

Adaptive evolution in Paleozoic coiled cephalopods

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Abstract.—Coiled cephalopods constitute a major part of the Paleozoic nekton. They emerged in the Early Ordovician but nearly vanished in the Silurian. The Emsian appearance of ammonoids started a story of evolutionary success of coiled cephalopods, which lasted until the end-Permian extinction event. This story is investigated by using a taxonomic database of 1346 species of 253 genera of coiled nautiloids and 1114 genera of ammonoids. The per capita sampling diversities, the Van Valen metrics of origination and extinction, and the probabilities of origination and extinction were calculated at stage intervals. The outcome of these estimations largely reflects the known biotic events of the Paleozoic. The polyphyletic, iterative appearance of coiled cephalopods within this time frame is interpreted to be a process of adaptation to shell-crushing predatory pressure. The evolution of the diversity of coiled nautiloids and ammonoids is strongly correlated with the time intervals. Once established, assemblages of coiled cephalopods are related to changes in sea level. The general trends of decreasing mean (or background) origination and extinction rates during the Paleozoic are interpreted to reflect a successive stabilization of the coiled cephalopod assemblages. Different reproduction strategies in ammonoids and nautiloids apparently resulted in different modes of competition and morphological trends. Significant morphological trends toward a stronger ornamentation and a centrally positioned siphuncle characterize the evolution of Paleozoic nautiloids.

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Introduction

Cephalopods were among the most highly developed animals and the topmost predators in the free water column during long intervals of the Paleozoic. Their role in the seas changed with the appearance of jawed fishes in the late Paleozoic, but until recent times, cephalopods remained a major part of the nektonic life of the seas. Over long periods in the Paleozoic, cephalopods with a coiled conch constituted the most common cephalopods, but they are represented today only by Recent *Nautilus*. Their fate, the ecological role of these ancient molluscs, and their niche in the water column remain poorly understood.

The ecological role and niche of coiled cephalopods can be studied by considering the common morphological characters of these fossils. The morphospace and the adaptational value of the characters of coiled cephalopods are particularly well investigated through the work of Raup (1966, 1967), Raup and Chamberlain (1967), Chamberlain (1980, 1993), and many others.

The fate of coiled cephalopods in the course

of evolution can be described in terms of taxonomic rates and trends in morphologic characters by using a species-based database. The technique of a data-based investigation of taxonomic rates has strongly improved in recent years (see Sims 2003, and references therein).

In this paper, I examine the hypothesis of a common niche of coiled cephalopods and address several questions. Can we speak of an adaptive evolution of coiled cephalopods? Is there any similarity between the first emergence of coiled cephalopods in the Ordovician and the emergence of ammonoids in the Emsian? Do the main representatives of coiled cephalopods—ammonoids and coiled nautiloids—exhibit any common pattern in their evolution? Finally, which factors drove the evolution of coiled cephalopods during the Paleozoic?

Development of a Hypothesis

The word “coil” comes from the Latin *colligere*, “to collect.” In geometric terms, it comprises a series of loops, a curve or circle of more than 2π . Following Teichert (1964), a

coiled cephalopod is defined by a spirally curved conch of more than one volution. There are both openly coiled cephalopods (gyrocones) and closely coiled cephalopods in which the volutions touch each other. Only the latter are considered here.

The logarithmic curved conch (cyrtcone) is considered to be the standard realization of the growth of a conchiferan with a constant but slightly irregular accelerated increment of material at its aperture (Bayer 1978; Lövtrup and Lövtrup 1988; Ackerly 1989; Ubukata 2003). An accretional growth system that builds the special logarithmic curve of the coiled conch requires a suite of parameters, which are maintained in a very narrow zone of tolerance (Raup 1961; Raup and Michelson 1965). As a consequence of this growth the, prominent Raup parameters W (whorl expansion rate) and D (position of the curve in relation to the axis) have to be in a relation such that $1/D \geq W$. (Raup 1967). A coiled conch is therefore a case of a logarithmic curved conch, whose chance to evolve only by totally random processes is very low. Therefore, we have to look for a constraint that causes the evolution of coiled conchs. Functional aspects that control selectional constraints could represent the main factors of the evolution toward a coiled conch.

In fact, the coiling of the conch offers a number of advantages over the ancient cyrtcone or the alternative gyrocone and orthocone shell. It mechanically strengthens the conch (theoretical evidence: e.g., Raup 1967; Saunders and Wehmann 1977; Currey 1988; Hewitt and Westermann 1990; Hewitt 1996; and empirical evidences: Zipser and Vermeij 1978; Vermeij 1982; Kröger 2002), increases the maneuverability (e.g., Trueman 1941; Raup 1967; Saunders and Shapiro 1986; Crick 1988; Jacobs and Chamberlain 1996; Westermann 1996; Westermann and Tsujita 1999), and offers a moderate hydrodynamic efficiency at the same time (Chamberlain 1980; Jacobs and Chamberlain 1996). The coiled conch additionally requires a minimum expense of energy for buoyancy regulation compared with other ectocochleate cephalopods (Crick 1988). These are strong arguments for an adaptive origin of coiling in the cephalopod conch.

Data Set and Methods

Within the current investigation I distinguish between a non-ammonoid database and an ammonoid database. The first data set, "coiled nautiloids," comprises all non-ammonoid coiled cephalopods; it represents a paraphyletic group with the shared characters "nautiloid" and "coiled." The second data set, "ammonoids," represents a monophyletic group of genera.

Both data sets are surveyed and treated differently. The basic version of both data sets used in the current investigation was part of the database of genera compiled by Sepkoski (2002). But, coiled nautiloids are only very incompletely treated in Sepkoski's database and thus required a complete revision. To do this, I used the partially published Data Retrieval System Fossil Nautiloidea, of Engeser (2003), followed by an additional search for all available citations of coiled nautiloids in the literature. The non-ammonoid database comprises at present 1346 species of 253 genera (see supplemental material online, at <http://dx.doi.org/10.1666/03079.s1>).

In contrast, the ammonoids, which are represented by 1114 genera in the database, are in general taxonomically well known and described, as Sepkoski's (2002) database reflects. To evaluate the usefulness of the entire data set of all coiled cephalopods, I concentrated on the weaker part of the compilation. Thus, in this study I use the data set of coiled nautiloids as primary reference. This is a data set that I compiled very thoroughly myself, whereas the ammonoid database is adopted directly from that of Sepkoski (2002).

Generally, the sum of the ranges of the species within a genus is considered to represent the time range of the genus. The stage definitions and their durations, which follow the IUGS-ICS (Remane et al. 1996), serve as the time grid (see Appendix). The estimation of per capita taxonomic rates follows the time intervals between stage boundaries; the estimation of probabilities follows the intervals between stages midpoints.

