Ammonoid Evolution
During the Critical Intervals
Before and After the Devonian-Carboniferous Boundary
and the Mid-Carboniferous Boundary

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Die Entwicklung der Ammonoiden während der kritischen Zeiträume
vor und nach der Devon/Karbon-Grenze
und der Mittelkarbonischen Grenze

Zusammenfassung

Berechnungen der Diversitäts-Entwicklung der Ammonoiden während des Karbons auf der Art-Ebene wurden ermöglicht durch die Nutzung der in der Datenbank GONIAT enthaltenen Daten. GONIAT ist als Hilfsmittel für die Erforschung der Systematik, der Evolution, der paläogeographischen Verbreitung und der biostratigraphischen Reichweiten eingerichtet worden.

Die quantitativen und qualitativen Analysen der vorliegenden Studie konzentrieren sich auf die Zeiträume vor und nach zwei ausgeprägten kritischen Epochen in der Evolution der Ammonoiden: die Zeiten um die Devon/Karbon-Grenze (DCB) und um die Grenze zwischen Unter- und Oberkarbon, die MCB. In beiden Fällen starben größere Gruppen kurz vor oder an der Grenze aus, und andere Gruppen setzten nach der Grenze ein. Nur wenige Arten scheinen die DCB und die MCB überlebt zu haben.


Abstract

Calculations of the diversity development of Carboniferous ammonoids on the basis of species have been made possible by utilising the data stored in the database GONIAT. GONIAT is especially designed as a tool for investigations on the systematics of Palaeozoic ammonoids, their palaeogeographic distribution and their biostratigraphic range.

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The quantitative and qualitative analysis of the present study concentrates on the epochs before and after two fundamental critical intervals in ammonoid evolution: the time around the Devonian/Carboniferous boundary (DCB) and around the Mid-Carboniferous boundary (MCB) between the Lower and the Upper Carboniferous subsystems. In both cases several major groups became extinct some time before or at the respective boundary, and other groups entered after the boundary. Only a few species may have crossed the DCB and the MCB, respectively.

The ammonoid changeover in both critical intervals have characteristics in common: The morphological differences concern mainly the shell characteristics of their early whorls; significant characters are also the ornamentation and the general outline of the conch including the size. The similarities in ammonoid evolution are

1) the stepwise decrease in diversity before the boundary from a high diversity phase to a low diversity phase,
2) after the low point the origin of new groups with wide, but small whorls and a low grade of involution,
3) the onset of a high diversity phase with complicated conch forms and ornamentation. Possible causes are discussed.

1. Introduction

During the late Palaeozoic periods several episodes of severe fluctuations in the composition of ammonoid faunas can be recognised. In the Devonian at least five critical episodes are known, and at the end of the Devonian almost the whole superorder Ammonoidea became extinct. The mode of the Devonian/Carboniferous turnover has been intensively discussed on the basis of genera and higher systematic categories (e.g. BECKER, 1993; HOUSE, 1983, 1985, 1993; KORN, 1993; PRICE & HOUSE, 1983). Also in the Carboniferous (KULLMANN, 1994; KULLMANN & NIKOLAÈVA, 1999) and the Permian (Zhou et al., 1997) some significant fluctuations can be observed which influenced greatly the course of the ammonoid evolution.

Calculations on the basis of the species level and an intense evaluation of the diversity development during these critical episodes have been made possible by using the data of the Database Management System GONIAT (Kullmann et al., 1998). GONIAT has been established in the University of Tübingen (Germany) and is available by downloading in the INTERNET in the homepages of the University of Tübingen (Germany) under the URL http://www.uni-tuebingen.de.

GONIAT is designed as a tool for investigations on systematics and evolution of Palaeozoic ammonoids, their palaeogeographic distribution and their biostratigraphic range. It provides not only determinations based on morphological characteristics but also extended information on occurrence, duration, literature and phylogenetic relationships of every taxon of the family, genus and species levels.

GONIAT is a relational database consisting of six independent databases connected by three link information files (Kullmann et al., 1993; Korn et al., 1994). The main databases TAX, MORPHA and MORPHB contain data of specific taxa, their taxonomic position and distinctive morphologic characteristics which are important for the determination of adult and different ontogenetic growth stages. The database BOUND contains the biostratigraphical data as time planes of boundaries based on approximate radiometric age assignments as well as the time-stratigraphic limits for the biostratigraphic range. The radiometric dates used in this study are estimations derived from several published time scales (e.g. Harland et al., 1990; Jones, 1995; Menning et al., 1996; Tucker et al., 1998). The database LOC which accommodates the information on the localities and beds of the species is relevant for the palaeogeographic distribution of the ammonoids.

