



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

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3 Text-Figures and 2 Tables

*Devonian
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Ammonoids
Evolution
Diversity*

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

Zusammenfassung

Berechnungen der Diversitäts-Entwicklung der Ammonoideen 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 Ammonoideen: 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.

Der Wechsel der Ammonoideen beider kritischer Perioden weist einige gemeinsame Eigentümlichkeiten auf: Die morphologischen Unterschiede betreffen hauptsächlich die Jugendstadien; wichtige Merkmale sind außerdem die Ornamentierung und die generelle Schalenform und Schalengröße. Die Ähnlichkeiten in der Ammonoideen-Evolution sind einmal eine stufenweise Verminderung der Diversität von einer Diversitäts-Hochphase zu einer Niedrigphase der Diversität. Nach dem Tiefpunkt erfolgt der Beginn neuer Gruppen mit extrem weitnabeligen, aber sehr kleinen Windungen mit geringer Involution. Der bald darauf folgende Beginn einer Diversitäts-Hochphase mit komplizierten Gehäuseformen und ausgeprägter Ornamentierung ist eine dritte Gemeinsamkeit. Mögliche Ursachen werden diskutiert.

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 & NIKOLAEVA, 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 Prolecanitida; 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 *Platyclymenia* Zone; Plat. = upper *Platyclymenia* Zone; Clym. = *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, *Gattendorfia* Zone), and in the following middle Tournaisian substage four new families were added stepwise. The diversity changeover is documented (Text-Fig. 3A) by counts of A, first appearances, B, last appearances and C, total frequency of species per million years.

During the middle and upper Famennian 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 number of taxa dropped tremendously after the extinction of almost all clymeniids (Text-Fig. 3A, B: last appearance). 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 Carboniferous the frequency of species increased 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 intervals (middle Tournaisian, Tn2; upper 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).

