Impact of Reproductive Strategy
on Cephalopod Evolution

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Einfluss der Reproduktionsstrategie
auf die Evolution der Cephalopoden

Zusammenfassung

Ammonoidea waren die bei weitem am schnellsten evoluierende und artenreichste Gruppe unter den fossilen Cephalopoden. Ein Grund für die Unterschiede in Diversität und Evolutionsrate unter den größeren Cephalopodengruppen könnte sein, dass Taxa innerhalb von Kladus mit kurzen stratigraphischen Reichweiten und hoher Diversität eine semelpare Reproduktionsstrategie (Absterben der Elterngeneration folgt auf kollektives Ablaichen) besaßen, während Taxa in Kladus mit großen stratigraphischen Reichweiten und geringer Diversität eine iteropare Reproduktionsstrategie hatten (wiederholte, getrennte Brutperioden).

Vorläufige Resultate aus dem Karbon der südlichen mittleren USA unterstützen diese Hypothese. Die stratigraphische Reichweite der Nautiloideen ist im Durchschnitt 4,3 mal länger als die Reichweiten der gleichzeitig auftretenden Ammonoideen, wobei die Embryonalgehäuse der Nautiloideen 6 bis 10 mal größer waren als die Ammonitellen. Der durchschnittliche Durchmesser der Ammonitellen war sehr ähnlich für Spezies nahe verwandter Goniatitenfamilien (~0,80 mm) und die Variation innerhalb der Spezies war gering (s.d. 0,03–0,06 mm). Diese Ergebnisse decken sich mit der Größe der Embryonen einiger rezenter semelparer und iteroparer Cephalopoden (z.B. *Loligo pealei* und *Nautilus pompilius*).

Abstract

Ammonoids were by far the most rapidly evolving and species-rich of major cephalopod groups in the fossil record. One reason for differences in diversity and in evolutionary rates among major cephalopod groups may be that taxa in clades characterized by short stratigraphic ranges and high total diversity had a semelparous reproductive strategy (parental mortality follows mass spawning event), whereas taxa in clades with long stratigraphic ranges and low total diversity had an iteroparous reproductive strategy (repeated, isolated breeding events).

Preliminary results from the Carboniferous of the southern midcontinent, USA, support this hypothesis. Stratigraphic ranges of the nautiloid taxa were on average about 4.3 times longer than the ranges of co-occurring ammonoid taxa, and nautas were typically 6 to 10 times larger than ammonitellas. Mean ammonitella diameter was very similar for species within closely related goniatitid families (~0.80 mm), and size variation within species was small (s.d. 0.03–0.06 mm). These results are consistent with embryonic size data from some extant semelparous and iteroparous cephalopods (e.g., *Loligo pealei* and *Nautilus pompilius*, respectively).

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1. Introduction

Evolutionary tree topologies for the Ammonoidea and the Nautiloidea are very different (Text-Fig. 1). In general, nautiloid taxa tend to have longer durations than ammonoid taxa, and fewer nautiloid taxa were generated despite having a longer evolutionary history. The duration of the Ammonoidea was approximately 330 million years, and in that time, more than 200 families and 1500 genera evolved, corresponding to an average family origination rate of 0.64 families per million years and an average genus origination rate of 4.7 genera per million years. In comparison, nautiloids have a longer taxon duration (~520 m.y.), yet only about half the number of families (~100) and genera (~1750), and the average family and genus origination rates are about one third of the ammonoid rates (0.21 fam./m.y. and 1.4 gen./m.y., respectively). A number of explanations for these differences have been proposed. In this paper, we develop the possibility that they are the consequence of differences in embryology and reproductive style. Important contributions to the study of cephalopod ontogeny and embryology (especially concerning fossil species) have been made by SCHINDE-WOLF (1933, 1934), ERBEN (1962, 1968), DRUSCHITS (1970), KULICKI (1974), BOLETZKY (1974, 1987, 1988), LEHMANN (1981), LANDMAN (1982, 1988, 1996), TANABE (1985), BANDEL (1986), WARD (1987), ENGESER (1990), DOGUZHAEVA (1999), as well as others. Here, we focus on diversity, evolutionary rates, and reproductive strategies.