In studies on diversity fluctuations a great number of restrictions and limitations have to be taken into account (Kullmann & Nikolaeva, 1999). Comparatively few species are precisely dated; the biostratigraphical records allow in many cases only nebulous estimations of the longevity of taxa. In addition to the imprecise dating the rather rough biostratigraphic scales prevent a clear global comparison of the occurrence of the taxa under consideration. The evaluation of the time spans involved is difficult because of the uncertainties of a detailed calibration of the biostratigraphic units. The database system GONIAT reveals deliberately the weaknesses and inconsistencies of the ammonoid fossil record. In many cases not only the biostratigraphic ranges of taxa are imperfectly recognised or imprecisely described but also the circumstances of the provenance of the described forms remain obscure. Most species must be regarded as "typologic" species, because their diagnoses do not contain sufficient information about the variability of the species. Hughes & Labandeira (1995) pointed out that most fossil species have been erected using brief descriptions of a very small number of specimens. In general, many of our conclusions appear to be based on insufficiently known species.

Almost 4000 valid ammonoid species are described from the Palaeozoic belonging to more than 110 families and 600 genera. The period in which ammonoids lived is thought to comprise about 160 million years [m.y.] (409–251 m.y. before present). The average frequency of Devonian ammonoids amounts to about 24 species assigned to 5 genera and 1 family per m.y.; the frequency of Carboniferous ammonoids differs not considerably: 25 species, 4 genera and 0.7 families per m.y., almost as many as in the Permian: 25 species, almost 5 genera and 0.75 families. As a general result, there does not seem to exist a significant difference in the general turnover rate of ammonoids during the Devonian, Carboniferous and Permian.

2. Quantitative Analysis of the Critical Intervals

2.1. Late Upper Devonian and Early Lower Carboniferous

The older critical epoch under consideration comprises 5 m.y. before the Devonian/Carboniferous Boundary (DCB), and 8 m.y. after the DCB (base of Platyclymenia Zone until late Tournaisian stage, Tn3, see Tab. 1). Nine ammonoid superfamilies existed below the DCB, four of the order Goniatitida, five of the order Clymeniida. After the DCB only two superfamilies were present, one belonging to the new order Prolecantitida; a third superfamily appeared in the middle Tournaisian (Text-Fig. 1).

The quantitative turnover becomes clear by separating families. Most families of both orders Goniatitida and Clymeniida became already extinct before the Devonian-Carboniferous boundary, at the "Stockum interval", in which at most only a few clymeniid species survived and
Text-Fig. 1. Chart showing the phylogeny and range of Upper Devonian and Lower Carboniferous superfamilies (between 370–350 m.y.). Cheil. = Cheiloceras Zone; Pr. = lower Platy- 
clymenia Zone; Plat. = upper Platylymenia 
Zone; Gym. = Clymenia Zone; Wo = lower 
Wocklumeria Zone; Ac = upper Wocklumeria 
Zone = “Stockum Interval”. 
Tn1 = lower Tournaisian; middle Tourn. 
(Tn2) = middle Tournaisian; upper Tourn. 
(Tn3) = upper Tournaisian.

some representatives of the family Prionoceratidae entered. After the 
DCB two new families arose during the lower Tournaisian (Tn1, Gatten- 
dorfia Zone), and in the following 
middle Tournaisian substage four 
new families were added stepwise. 
The diversity changeover is docu- 
mented (Text-Fig. 3A) by counts of 
A, first appearances, B, last ap- 
pearances and C, total frequency of 
species per million years.

During the middle and upper Fa- 
mennian stage a constant increase 
of the diversity can be observed 
(Text-Fig. 3A, A: first appearance; C: 
frequency). The highest diversity 
was reached during the Wocklumeria 
Zone (before the Stockum interval) 
with 149 species after intervals with 
60 or 70 species per m.y. The num- 
ber of taxa dropped tremendously 
after the extinction of almost all cly- 
eniids (Text-Fig. 3A,B: last appear- 
ance). With the entry of Acutimitoceras 
only 30 species/m.y. are described. 
Three species (of only one genus) 
seem to have survived the DCB.