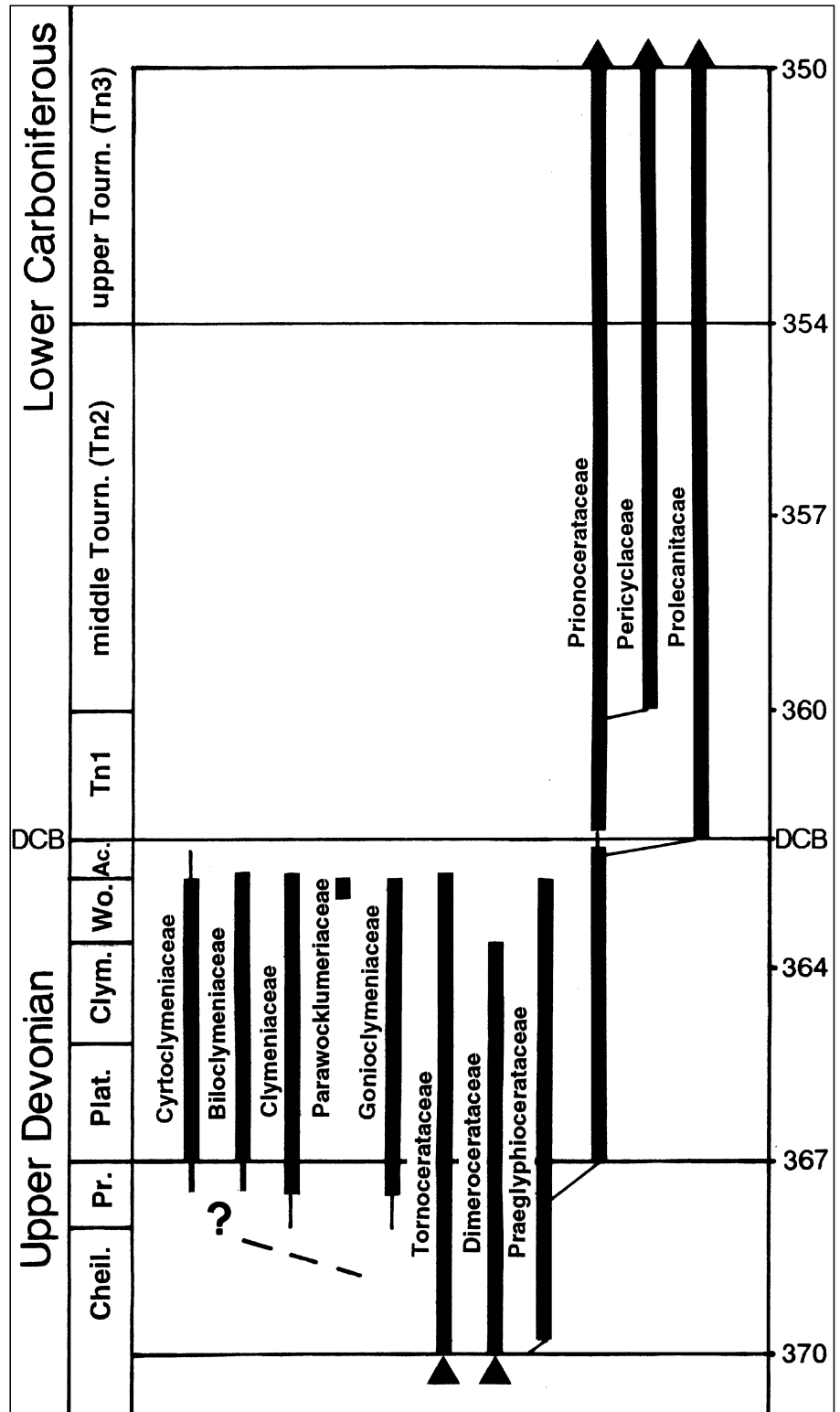


Table 1.
 Time planes around the Devonian-Carboniferous Boundary (DCB) used in this paper representing boundaries on the basis of biochrones as used in database BOUND of the Database System GONIAT between base of *Platyclymenia* Zone (middle Famennian stage) until upper Tournaisian stage (left of hyphen: older interval; right: younger interval).

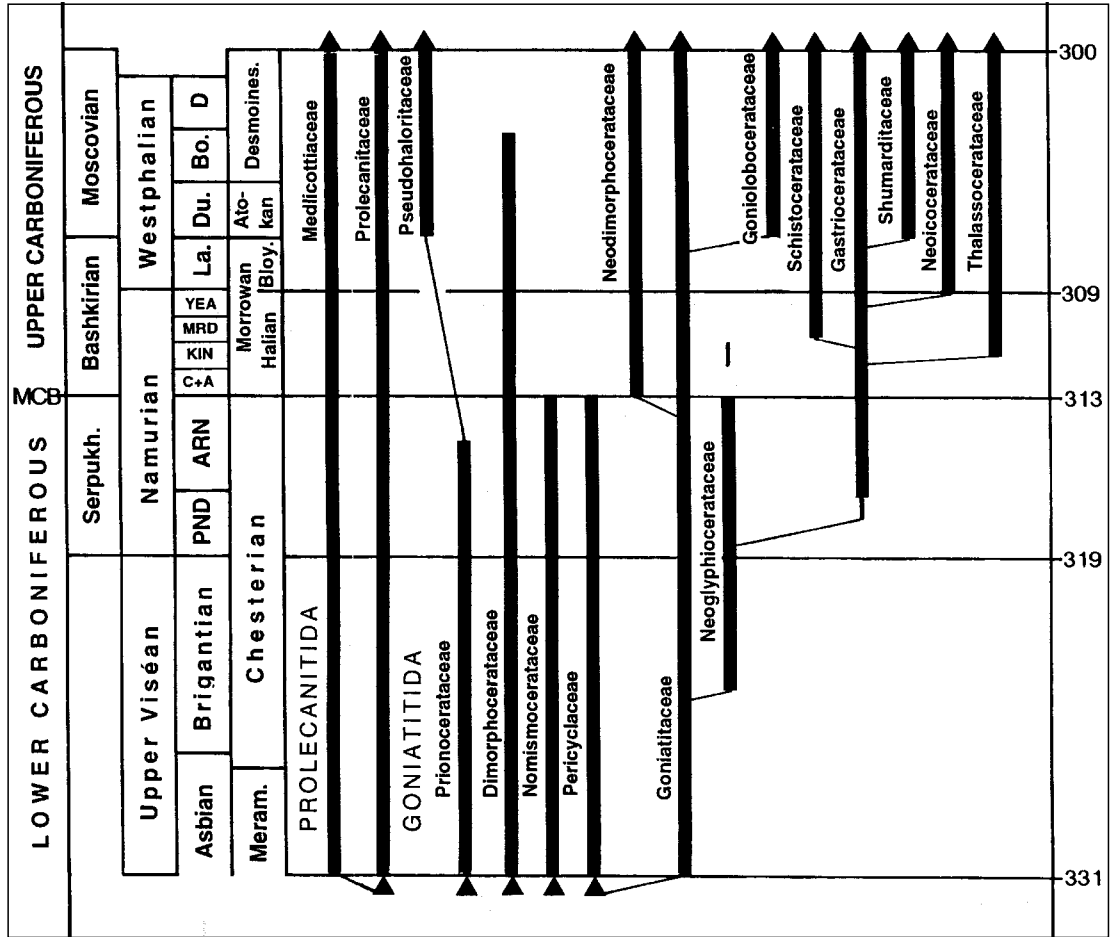
354	Boundary middle Tournaisian (Tn2)--upper Tournaisian (Tn3)
360	Boundary lower Tournaisian (Tn1)--middle Tournaisian (Tn2)
362	DCB, Devonian--Carboniferous Boundary, base of Tournaisian(Tn1)
362,6	First appearance of <i>Acutimitoceras</i>
363,6	Boundary <i>Clymenia</i> Zone-- <i>Wocklumeria</i> Zone
365,2	Boundary <i>Platyclymenia</i> Zone-- <i>Clymenia</i> Zone
367	Boundary <i>Prolobites</i> Zone-- <i>Platyclymenia</i> Zone