Semelparity is a reproductive strategy in which individuals reproduce once, usually in a coordinated breeding effort by all mature members of the population, then die soon afterwards. Iteroparity, by contrast, is a reproductive strategy in which individuals may reproduce repeatedly, usually in isolated breeding events, and death is not normally associated with reproduction. Considering reproductive strategy as either semelparous or iteroparous may be an over-simplification, for the two reproductive strategies actually represent end-members in a continuum ranging from reproducing once (uniseasonal uniparous) to reproducing continuously (continuous iteroparous) (KIRKENDALL & STENSETH, 1985). However, given the observable differences in species representing the end-members, the dichotomy is useful in this case. In
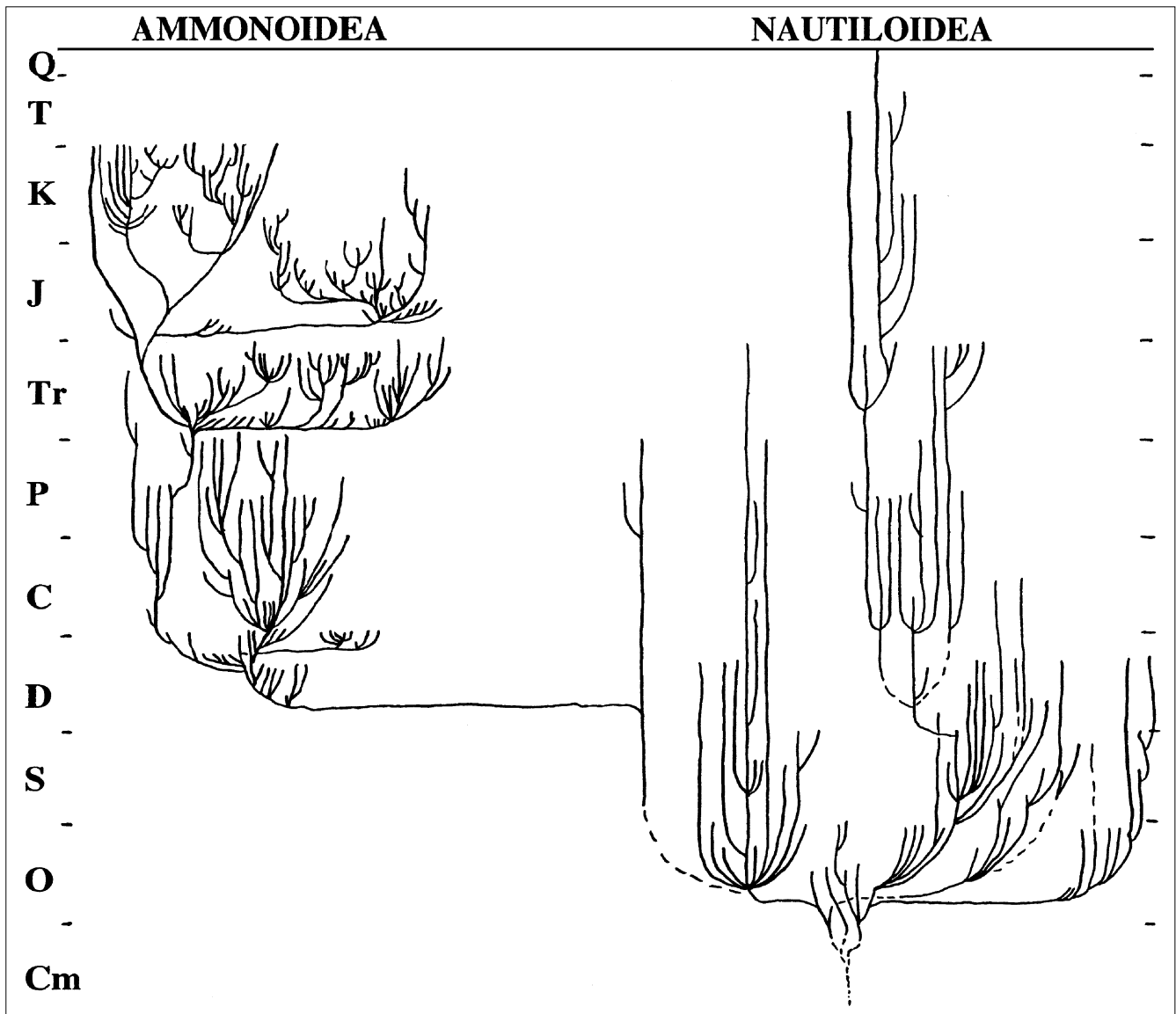
Text-Fig. 1.
Evolutionary tree (family level) for Ammonoidea and Nautiloidea.
Modified from TEICHERT (1967, Fig. 20).