In the first stage of the Carboni- 
ferous the frequency of species in- 
creased constantly, but not to the 
extent of the last unit (Wocklumeria 
Zone) of the Famennian stage: in 
average about 45 species/m.y. can 
be counted. In the following inter- 
vals (middle Tournaisian, Tn2; up- 
per Tournaisian, Tn3) the decrease 
of diversity continued throughout 
the rest of the Tournaisian stage; 
origination rate, extinction rate and 
the ammonoid frequency remained 
lowest almost until the end of the 
Tournaisian (KULLMANN, 1994).

Table 1.

| Time planes around the Devonian-Carboniferous Boundary (DCB) used in this paper representing boundaries on the basis of biochrones as used in database BOUND of the Database System GONIAT between base of Pla- 
tyclymenia Zone (middle Famennian stage) until upper Tournaisian stage (left of hyphen: older interval; right: younger interval). |
|IRD values of HARLAND et al. (1990), JONES (1995), MENNING et al. (1996) and TUCKER et al. (1998); radiometric date of the DCB after TU- 
cker et al. (1998). |
| 354 | Boundary middle Tournaisian (Tn2)--upper Tournaisian (Tn3) |
| 360 | Boundary lower Tournaisian (Tn1)--middle Tournaisian (Tn2) |
| 362 | DCB, Devonian--Carboniferous Boundary, base of Tournaisian(Tn1) |
| 362.6 | First appearance of Acutimitoceras |
| 363,6 | Boundary Clymenia Zone--Wocklumeria Zone |
| 365,2 | Boundary Platylymenia Zone--Clymenia Zone |
| 367 | Boundary Prolobites Zone--Platylymenia Zone |
Text-Fig. 2. Chart showing the phylogeny and range of mid-Carboniferous superfamilies (331 to 300 m.y.).

PND = Pendleian; ARN = Arnsbergian; C = Chokierian; A = Alportian; KIN = Kinderscoutian; MRD = Marsdenian; YEA = Yeadonian; La. = Langsettian; D = Duckmantian; Bo. = Bolsovian; D = Westphalian D; Bloy. = Bloydian.

Text-Fig. 3.

A) Frequency distribution of the ammonoid species during the critical interval around the DCB between 367 and 354 m.y.

B) Frequency distribution of the ammonoid species during the critical interval around the MCB between 319 and 309 m.y.

Abscissa: absolute time scale as used in the Ammonoid Database GONIAT version 2.80 (KULLMANN et al., 1998), radiometric time scales of HARRLAND et al. (1990), JONES (1995), MARRING et al. (1996), TUCKER et al. (1998) and others.

A = First appearance of new species; B = Last occurrence of existing species; C = Absolute frequency of species.

Values of intervals longer or shorter than 1 million years are converted into 1 m.y. Radiometric age of Devonian/Carboniferous boundary based on TUCKER et al. (1998).
2.2. Late Lower Carboniferous and Early Upper Carboniferous

The younger critical epoch under consideration comprises 6 m.y. before the Mid-Carboniferous boundary (MCB) and 4 m.y. after the MCB (Viséan/Namurian boundary, Chesterian until Namurian/Westphalian or Halian/Bloydian boundary, see Tab. 2). Three out of nine superfamilies of the order Goniatitida became extinct at the MCB, and five superfamilies arose a short time after the MCB (Text-Fig. 2). About ten families disappeared at the MCB, eight families continued, and one family (Homoceratidae) arose immediately at the MCB. The diversity changeover (Text-Fig. 3B) shows the following development: The number of new species (first appearances) which was highest in the late Lower Carboniferous was slightly on the decline some million years before the MCB. After the MCB the origination of new species increased stepwise to a maximum. The peaks of the extinction rate correspond only partly to the rate of the first appearances; about 4 million years before the MCB (in the Pendleian substage) the extinction rate had a maximum, dropped at the beginning of the following substage (early Amsbergian) and reached a new maximum at the MCB.

Four species are known from beds below and above the MCB. A number of "Lazarus species" must have survived, because in addition nine older long-living genera are known from a later interval. Also, the important superfamily Prionocerataceae, which disappeared below the MCB, recurred not until the Atokan or Moscovian of the Upper Carboniferous period; the majority of species belonged to the siphuncle; the majority of species belonged to this superfamily Pseudohaloritaceae.