For all coiled nautiloids I compiled geographical species occurrences. The sum of the species occurrences represents the paleo-geo-

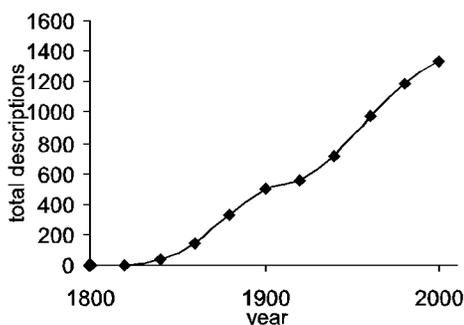


FIGURE 1. Cumulative frequency plot of species of Paleozoic coiled nautiloids described since the eighteenth century. The nearly linear increase of described species since the mid-nineteenth century gives evidence for some potential of discovery of new species in the future and for the relative incompleteness of the sampled record.

graphical occurrence of a genus. If available, the dimension of the adult conch, the ornamentation of shell, and the position of the siphuncle of coiled nautiloids were compiled from the literature. The resulting database was tested for sampling bias.

Completeness of the Record.—In contrast to other fossil groups, the Paleozoic nautiloids are poorly known. Figure 1 gives a cumulative image of all species of coiled nautiloids described since the eighteenth century. A nearly complete record of the fauna based on taxonomic work through the last centuries would produce a simple logarithmic growth function of all known species with few initial descriptions in early times, a strong increase in the nineteenth and twentieth centuries, and only few new descriptions in recent times. Figure 1 is distinguished from such an ideal picture by lacking a significant decrease in new descriptions in recent times, thus demonstrating a strong potential for discovering new species.

The database can be tested to determine whether the record adequately describes the succession of coiled nautiloids. It is well known that spatial and temporal diversity for most taxa is a function of latitude. With few geographical exceptions, species diversity is highest near the equator and lowest at the poles in modern marine environments (e.g., Schopf et al. 1978; Wilson 1988) as well as in the fossil record (e.g., Stehli et al. 1969; Bambach 1990; Crame 2002). Any representative database should reflect this effect. Figure 2

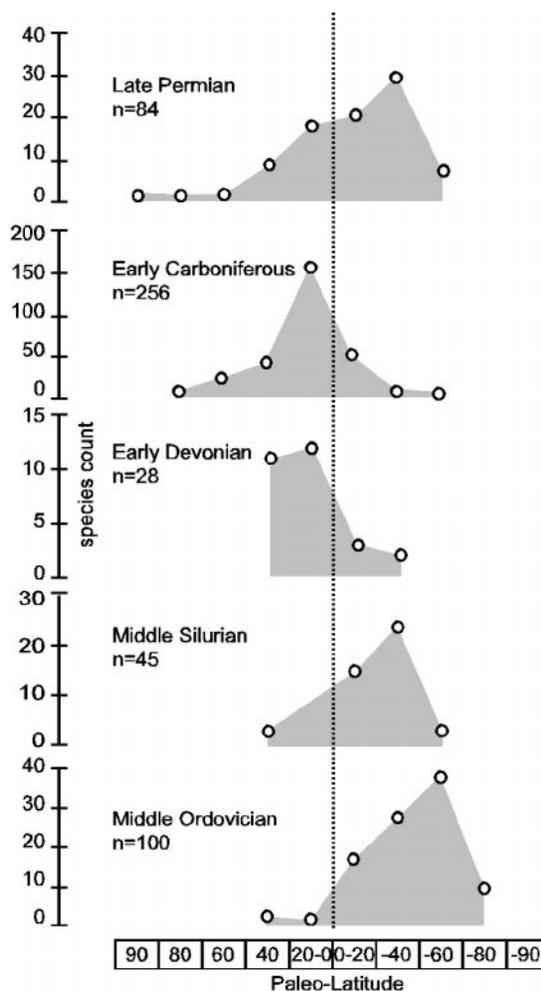


FIGURE 2. Frequency distribution of described species of Middle Ordovician, middle Silurian, Early Devonian, Mississippian and late Permian time interval per paleo-latitude. The shift of frequency peaks from the Southern Hemisphere in the early Paleozoic toward the equator and back toward the Southern Hemisphere in the late Paleozoic reflects a mixture of sampling bias and a real latitude effect with an equatorial frequency peak.

gives the diversity per latitude for five time intervals as recorded in the species database for coiled nautiloids. A strong latitudinal effect is visible during the late Paleozoic, which demonstrates a rough adequacy of the species database during this period. The early Paleozoic is not as well represented. Here the concentration of data in the Southern Hemisphere is an effect of the well-explored assemblages of the Baltoscandic area and North America. This uneven focus suggests some potential for discovering new nautiloid assemblages in re-

TABLE 1. Quality of the coiled cephalopod database. The top five cephalopod taxonomists erected a total of only 312 species of coiled nautiloids. This gives evidence of a relatively independent practice in describing coiled nautiloids.

	No. of authors	No. of species
Total	206	1356
No. of authors with <5 descriptions	151 (73%)	295 (22%)
No. of authors with >40 descriptions	5 (2.4%)	312 (23%)

gions like Antarctica, Australia, the Russian Far East, and North Africa. If the measured taxonomic rates simply reflect the shifting of paleogeographical positions of centers of strong collecting activities (e.g., Baltoscandia) during earth history, a simple correlation between sampling diversity and sampling latitude is expected. To test the bias introduced by that sampling effect, I plotted the mean latitude of a subsample of a time interval against its corresponding diversity values. But I found no correlation between the values ($r^2_{\text{diversity/latitude}} = 0.017$), suggesting that biased sampling in the early Paleozoic has not introduced a recognizable bias in evolutionary taxonomic rates.

Ease of Collection.—The unevenness of paleontological study in different regions and time intervals may have led to a strong variation in the numbers of described taxa and an inadequate knowledge of certain time intervals and regions (see, e.g., Adrain and Westrop 2003). To assess the quality of the coiled nautiloid database, I analyzed the number of workers and their main research field (Table 1). The 1356 species of coiled nautiloid species were erected by a total of 206 authors. Authors who erected no more than five species in their career erected approximately one-fourth of all types. Specialists who erected in their entire career more than 40 species added another quarter of the species total. These few cephalopod specialists worked relatively independently from a preferred stratigraphic interval, but they did focus regionally. Because of the high diversity of cephalopod workers, sampling error caused by oversplitting of taxa and hidden synonymies is expected to be randomly distributed over the database (see also Adrain and Westrop 2000).