general, r-selected species tend to be semelparous, with little or no parental care provided for the many offspring that are of relatively small size at birth/hatching (MACARTHUR & WILSON, 1967); embryonic development is fast, and life spans are short. Conversely, many K-selected species are iteroparous, and parental care is commonly provided for the few, relatively large offspring (MACARTHUR & WILSON, 1967); embryonic development is slow, and life spans are long. Although the correlation between reproductive strategy and r versus K population dynamics is not without exception, it has been hypothesized that the size of the cephalopod embryo correlates with reproductive strategy (small embryos indicating semelparity and large embryos indicating iteroparity), and that ammonoids are r-selected, semelparous, etc., and nautiloids are K-selected, iteroparous, etc. (LANDMAN, 1988; LANDMAN et al., 1996; MANGER et al., 1999). Among extant cephalopods, many coleoid species have characteristics of r-selected taxa, whereas the species of Nautilus appear to reflect the opposite extreme.

Building on the apparent difference in reproductive strategies for ammonoids and nautiloids, the goal of this study is to investigate whether reproductive strategy might also have controlled life history traits and evolution of Carboniferous cephalopods. LAIRD et al. (1969) and KOHNE (1970) presented evidence that species with longer generation times tend to have slower evolutionary rates, and vice versa. The logic behind the inverse relationship between generation times and evolutionary rates – the generation-time effect – is very straightforward: since errors in nuclear DNA replication during germ-cell divisions are considered the primary source of heritable mutation (LI, 1998), the more reproductive events per unit time, the more mutations possible. Thus, organisms with shorter generation times will tend to have higher rates of evolution. Semelparous organisms usually have relatively short life spans, whereas iteroparous organisms usually have long life spans. Therefore, the differences in diversity and in evolutionary rates between ammonoids and nautiloids may be the result of having different reproductive strategies.

2. Materials and Methods

Specimens were collected from Upper Mississippian (Chesterian) and Pennsylvanian (Morrowan and Missourian) strata at 11 localities in northern Arkansas and one locality in eastern Oklahoma. The lithology of these strata is diverse, including concretionary black shale and high energy, calcareous, conglomeratic sandstone. The strata were all deposited in a stable cratonic setting. The cephalopod-bearing horizons are isolated both geographically and stratigraphically. Cephalopods are abundant at each locality, and these cephalopod occurrences have been interpreted previously as reflecting mass mortality of populations of sexually mature individuals, possibly following a reproductive event (MANGER et al., 1999).

Representative specimens were sectioned longitudinally and ground carefully to the medial plane in order to observe the maximum ammonitella (or nauta) diameter (Text-Fig. 2). The ammonitella is the portion of the shell that represents the embryonic stage of growth, after
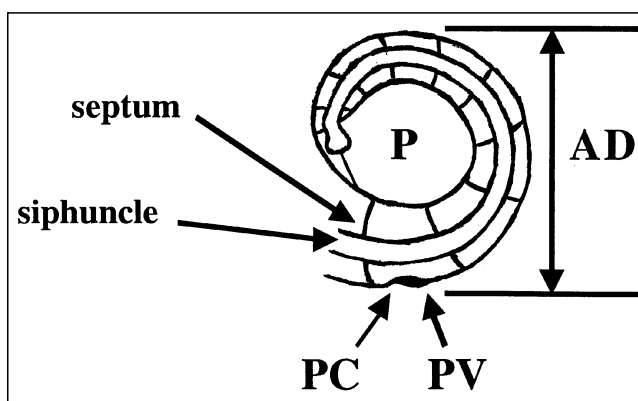
Text-Fig. 2.
Diagram of a longitudinal section of an ammonitella (or nauta) showing several common embryonic shell features.
Protoconch (P), primary constriction (PC), primary varix (PV), and ammonitella diameter (AD).
Note: Only the first few septa are secreted during the embryonic phase of growth (after LANDMAN et al., 1996, Fig. 1).

Table 1.
Cephalopod taxa included in the study (* indicates insufficient sample size for calculation of standard deviation).