3. Qualitative Analysis of the Critical Intervals

3.1. Late Upper Devonian and Early Lower Carboniferous

The qualitative analysis reflects a twofold change of the diversity before the DCB. The clymeniid episode ended during the last ammonoid biozone of the Upper Devonian, the Wocklumeria Zone, at the “Stockum interval”, a short time before the DCB as defined by the Stratigraphical Commission. The rapid and almost complete extinction of the clymeniids marks the first step of the changeover. The special character of the triangular coiling of their whorls sometimes restricted to their inner whorls. This character is mostly connected with the formation of three strong shell constrictions per whorl at a distance of 120°. About a third of the clymeniid species belonging to eight genera possesses this feature, but at the same time one species of the Goniatitida, Mimimitoceras trizonatum, exposes the same characteristic. In the units before the “Stockum interval” the general shell outline and the suture-lines of Clymeniida and Goniatitida differ greatly. Shell ornamentation is common only among the clymeniids (about 25 % of the clymeniid species).

In the “Stockum interval” the remaining species display an extremely uniform conch form. Except for two species they belong to the new genus Acutilimitoceras. This genus differs from most representatives of the Wocklumeria Zone by its different ontogenetic development on early growth stages: the first whorls are extremely evolute, and they change their growth parameters at a later stage. The adult whorl form may become involute. Biometric studies have revealed that the mode of the ontogenetic conch development is triphasic in contrast to that of the majority of older ammonoids with monophasic or diphasic growth patterns (KANT & KULLMANN, 1988). The triphasic mode became predominant in the Carboniferous period.

In the earliest Carboniferous the majority of the Goniatitida as well as the members of the new order Prolecanitida are discoidal, almost half of them with a wide umbilicus. The conch form of the Prolecanitida resembles strikingly to the general form of the Clymenida: they are discoidal, with wide umbilicus; their surface is smooth, but the position of the siphuncle is ventral. The Goniatitida, however, display a great diversity in conch form and ornamentation: about 25 % of the goniatitids are ornamented, and 15 % have an oxycone ventral side.

3.2. Late Lower Carboniferous and Early Upper Carboniferous

The ammonoids of the Lower and Upper Carboniferous are fundamentally different. The morphologic differences concern ornamentation, suture-line and, as at the DCB, the shell characteristics of their early whorls. The last Lower Carboniferous forms are rather diverse, usually widely umbilicate at the early stages, but their coiling displays an advanced tendency towards involute of the relatively large whorls. Many of the species are characterized by a rather complicated ornamentation. The suture-lines of the many advanced older forms show inflated or even pouched parallel-sided “gastrioceran” prongs of the ventral lobe which became predominant later in the Upper Carboniferous period; the majority of species belonged to groups with more simple ventral lobes which disappeared at the MCB.

<table>
<thead>
<tr>
<th>Time planes around the Mid-Carboniferous Boundary (MCB) as in Tab. 1, between base of Pendleian substage and the end of Yeadonian substage, Namurian (left of hyphen: older interval; right: younger interval)</th>
<th>Radiometric dates of HARLAND et al. (1990), JONES (1995), MINNING et al. (1996) and others.</th>
</tr>
</thead>
<tbody>
<tr>
<td>309</td>
<td>Yeadonian—Langsettian (base of Bloydian, Westphalian)</td>
</tr>
<tr>
<td>310</td>
<td>Marsdenian—Yeadonian</td>
</tr>
<tr>
<td>311</td>
<td>Kinderscoutian—Marsdenian</td>
</tr>
<tr>
<td>312</td>
<td>Alportian—Kinderscoutian, base of Reticuloceras</td>
</tr>
<tr>
<td>312.5</td>
<td>Chokierian—Alportian</td>
</tr>
<tr>
<td>313</td>
<td>MCB, Mississippian—Pennsylvanian, base of Homoceras</td>
</tr>
<tr>
<td>313.5</td>
<td>E2b—E2c (England), base of Nuculoceras</td>
</tr>
<tr>
<td>314.5</td>
<td>E2b1—E2b2 (England), N1c1—N1c2 (Russia)</td>
</tr>
<tr>
<td>316.5</td>
<td>Pendleian—Amsbergian</td>
</tr>
<tr>
<td>317,5</td>
<td>N1b1—N1b2 (Russia), base of Dombairites tectus</td>
</tr>
<tr>
<td>319</td>
<td>Viséan—Namurian, base of Pendleian, Serpukhovian, Eumorphoceras</td>
</tr>
</tbody>
</table>
Immediately after the MCB relatively small forms appeared which did not display any ornamentation but only coarse or lamellate growth lines. The suture had the same number of elements as before, but consisted of relatively simple ventral lobes with acute prongs which were not inflated or pouched. The main difference of the conch shape can be observed at the characteristic form of the early growth stages. The genus Homoceras and some other homoceratid genera are characterised by early whorls with a wide and low whorl section and with a sharp umbilical shoulder forming the specific outline of the young whorls called “calyx stage”.