Processing of Data.—I measured the per-genus standing diversity (d) as the total number

of boundary crossers (N_{tot}), ignoring the single-interval genera (singletons) per lineage-million years (Lmy). The singletons are expected to be very sensitive to preservation rates (Foote 2000, 2001 and references therein).

Additionally I measured origination and extinction rates. There are several measures of origination and extinction, each with different advantages and disadvantages (see Foote 2000). I used the metrics of origination (p) and extinction (q) of Van Valen (1984) because they proved to be most practical in the specific data sets, which consist of relatively few genera that cross both the lower and upper boundaries of the chosen time intervals. The origination rate is thus estimated by $p = N_{\text{Fi}} / ((N_{\text{b}} + N_{\text{t}}) / 2) / \Delta t$ where Δt is the length of the time interval per Lmy, N_{Fi} is the number of taxa that cross only the top boundary of the time interval, N_{b} the total number of taxa that cross the bottom boundary of the time interval, and N_{t} is the total number of taxa that cross the top boundary of the time interval. The extinction rate is estimated by $q = N_{\text{bi}} / ((N_{\text{b}} + N_{\text{t}}) / 2) / \Delta t$, where N_{bi} is the number of taxa that cross only the bottom boundary of the time interval.

The simple measure of extinction rates does not consider the variation in the quality and completeness of the fossil record. Therefore, Van Valen (taxonomic) metrics are in a strict sense sampling rates, which may represent a mixture of preservation and sampling effects, as well as “true” taxonomic rates. Two different approaches consider the common confounding of sampling and taxonomic rates (Nichols and Pollock 1983; Foote 2001). In this study, I favored the ignoring of singletons, which is inherent in the method of Nichols and Pollock (1983), against the alternative approach of Foote (2001). Nichols and Pollock (1983) use capture-mark-recapture models (CMR) borrowed from demographical and

TABLE 2. Scaling of morphological data in the coiled cephalopod database. The morphological data were translated into different scales in order to process them statistically.

Data	Scale
Umbilicus of the conch	Nominal: 0 = umbilical window absent; 1 = umbilical window present
Ornamentation	Ordinal: 0 = smooth; 0.25 = max. ornamentation striae; 0.5 = max. ornamentation ribs; 0.75 = max. ornamentation longitudinal ribs; 1 = max. ornamentation nodes and/or spines
Relative position of the siphuncle	Interval: 0 = ventral; 0.25 = subcentral; 0.5 = central; 0.75 = subdorsal; 1 = dorsal
Dimension of the conch	Ratio: adult diameter in millimeters

ecological studies. These models are used to estimate sampling probabilities. Connolly and Miller (2001, 2002), using the freeware computer program MARK (White and Burnham 1999), further developed the method of Nichols and Pollock to measure probabilities of origination and extinction. I calculated the probabilities of origination (p) and extinction (q) by using Jolly-Seber-type models (Pollock et al. 1990) within MARK. A detailed description of the method is given by Nichols and Pollock (1983), White and Burnham (1999), and Connolly and Miller (2002).

Morphometric Data.—I investigated some morphological characters and their trends. The values considered here are (1) the coiling itself (planispiral coiled, which comprises conchs that coil at a plane, and trochospiral, which comprises conchs that coil in a plane and an additional third axis); (2) the nature of the origin of the conch's spiral (openly or closely coiled around the coiling axis, which gives an umbilical window); (3) the relative position of the siphuncle (ventral, dorsal, central); (4) the dimension of the conch; and (5) its ornamentation. In order to interpret trends and their context, the rough data were translated into a nominal, ordinal, or interval scale. Table 2 offers detailed information on the property of the data. The status of the umbilicus is given simply as a nominal value (umbilical window absent = 0, umbilical window present = 1). Following Ward's (1981) description of ornamentation, I divided the cephalopods into groups of different ornamentation. Thus, for example, all cephalopods with longitudinal ribs are represented in the database by the ordinal value 0.75 (see Table 2). If both striae and ribs were developed, the maximum

ornamentation was scored. The higher the value, the rougher is the ornamentation of the conch. The position of the siphuncle is given in the database by interval values. Thus, if the siphuncle is positioned near the center of the cross-section toward the concave side of the conch, the value is 0.75, and so forth (see Table 2). The higher the value, the nearer the siphuncle is toward the concave (dorsal) side of the conch. The recognized trends result from a simple plot of the mean values or standard deviations of the morphological distributions at specific time intervals against time. Because the data set reflects a multitude of lineages, it gives among-lineage trends.

Results

Sampling Diversity Curve.—The sampling diversity increases in the coiled nautiloids as well as in the ammonoids during the Paleozoic as a whole (Fig. 3). This trend is not a simple increasing curve but comprises different intervals of increase and decrease. Four main phases of diversity trends of coiled cephalopods are recognizable in the Paleozoic: in the Tremadocian the first coiled nautiloids appeared and quickly reached a high taxonomic richness during the Middle Ordovician. By the end of the Ordovician this early community virtually disappeared. Only one coiled cephalopod genus is known to cross the O/S boundary: *Barrandeoceras* Hyatt of the Tarphyceratida. A second minor flourishing of coiled nautiloids occurred during the Middle Silurian, followed by a quick decrease until the Early Devonian. From the Lochkovian and Pragian only three genera were reported: *Centroceras* Hyatt of the Nautilida and *Lorieroceras* Foerste and *Naedyceras* Hyatt of the Oncoceri-