Radiometric dates of HARLAND et al. (1990), JONES (1995), MENNING et al. (1996) and TUCKER et al. (1998); radiometric date of the DCB after TUCKER et al. (1998).

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. = Langsetian; Du. = Duckmantian; Bo. = Bolsovian; D = Westphalian; Bloy. = Bloydian.



Text-Fig. 3.

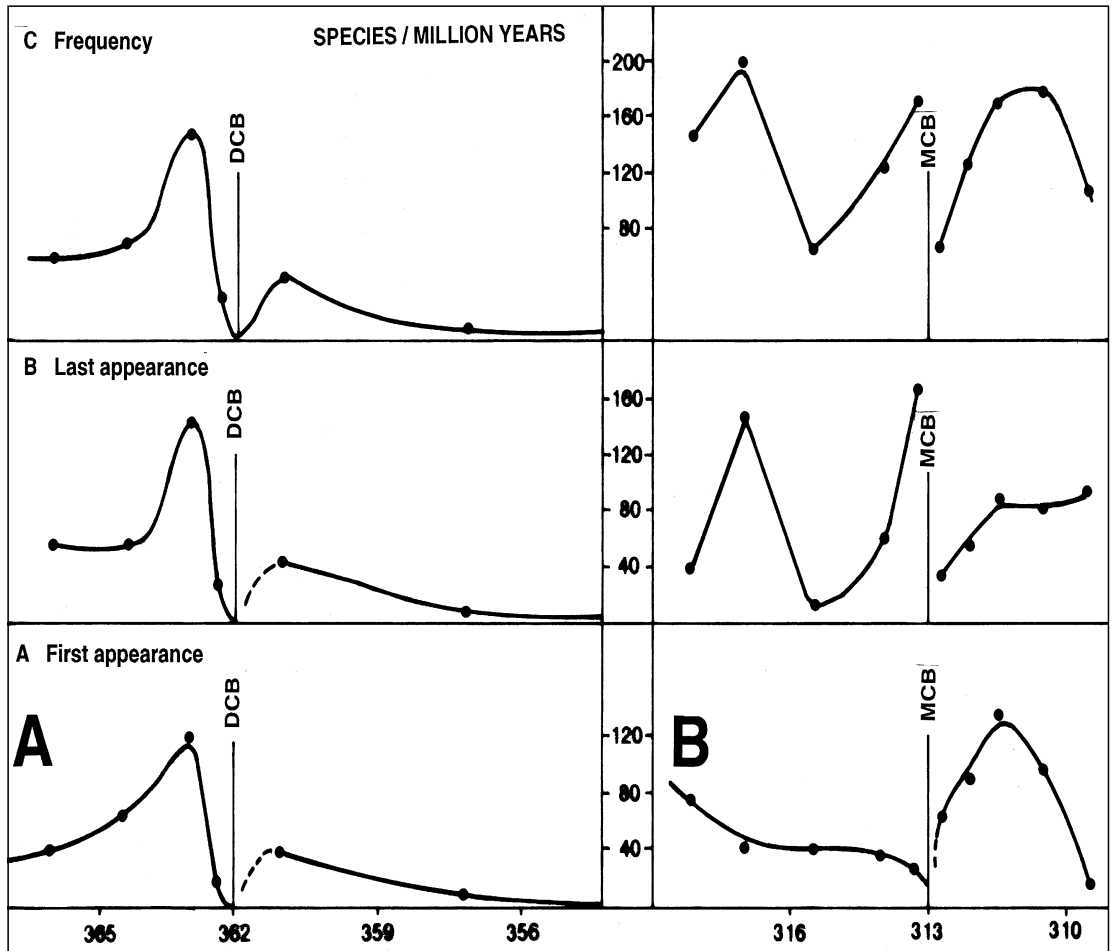
A) Frequency distribution of the ammonoid species during the critical interval around the DCB between 367 and 354 m.y.