Order	Family	Genus and species	Sample number	Mean embryonic size (mm)	Size range (mm)	St. dev.	Strat. range	Est. sp. duration (m.y.)
Prolecanitida	Pronoritidae	*Pronorites arkansasensis*	9	0.99	0.92-1.03	0.06	Morrowan–Desmoinesian	8
Goniatitida	Glaphyritidae	*Syngastrioceras oblatum*	41	0.83	0.75-0.92	0.03	Morrowan	3
		Eoasianites angulatus	3	0.78	0.78	*	Desmoinesian–Missourian	6
	Gastrioceratidae	*Cancelloceras huntsvillense*	6	0.81	0.78-0.85	0.03	Morrowan (part)	2
	Reticuloceratidae	*Verneuilites pygmaeus*	6	0.78	0.75-0.82	0.03	Morrowan (part)	2
		Arkanites relictus	47	0.78	0.71-0.87	0.03	Morrowan (part)	2
		Retites semiretia	22	0.80	0.73-0.87	0.04	Morrowan (part)	2
	Schistoceratidae	*Branneroceras branneri*	6	0.81	0.78-0.85	0.03	Morrowan (part)	1
Nautilida	Trigonoceratidae	*Aphelaeceras arkansanum*	1	5.49	5.49	*	Chesterian	10
	Tainoceratidae	*Metacoceras vagans*	1	8.52	8.52	*	Morrowan–Missourian	18

which the ammonoid hatched from its egg; nauta is the equivalent term for nautiloids. The ammonitella (and nauta) consists of the initial chamber, or protoconch, and approximately one whorl (Text-Fig. 2). Changes in shell micro-structure and ornamentation occur abruptly beyond the ammonitella (and nauta). The edge of the ammonitella (and nauta) is demarcated by a shallow depression called the primary constriction, which occurs just adaperturally of a thickening of the shell called the primary varix (Text-Fig. 2).

The taxa studied include 8 ammonoid species (1 prolecanitid, 7 goniatitid) and 2 nautiloid species (Table 1). Of the 7 goniatitid species, all but *Branneroceras branneri* are classified in the superfamily Gastriocerataceae, and *B. branneri* is the likely descendant of *Retites semiretia*; thus, all of the goniatitid species are fairly closely related. Prolecanitids are rare in most assemblages, and *Pronorites arkansasensis* was the only species abundant enough to sample. Only 2 nautiloid species from these localities were sufficiently abundant and well preserved in the apical portion of the phragmocone to be sampled.

The stratigraphic ranges for these species are well-known because of the biostratigraphic work on the cephalopod taxa in the study area (e.g., SAUNDERS et al., 1977). Therefore, stratigraphic ranges for most taxa can be assigned to the formation (or even the member) level. However, there has been much controversy recently regarding some of the absolute dates on the geologic time scale, particularly for the Carboniferous. Age values in Table 1 and Text-Fig. 3 are derived from the time scale of GROVES et al. (1999).

3. Results and Discussion

Embryonic sizes and stratigraphic ranges of the species included in this study are shown in Table 1. Ranges of the ammonoid species studied are on average about 4.3 times shorter than ranges of co-occurring nautiloids, and ammonitella sizes are approximately 6 to 10 times smaller than nauta sizes, as can be seen graphically in Text-