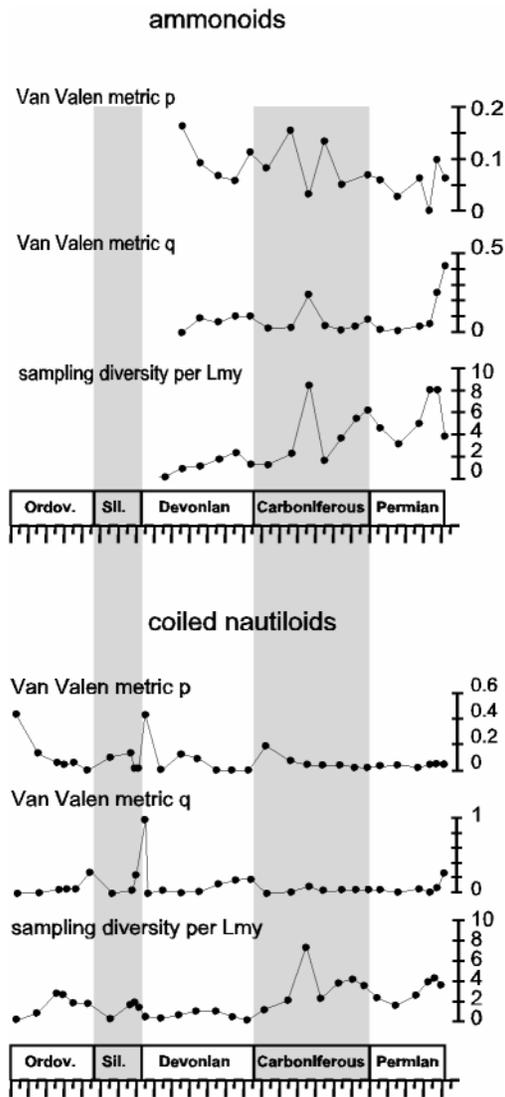


FIGURE 3. Estimated taxonomic rates for ammonoids and coiled nautiloids without singletons. The parallelism of event pattern in both databases is striking. A major diversity peak is developed in the Serpukhovian. Note the high extinction and origination rates at the Siluro/Devonian boundary for nautiloids and the very low and constant rates in the late Paleozoic. The taxonomic rates of the ammonoids show a higher amplitude in the late Paleozoic. Ammonoid data are from Sepkoski 2002. Points reflect stage boundaries. Abbreviations: Lmy = lineage million years, q = Van Valen metric of extinction, p = Van Valen metric of origination.

da. A third short minor peak in diversity occurs during the Middle Devonian. During the Emsian and Eifelian the ammonoids and several new coiled nautiloids appeared. A sudden decrease of diversity of coiled nautiloids and ammonoids occurred in the Late Devonian Frasnian/Famennian boundary. Again

only one coiled nautiloid is reported to have survived the crisis: the oncocerid *Mitroceras* Hyatt (Dzik 1984). After that crisis a fourth phase of evolution of coiled nautiloids is recognizable, which lasts until the Late Permian. This interval is characterized by a steady, comparatively stable increase of diversity with a significant short-term diversity peak in the Serpukhovian.

Three of these phases are marked by major Paleozoic extinction events. These are the late Ashgillian bio-event (see, e.g., Barnes et al. 1996), the Frasnian/Famennian crisis (see, e.g., McGhee 1996), and the end-Permian mass extinction (see, e.g., Erwin 1993). The significant Early Devonian diversity minimum is not correlated with a recognized major bio-event. This time interval did not exhibit neither strong extinction pulses in the global extinction curve of Sepkoski and Koch (1996) or a significant minimum in the global diversity curve (see Sepkoski 1979; Alroy et al. 2001); nor is it marked by a significant minimum in exposed number of formations (see Peters and Foote 2002), or by evidence of an accumulation of bio-events (see, e.g., Walliser 1996). Nevertheless, the Early Devonian diversity minimum is traceable not only in coiled nautiloids but in the Nautiloidea in general (see House 1988).

Within this time frame three main events of radiation: the Tremadocian–Arenigian radiation, the mid-Devonian radiation, and the Mississippian radiation. It is notable that these times of diversification do not follow a logistic (logarithmic) population growth curve that tapers to an equilibrium size (carrying capacity, K , of population ecology). Instead, the growth process in all cases is a slow, roughly linear one, which is strongly disturbed by extinction events. Comparison of the diversity curves of the Ammonoidea and the coiled Nautiloidea reveal a strong correlation between the trend of both estimates. Figure 4 shows $\Delta d_{\text{ammonoids}}$ plotted against $\Delta d_{\text{coiled nautiloids}}$ which have an r^2 of 0.82. Thus the phylogenetically independent but morphologically linked data sets of coiled nautiloids and ammonoids show nearly identical diversity patterns. The Serpukhovian diversity peak (cf. Kullmann and Nikolaeva 2003) as well as a minor early Permian diversity minimum are developed. This parallel pattern

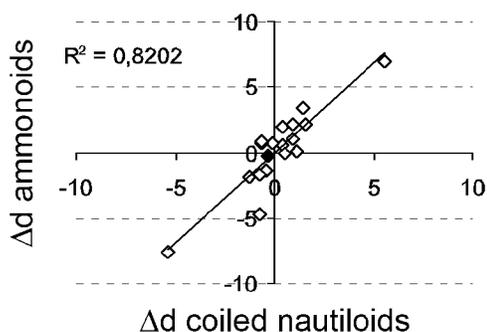


FIGURE 4. Plot of $\Delta d_{\text{ammonoids}}$ against $\Delta d_{\text{coiled nautiloids}}$. The change of sampling diversity (d) in ammonoids is strongly positively correlated with the change of sampling diversity in coiled nautiloids. Considering that both data sets show no direct phylogenetic relationship, the strong morphological signal in the entire data set is evident.

demonstrates a strong morphological signal in these trends.

The mean per-genus diversity in coiled nautiloids is generally lower than that of the ammonoids. Additionally, diversity increases much more slowly in this group than in the ammonoids. Nevertheless there are two time intervals, the Eifelian and Bashkirian, in which the average diversity of nautiloids is higher than that of ammonoids. Remarkable also is the Mississippian, which is characterized by equally balanced diversity values.

Extinction Curve.—The curve of per capita rate of extinction (Fig. 3) and the curve of extinction probability (Fig. 5) in both coiled nautiloids and ammonoids are generally composed of strong punctuated extinction pulses and a very low background extinction rate. The mean extinction probabilities and rates are higher at the beginning of the group radiation (e.g., the early Middle Ordovician in coiled nautiloids, the early Middle Devonian radiation of ammonoids) and tend to get lower toward the end of the Paleozoic. The wide confidence intervals, which appear in the probability peaks of Figure 5, reflect the low sample number used in the calculation; they therefore reflect simply an artifact of the computing via the CMR-method.

