm

Stoliczkaia

Stoliczkaia texana

M: 56 mm, 74 mm, 100.5 mm

m: 37.5 mm, 44 mm

Appendix IV: List of References of Diameter Measurements

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