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 HARLAND et al. (1990), JONES (1995), MENNING 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 Arnsbergian) 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 giving rise to the peculiar 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 key character of the Clymeniida is the dorsal position of the siphuncle; the percentage of clymeniids amounts to about two third of the ammonoids, increasing to 88 % in the Clymenia Zone and 80 % in the *Wocklumeria* Zone (except for the "Stockum interval"). A number of genera have the special character of the triangular coiling of their whorls sometimes restricted to their inner whorls. This character is mostly connected with the forma-

Table 2.
Time planes around the Mid-Carboniferous Boundary (MCB) as in Tab. 1, between base of Pendleian substage until the end of Yeadonian substage, Namurian (left of hyphen: older interval; right: younger interval).; Radiometric dates of HARLAND et al. (1990), JONES (1995), MENNING et al. (1996) and others.

309	Yeadonian--Langsetian (base of Bloydian, Westphalian)
310	Marsdenian--Yeadonian
311	Kinderscoutian--Marsdenian
312	Alportian--Kinderscoutian, base of <i>Reticuloceras</i>
312,5	Chokierian--Alportian
313	MCB, Mississippian--Pennsylvanian, base of <i>Homoceras</i>
313,5	E2b--E2c (England), base of <i>Nuculoceras</i>
314,5	E2b1--E2b2 (England), Nm1c1--Nm1c2 (Russia)
316,5	Pendleian--Arnsbergian
317,5	Nm1b1--Nm1b2 (Russia), base of <i>Dombarites tectus</i>
319	Viséan--Namurian, base of Pendleian, Serpukhovian, <i>Eumorphoceras</i>

tion 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 *Acutimitoceras*. 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 conch 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 Clymeniida: 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 involution of the relatively large whorls. Many of the species are characterised by a rather complicated ornamentation. The suture-line of many of the advanced older forms shows inflated or even pouched parallel-sided "gastroceran" 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.

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 evolute 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 catastrophies SCHÖNLAUB (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 SCHÖNLAUB as belonging to the five large mass extinctions in the history of the earth. SCHÖNLAUB discussed greatly the Frasnian/Famennian boundary in the Upper Devonian period, which remains until now controversial (RACKI, 1999). According to SCHÖNLAUB's list the DCB at the end of the Devonian system seems to be of secondary importance be-

cause 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 (REYNO & RUDDIMAN, 1992). The reduced content of CO₂ in the atmosphere as can be seen in SCHÖNLAUB (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 extinction events amidst an already stressed environment.

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