Easily observable are the major extinction events at the O/S boundary for coiled nautiloids and at the Frasnian/Famennian boundary in both data sets. The coiled nautiloids show additionally strong extinction pulses at the Silurian–Devonian transition, which reflect

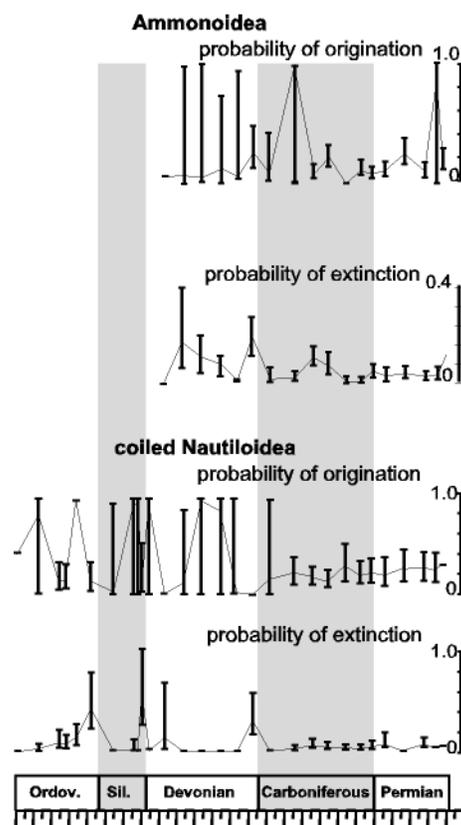


FIGURE 5. Estimated probabilities of origination and extinction for ammonoids and coiled nautiloids without singletons. Ammonoid data are from Sepkoski 2002. The large confidence intervals in many intervals reflect the few counts in these intervals. The Kungurian probability of origination in ammonoids is an artifact, reflecting a rough stratigraphic timing of Permian counts in the database of Sepkoski (2002). Points reflect midpoint of stages. Bars give confidence interval of 96%.

the global trend of enhanced extinction rates in the Pridolian in several biotas (see, e.g., Kaljo et al. 1996; Porebska and Sawlowicz 1997) and a minor peak at the Lochkovian–Pragian transition, which possibly reflects the Lo/Pr-Event of Walliser (1996). The major end-Permian event affected the coiled nautiloids less strongly than the ammonoids. One peak needs special attention. This is the Serpukhovian peak in extinction probability in ammonoids, which mimics a strong positive signal in sampling diversity in coiled nautiloids and ammonoids as well as in its magnitude of origination (see Figs. 3, 5). Sepkoski (1996) recognized this event, but he noted an associated drop in global diversity. In contrast to this observation, the coiled cephalopods and ammonoids show an increased diversity at that time. The event was recognized

as an ammonoid faunal transition by Ramsbottom (1981) and was studied in detail by Kullmann and Nikolaeva (1999; 2003) for ammonoids. The authors show a stepwise faunal turnover accompanied by a significant morphological change of ammonoids in the Serpukhovian toward the Mississippian/Pennsylvanian boundary. It is notable that unlike the ammonoids, the coiled nautiloids show no significant peak in extinction probability (Van Valen rate) in the Serpukhovian.

Origination Curve.—The Van Valen metric of origination of coiled nautiloids shows a pattern that starts in the Early Ordovician with high values but becomes successively lower during the recognized time interval (see Fig. 3). This pattern is slightly disturbed by intervals of comparably high origination rates in the middle Silurian, the Emsian–Eifelian, and the Mississippian. A very distinct peak in the Lochkovian reflects the observation that no genus of coiled nautiloids is reported to cross the Silurian boundary. A completely new fauna of coiled nautiloids emerged later in the Early Devonian: coiled oncocerids and the enigmatic genus *Centroceras* Hyatt. The ammonoids originated in the Emsian; their Van Valen metric of origination in general slowly decreases during the Paleozoic, but strong positive peaks occur in the Visean and Bashkirian.

It is important to note that after the Emsian–Eifelian radiation, both in ammonoids and nautiloids synchronously, the origination rate decreased strongly. But after the Frasnian/Famennian extinction event, which affected both ammonoids and coiled nautiloids, the origination rate increased more in nautiloids than in ammonoids. A clear minimum in origination rate, which is developed in ammonoids at the Serpukhovian, is not found in nautiloids.

The probabilities of origination are characterized by very wide confidence intervals in great parts of the data set (see Fig. 5). This observation simply reflects the low sample number, which was used in the computing. The low sample number in fact reflects a real recognized sampling diversity (see Fig. 3) and therefore shows the limitations of the CMR-method in palaeontology. Nevertheless, the probability curves of origination provide use-

ful information if the sampling diversity is considerably high. In these intervals the origination probabilities largely reflect the Van Valen metrics, which share extraordinarily high rates in the Mississippian for coiled nautiloids and extraordinarily low rates for ammonoids in the middle Carboniferous. In summary, ammonoids and coiled nautiloids show very little correspondence in their origination pattern.

Comparison of origination probabilities against extinction probabilities reveals a strong difference between ammonoids and the coiled nautiloid data set: ammonoids show a relatively good positive correlation between probability of q and p and additionally between Δp and Δq ($r^2 = 0.38, 0.4$, respectively). Thus, high origination rates in ammonoids were coupled with high extinction rates and vice versa, whereas no such relationship is visible in coiled nautiloids.

Discussion

The evolution of coiled cephalopods is, like that of all other organisms, affected by the functional interaction with their external environment, including competitors and predators. Their evolution is also affected by endogenous or internal factors of the organism group itself, such as fecundity or structural constraints. The results of the investigation are discussed below in order to evaluate the impact of these effects.

Effects of Functional Morphology

Coiling.—Differences in coiling of cephalopods were recognized only insofar as there were deviations from the planispiral coiling plane (trochospiral coiling) and differences in the starting values of the spire, which would give a closed umbilicus or an umbilical window.

A coiled conch develops a closed umbilicus only when certain very limited conditions are fulfilled, thus permitting only very limited degrees of freedom (e.g., Raup 1967). Building a coiled conch with a closed umbilicus is, therefore, a highly unlikely process. In fact, as seen in Figure 7, a closed umbilicus is developed in coiled nautiloids only in very limited time intervals. It is interesting to notice that the old-

est coiled cephalopods were the closely coiled Tarphyceratida. In the Early and Middle Ordovician this group represented the dominant type of coiled cephalopods. There is a gap of more than 15 Myr in the early Silurian without any closely coiled cephalopods recorded.

This initial dominance of closely coiled cephalopods can be interpreted functionally and ecologically. A cephalopod with an openly coiled conch always would have a juvenile conch with a large hole in the middle, causing an unsteady locomotion with common periods of acceleration (Jacobs and Chamberlain 1996). The locomotion of the small, juvenile cephalopods would therefore have been much more unstable than in large or adult cephalopods, owing to a much higher drag coefficient than in larger conchs. Consequently, a closely coiled conch would enhance juvenile locomotion. The exceptionally high fraction of closely coiled cephalopods in the Ordovician (see Fig. 7) may indicate a selectional advantage of this effect. The phenomenon can also be expressed as a high percentage of coiled shells within the fraction of the smallest cephalopod shells of that time. It is then remarkable that in the Lituitidae, which comprises a large proportion of coiled Ordovician cephalopods, invariably only the juvenile part of the conch is coiled. This implies that mobility and mechanical strength were advantageous to the small shell fraction, possibly as a response to durophagous predators with only a limited prey range. In fact, cephalopods themselves were the only Ordovician nektonic durophagous predators.