This new type of ammonoids, the homoceratids dominated the earliest Upper Carboniferous ammonoid faunas, at the beginning with three cosmopolitan genera and 15 species. In the following interval (Alportian substage) the ammonoid diversity increased to nine genera with more than forty species. The second most important new group was the family Ramositidae comprising more than 10% of the species. The faunal composition remained the same during the whole Homoceras Stage (lower Bashkirian) but was changed later by the first appearance and expansion of the ornamented Reticuloceratidae which reached in the middle Bashkirian (Kinderscoutian substage) almost 50% of the fauna.

4. Faunal Characteristics of the Boundary Events

In both compared cases an almost complete change over of the faunal elements took place within a comparatively short time span. Considering the morphologic changes of the faunal composition the events at the DCB and MCB can be regarded as a paradigm shift.

Below the boundaries: The diversity of shell types was high, the advanced involute conch forms were widespread; many species were ornamented. Advanced suture-lines were also common. The faunas with diverse conch types collapsed, the diversity decreased to a minimum. Only a few species with eulophyseal and widely umbilicate conchs on early or adult growth stages appeared. During this exchange interval strongly ornamented forms were absent. The number of species was extremely diminished.

After the changeover the former diversity of ammonoids was stepwise re-established on the basis of a different root group. New faunas similar to those before the respective boundary, with diverse conch types and suture-lines, arose considerably later.

5. Possible Causation of the DCB and MCB Events

In a profound essay on Proterozoic and Palaeozoic catastrophes Schönlau (1996) gave an extended review on possible causes for environmental events. The list of possible reasons for such events seems to be endless, and arguments in favour or against specific factors remain in most cases open to further discussion.

Both critical intervals are not regarded by Schönlau as belonging to the five large mass extinctions in the history of the earth. Schönlau discussed greatly the Frasnian/Famennian boundary in the Upper Devonian period, which remains until now controversial (RACKI, 1999). According to Schönlau’s list the DCB at the end of the Devonian system seems to be of secondary importance because of the lack of significant changes in trace elements or isotope composition at the DCB. A sequence of black shales ("Hangenberg shales") shortly before the DCB, at the end of the Clymeniid-bearing Wocklumeria Zone resembles the euxinic intercalations in late Devonian sequences known as “Kellwasser” horizons. In Germany the black “Hangenberg shales” of uppermost Devonian age are overlain by limestone or sandstone layers with the impoverished faunas of the “Stockum interval”, and fluctuations of the sea-level by tectonic activity or glaciation seem to be documented.

The causes for extinction were probably multitudinous. Tectonic as well as volcanic activity occurred during both periods under consideration causing disturbances of rock sequences world-wide in many areas. One obvious factor commencing at the beginning of the Carboniferous may be connected with the onset of extremely extended limestone production in the Lower Carboniferous period. Tectonic uplift led to the regional and global increase of chemical erosion of siliciclastics resulting in the high sedimentation rate of CaCO₃ in large areas (REYN & RUDDIMAN, 1992). The reduced content of CO₂ in the atmosphere as can be seen in Schönlau (1996, Figs. 9, 3) must have caused a global cooling during the whole Carboniferous period. Drastic changes of the temperature towards an ice-house climate influencing thereby the ocean habitats may explain the relatively low number of ammonoid taxa throughout almost the whole Lower Carboniferous period.

The apparently short intervals of the absolute low diversity phases cannot be explained easily by global sea-level changes. At the DCB as well as at the MCB the extinction rate came close to the complete extinction of the entire superorder Ammonoidea that finally occurred at the end of the Cretaceous period. As in many similar cases it has to be considered whether asteroid impacts may have taken place at the DCB and MCB contributing to the extinctions amidst an already stressed environment.

Acknowledgements

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References


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