Fig. 3. The embryonic size data agree well with previously published evidence from Mesozoic ammonoids and nautiloids (LANDMAN, 1988). In addition, these results are consistent with embryonic size data from some extant semelparous and iteroparous cephalopods (e.g., *Loligo pealei* and *Nautilus pompilius*, respectively).
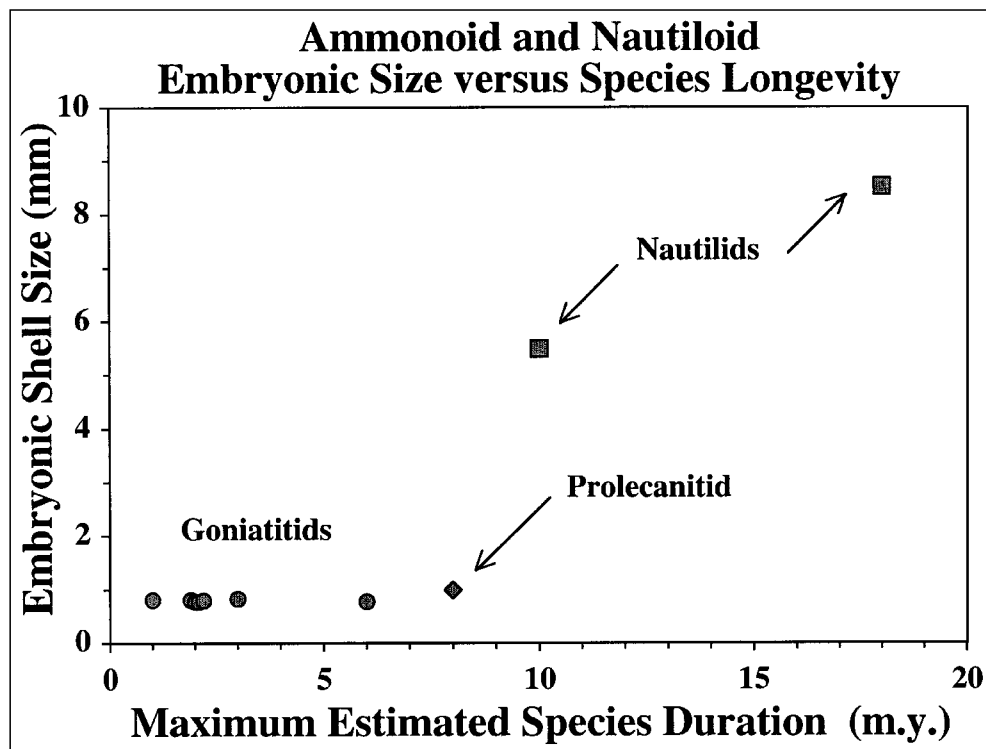
This and previous work (STEPHEN, 1998) has shown that variation of ammonitella size within a species is small (s.d. 0.03–0.06 mm). This is an important finding because it allows the comparison of small differences in mean ammonitella size between species. It also indicates that large population sizes (> 100) are not necessary for meaningful statistical analyses.

We now have data for 5 species with multiple populations separated in time: *Arkanites relictus, Cancelloceras huntsvillense, Retites semiretia, Syngastrioceras oblatum,* and *Pronorites arkansasensis.* In each case, ammonitella size within a species is relatively stable (s.d. <0.06 mm) throughout its stratigraphic range.

This means that ammonitella size may be a useful character and should be considered in future phylogenetic analyses. Furthermore, in our data for the superfamily Gastriocerataceae, ammonitella diameters for species within and among families are not significantly different. Mean ammonitella sizes for all goniatitid species are significantly different from the prolecanitid *P. arkansasensis,* and all ammonoid species are significantly different from the nautiloid species.

A simple t-test was used to determine whether differences of the means between species were significant; in some instances, the normality and/or equal variance criteria failed, and in those cases, a Mann-Whitney rank sum test was performed instead.

In general, ammonitella sizes for the goniatitid species in this study are similar to those published in the comprehensive study of LANDMAN et al. (1996). The mean ammonitella diameter for all goniatitid species in this study is 0.80 mm, versus 0.96 mm in the study by LANDMAN et al. (1996) which showed data for many more species, including many measurements for taxa with very large ammonitellas, e.g., *Perrinites* at 2.31 mm. It should be noted that LANDMAN et al. (1996) reported large intra-specific variation in ammonitella diameter, with size ranges of up to 0.7 mm, for some Cretaceous Lytoceratina species (e.g., *Tetragonites glabrus*); in comparison, the average ammonitella size range for the species in our study is 0.1 mm. There are several potential causes of intra-specific variation in ammonitella size, either within a population or between populations (contemporaneous or separated in time): phylogenetic

Ammonoid and Nautiloid Embryonic Size versus Species Longevity

Nautilids

Goniatitids

Prolecanitid

Text-Fig. 3.
Species longevity versus embryonic shell size for the cephalopod taxa included in this study.

variation, ecophenotypic variation, taphonomic biases, taxonomic uncertainty, and difficulty in obtaining accurate measurements. Our research indicates that significant changes in ammonitella size most likely reflect phylogenetic trends due to selection pressure, perhaps related to reproductive strategy.

4. Conclusions

The results of this study support the hypothesis that taxa in clades characterized by short stratigraphic ranges and high total diversity had a semelparous reproductive strategy, whereas taxa in clades with long stratigraphic ranges and low total diversity had an iteroparous reproductive strategy.

In the future, in addition to collecting more nautiloid data, we would like to investigate the variability of embryonic shell size within cephalopod clades. We would also like to focus on species transitions, especially where embryonic shell size is reported to change.

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