The characteristic Silurian and Early Devonian coiled nautiloids are the trochospirally coiled Lechritrochoceratidae. Trochospiral nautiloids never had a higher diversity than in this time. Moreover, planispiral coiled shells like that of the tarphyceratids and lituitids seem to be exceptional in the Silurian. Considering that trochospiral conchs allow more degrees of freedom for growth than planispiral ones, their probability of origination per se is much higher. Thus, the high percentage of trochospiral cephalopods can be interpreted as a lack of a constraint on the evolution toward planispiral cephalopods. Trochospiral cephalopods represented more or less planktonic animals with

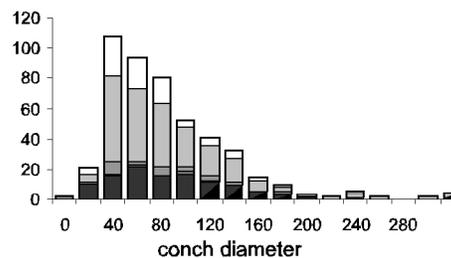


FIGURE 6. Frequency distribution of coiled nautiloid adult conch size, measured from adult or nearly adult representatives of a total of $n = 478$ species; Ordovician species black, Silurian species dark gray, Devonian species medium gray, Carboniferous species light gray, Permian species white. Note the nearly similar distributions in the different time intervals.

a limited ability for locomotion (see Westermann 1999). Possibly, the Siluro-Devonian trochospiral cephalopods represent a lack of adaptive pressure toward an effective locomotion for foraging and escape, for example. Keupp (2000) interpreted the occurrence of the Late Cretaceous heteromorph (including trochospiral) ammonoids as a reflection of high relative sea level and large areas of flooded shelves, which is true for the Silurian too.

In the early Middle Devonian the group of closely coiled cephalopods that began to dominate was the ammonoids, which increased in diversity during the Paleozoic. As pointed out by Jacobs and Chamberlain (1996) the closely coiled conchs of ammonoids were especially advantageous for the very small ammonoid hatchlings. It may be noted here that this effect may have contributed to the relatively fast evolution from the straight bactritoid hatchlings toward the closely coiled ammonoid hatchlings in the early Middle Devonian, as was shown by Erben (1964).

Body Size.—There is no general trend in the evolution of body size of coiled nautiloids expressed in the conch diameter (Fig. 6). However, with the emergence of ammonoids, coiled nautiloids represented the cephalopods of relatively larger body size, with average adult conch diameter of 70–80 mm. The largest coiled cephalopod recognized here was the Serpukhovian *Domatoceras gigas* Tzvetayev, with a measured adult diameter of 540 mm; very few Paleozoic ammonoids reached this dimension.

Ornamentation.—Ornamentation underwent

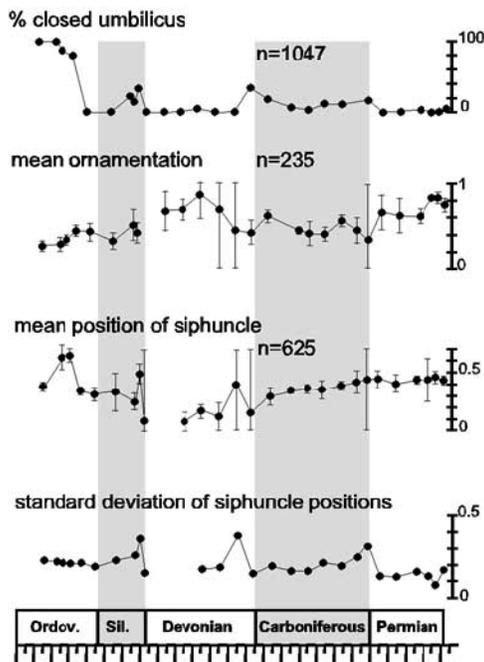


FIGURE 7. Morphological trends in single characters of coiled nautiloids during the Paleozoic. Table 2 gives scales for the measured characters. The figure shows that nautiloids with closed umbilici constitute the majority of Ordovician cephalopods, but much smaller proportions in the middle and late Paleozoic. A trend toward increasing ornamentation during the entire Paleozoic is striking. The position of the siphuncle gradually shifts toward a central position in the late Paleozoic with simultaneous decrease of standard deviation of siphuncle position. Points reflect midpoint of stages.

a general trend of a roughening during the Paleozoic. This roughening is illustrated in Figure 7 by an increase in the mean value of the index, which represents the ornamentation (Table 2). Thus, coiled nautiloids with a large ornament occurred more frequently in the late Paleozoic than in the early Paleozoic (see also Vermeij 1987). Because the main functional effect of sculpture is the strengthening of the shell against predators (e.g., Vermeij 1987; Jacobs and Chamberlain 1996), this trend reflects the increasing need of coiled cephalopods for defense against durophagous predators. In contrast, the ammonoids were only weakly ornamented during the entire Paleozoic (Ward 1981). The reason for this difference may be the general size difference between ammonoids and coiled nautiloids in the Paleozoic. A detailed analysis is lacking for this phenomenon, but Paleozoic ammonoids

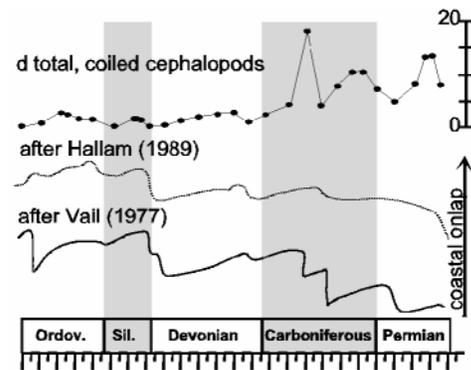


FIGURE 8. Relationship between total sampling diversity of coiled cephalopods in the Paleozoic and changes in sea level. Note the high correspondence of the different curves. *d* = sampling diversity without singletons.

were generally smaller than nautiloids, and thus were confronted with much higher drag, a strong constraint on a hydrodynamic shell.

External Effects

Sequence Stratigraphy.—Direct evidence from global sea level changes comes from sequence stratigraphic compilations (see, e.g., Vail et al. 1977; Hallam 1989). Generally sea level variation and diversity of coiled cephalopods are positively correlated (see Fig. 8). Thus, when the sea level rises, their diversity rises; when sea level drops, their diversity drops. Additionally the major extinction events of coiled cephalopods are coupled with punctuated sea level drops (O/S boundary, S/D boundary, Frasnian/Famennian boundary, and the middle Carboniferous event). This observation agrees with that of Hallam and Wignall (1999), who emphasized the role of sea level fluctuation in global diversity, especially the relationship between sea level drops and mass extinctions. However, Smith (2001) and Peters and Foote (2002), who emphasized the strong connection between sampling area, sampling diversity, and sea level, were clearly skeptical of this interpretation of the correlation between diversity and sea level. From a methodological viewpoint, though, they simply pointed toward the Popperian “disprove.” Only a thorough analysis of extensive sampling can address this question.

Climate.—Worsley et al. (1994) and Berner (1987, 1991) showed some major trends for

global Paleozoic CO₂ levels and provided some atmospheric temperature estimations. Marshall et al. (1997) and Grossmann et al. (2002) included some relevant Paleozoic $\delta^{18}\text{O}$ curves. But comparison of these data with the taxonomic rates of coiled cephalopods yielded no apparent correspondence. Thus, the climate analyses do not demonstrate any influence of even drastic climatic changes on coiled cephalopod evolution.

Tectonics and Volcanics.—Vermeij (1995) argued that a rise in primary productivity, which should be an effect of high orogenic activity, could raise species diversity. The enhanced weathering during orogenic events such as the culmination of the Taconic and Acadian orogens must have increased the primary productivity of the oceans (see, e.g., Ribessel et al. 1993). But no correspondence between taxonomic rates of coiled cephalopods and times of increased orogenic activity is recognized. This observation coincides with the investigation of Connolly and Miller (2002), who found no productivity dependence in the Ordovician Radiation for benthic organisms.

However, the interrelationship between tectonic activity, global sea level change, and the change of paleogeography played a significant role. The very distinct diversity peak of coiled cephalopods in the late Mississippian and the subsequent faunal change at the Bashkirian may reflect these interactions between tectonic activity and sea level. At the Bashkirian the initialization of the Pangean supercontinent began, and the high provinciality of the Mississippian world, which may have caused the Viséan–Serpukhovian diversity peak, disappeared. Additionally the Allegheny orogen culminated and the mid-Carboniferous glaciation started. These events may have driven the mid-Carboniferous faunal change recognized in coiled cephalopods.

Competitors and Predators.—Investigations of beaks of Paleozoic ammonoids (e.g., Bandel 1988; Doguzhaeva et al. 1997; Doguzhaeva 1999) and nautiloids (e.g., Mapes 1987; Mapes and Chaffin 2003) showed that coiled Paleozoic cephalopods played a role as prey, predator, and competitor in their environment. Moreover, in the early Paleozoic, nautiloids were the only large predators of the nekton.

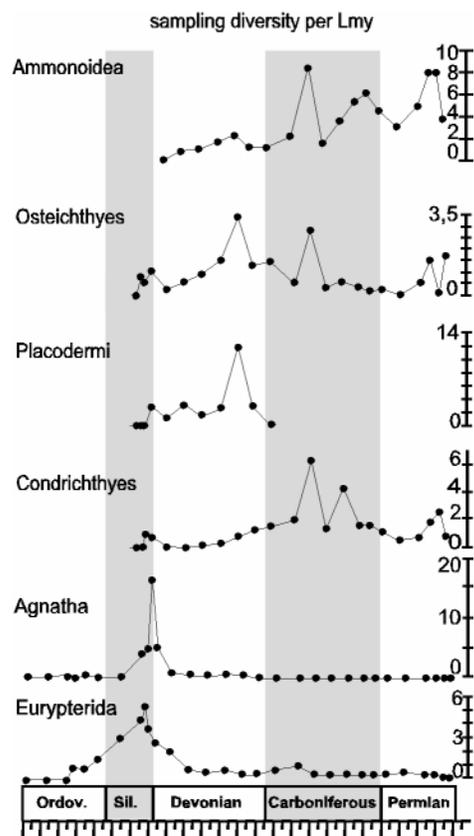


FIGURE 9. Sampling diversity of ammonoids within elements of the competitive/predatory nekton of the Paleozoic (data from Sepkoski 2002). Note the correspondence of the curves with major faunal change in the Early Devonian, and diversity peaks in the Givetian and Serpukhovian.

Traces of predation are found in Middle Ordovician orthocerids and tarphycerids (Kröger 2004; Kröger and Keupp unpublished). Most probably these injuries were caused by large endoceratids or actinoceratids, which both reached their acme in the Middle Ordovician (Teichert 1964). The role of the benthonic eurypterids must have been marginal except for the Late Silurian interval, which is characterized by a strong but short radiation of this group (see Fig. 9). The correspondence of the diversity curves of coiled nautiloids (Fig. 3) with those of Endoceratida, Actinoceratida (see Teichert 1964), and Eurypterida (see Fig. 8) demonstrates a parallel appearance of coiled nautiloids and large predators, thus suggesting that coiling may be largely an adaptation to predatory pressure.

The most important event in the history of the nekton of the Paleozoic is the initial radiation of gnathostomes in the Early Devonian. Therewith appeared simultaneously the Chondrichthyes, Placodermi, and Paleoniscides (Fig. 9), the main Paleozoic competitors and predators of cephalopods (Mapes et al. 1995; Mapes and Chaffin 2003). This is exactly the time of a renewed appearance of coiled nautiloids and the emergence of ammonoids (peaks of origination rates; see Figs. 3, 8). The high origination rates of coiled nautiloids and ammonoids in the Emsian–Eifelian correspond neither to significant sea level changes nor to increased extinction rates. They seem to be purely an outcome of the radiation of gnathostomes in this time interval.

In the context of the later evolution of the Paleozoic nekton in general the end-Silurian extinction interval seems to have played the major role. This event initiated a complete faunal change from dominance of orthoconic cephalopods, graptolitids, and tentaculitids to the dominance of fishes and coiled cephalopods in the free water column of the late Paleozoic, opening a brief evolutionary window for the agnathans (see Fig. 9).

The subsequent evolution of the nekton is largely determined by a parallel development of the diversity of its components, which together reflect the pattern of sea level change (see Fig. 8). This shows on one hand a strong correspondence of nektonic life with sea level changes and, on the other, the strong interrelationship (competitive and/or predatory) of the nektonic biota. However, the freshly emerged nektonic fauna was strongly disturbed by the Late Devonian extinction events: the Placodermi vanished, only one family survived in the ammonoids, only three genera of coiled nautiloids crossed the Devonian/Carboniferous boundary, and the paleoniscids were decimated. This time interval led to a significant increase in the importance of coiled nautiloids in the nekton.

Endogenous Effects

Dynamics of Diversification.—The growth of an interacting, competing population can be described by the Verhulst and Lotka-Volterra equations, which summarize a logarithmic

growth against a factor K , which represents the limiting resource. Similarly, models of complex adaptive systems describe diversification patterns by saturation functions (Brock 2000). Eble (1998) demonstrated such a growth curve for the model of the rugged fitness landscape (Kauffman 1989) and showed a logarithmic growth for the cumulative genera of marine invertebrate phyla during the Phanerozoic. Two intervals in the evolution of coiled nautiloids match this predicted pattern, the Tremadocian to Ludlowian and the Tournaisian to Tartarian. There, the cumulative number of genera increases significantly linear ($R^2 = 0.93$, Durban-Watson test $v = 1.01$, and $R^2 = 0.96$, Durban-Watson test $v = 0.92$, respectively) when plotted in a logarithmic scale, which give evidence for an adaptive radiation in the Early Ordovician and Mississippian. This phenomenon reflects the drastic increase in origination rates in these times, after initial high values (Figs. 3, 4). Interestingly, no logistic growth pattern is observed in the Devonian coiled nautiloids, and generally no logistic growth pattern is observed in the diversification of ammonoids; the cumulative number of ammonoid genera is less consistent with logarithmic expectation for the entire observed time interval (Durban-Watson test $v = 0.736$) as well as for different subintervals. This may be an effect of resolution; probably the ammonoid radiation and its recovery after extinction events appear in a very narrow time frame, which is not within the resolution of the current investigation. Yacobucci (2002) showed that ammonoid evolutionary dynamics appear to be similar to those of other marine invertebrates, but on much shorter time-scales. This phenomenon, however, deserve further consideration in future observations.

Fecundity.—In the current observational grid, the extinction events run along with origination peaks, showing high turnover rates in time intervals with extinction events. But there are visible differences between ammonoids and coiled nautiloids in these time intervals. In ammonoids the amplitude of extinction is much higher than in coiled nautiloids, but both origination curves oscillate in similar dimension (see Fig. 3). This is assumed

to be an effect of the different fecundity regimes of both groups.

The hatchlings of ammonoids (see, e.g., Landman 1988; Landman et al. 1996b) were many times smaller than those of the Nautilida (e.g., Arnold 1987; Chirat 2001). Thus ammonoids are presumed to reflect a typical *r*-strategy in reproduction, whereas coiled nautiloids are assumed to reflect the *K*-strategy. Following Brock (2000), *r*-strategists are always linked with changes in fecundity within the adaptive niche as a pure offset to stochastic mortality, whereas in *K*-strategists a strong heritable differential exists between genotypes. The different reproduction strategies generate different competition modes within the shared adaptational niche.

Competition Modes.—Figure 7 shows that the mean position of the siphuncle in coiled nautiloids varied between ventral and subdorsal. The position, as well as the variance (given as standard deviation of the siphuncle in a given time interval), shows an unstable trend until the Early Devonian. However, after the Late Devonian a clear trend toward a medial siphuncle position and a lower standard deviation of the siphuncle positions is visible. Additionally a strong trend toward a longitudinal ornamentation is developed by the late Paleozoic coiled nautiloids. Both features demonstrate clear trends toward a functional optimum. Thus, a central siphuncle is the best compromise between demands of buoyancy regulation and defense against predators (Kröger 2003), and a longitudinal ornamentation is the best compromise between demands of hydrodynamic efficiency and predator defense (Jacobs and Chamberlain 1996). The functional optimum represents, in macroevolutionary terms, an adaptive equilibrium, which means the boundary condition in a logistic growth curve. Consequently, after the strong extinction pulse in the Late Devonian the Nautilida show a constant trend toward an adaptive equilibrium.

The ammonoids suffered a widespread extinction in the Late Devonian, too (only a few Prionceratinae survived [House 1985]). But, by contrast, the ammonoids iterate their morphotypes only in a very narrow morphological field during the late Paleozoic, and over a

much shorter period (e.g., Saunders et al. 1999; Erwin 2001). This difference is interpreted as a consequence of a different reproduction strategy. Ammonoids reflected changing environmental conditions by changing their fecundity, whereas in nautiloids a strong heritable differential occurred between genotypes.

In other words, ammonoids and coiled nautiloids reflected different competition modes within the shared adaptational niche. Ammonoids may be described as following a passive logistic competition whereas coiled nautiloids followed an active selectional competition.

Conclusions

The development of a coiled conch by only stochastic variation, or as a result of structural constraints alone, is considered highly improbable. An adaptive evolution of the coiled conch is the most probable explanation for its existence.

In fact, the diversity of coiled cephalopods correlates directly with the diversity of durophagous predators (especially arthropods and vertebrates), and thus coiling in cephalopods appears to have developed largely as a consequence of the predatory pressure in the water column. Once a fauna of coiled cephalopods was established, its diversity followed the course of sea level fluctuations. High coastal onlap probably resulted in increased diversities because of greater availability of habitable area.

Two main events are notable in the Paleozoic: (1) the first emergence of coiled cephalopods in the late Early Ordovician simultaneous with a multitude of varied (even predatory) nautiloids; and (2) after a time interval of virtually no coiled cephalopods in the Early Devonian, a strong origination pulse of coiled nautiloids and the emergence of ammonoids simultaneous with the radiation of gnathostomes in the Emsian.

Even when the evolution of the diversity runs largely parallel in ammonoids and nautiloids, striking differences in the intensity of extinction and origination are visible. These differences are interpreted as an outcome of different reproductive strategies.

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Appendix

Interval length of stages used for estimation of taxonomic rates (after Remane et al. 1996).

No.	Stage	Interval length (in Myr)	Duration from mid-time to mid-time
1	Tremadocian	5	—
2	Arenigian	15	10
3	Llanvirnian	6	11
4	Llandeilian	6	6
5	Caradocian	9	7.5
6	Ashgillian	6	7.5
7	Llandoveryan	15	11
8	Wenlockian	5	10
9	Ludlowian	4	4.5
10	Pridolian	2	3
11	Lochkovian	5	3.5
12	Pragian	12	8.5
13	Emsian	9	11
14	Eifelian	11	10
15	Givetian	10	11
16	Frasnian	6	8
17	Famennian	10	8
18	Tournaisian	12	11
19	Viséan	15	14
20	Serpukhovian	4	9.5
21	Bashkirian	12	8
22	Moscovian	8	10
23	Kasimovian	6	7
24	Gzhelian	6	6
25	Asselian	8	7
26	Sakmarian	13	11
27	Artinskian	9	11
28	Kungurian	4	6.5
29	Ufimian-Kazanian	4	4
30	Tatarian	4	4