Ministry of Economic Affairs, Adm. of Mines, Belgian Geological Survey
Annales de la Société géologique de Belgique, T. 109 - 1986, pp. 49-54

Special volume "Aachen 1986"
Avril 1986

AMMONOID EVOLUTION IN LATE FAMENNIAN AND EARLY TOURNAISIAN

by

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(2 figures and 1 table)

ABSTRACT. - In the Famennian, ammonoids reached an acme of evolutionary diversification. While the order Clymeniida appeared, diversified and disappeared in this time, goniatites were more stable. Apparently, phylogenetic events are not restricted to only one or a few stratigraphical levels, and cannot be related to a trend-setting influence of global events.

RESUME. - Au Famennien, les ammonoïdés atteignent un optimum de diversification évolutive. Tandis que l'Ordre des Clymeniidés apparaît, se diversifie et disparaît pendant cet intervalle de temps, les goniatites restent stables. Apparemment, ces étapes phylogénétiques ne paraissent pas restreintes à un seul ou à un petit nombre de niveaux stratigraphiques et ne fournissent donc pas d'arguments qui permettent de croire qu'elles sont influencées par des événements mondiaux.

INTRODUCTION AND HISTORICAL REVIEW

The latest Devonian and earliest Carboniferous are characterised by irregular ammonoid evolution, with maxima and minima quickly following one another. There is a repeated explosive occurrence of new genera with a multitude of new species, following the extinction of entire groups.

Both Famennian groups, clymeniids and goniatites, are distinguished by the position of the siphuncle (which played a role in locomotion) : it is located at the ventral side of the whorl in goniatites and at the dorsal side of the whorl in clymeniids. Only one group, the Clymeniida, has a high rate of phylogenetic diversification during the Famennian. Together with the "sudden" appearance and the "abrupt" extinction of the clymeniids this makes these particularly promising for investigations on the influences of global events.

Ammonoids are known from appropriate Famennian environments throughout the world. Because of their quick evolution during this time span one needs a highly exact collecting and the discrimination of horizons often less than 50 cm thick. This scale of observation is still unusual in Paleozoic rocks of several parts of the world. Therefore this paper has to concentrate mainly on the results found in central Europe, although there is clear evidence of similar (but still being studied) developments in other parts of the globe.

The basis for studies of the irregular faunal evolution is a detailed understanding of ammonoid systematics, and thorough knowledge of the stratigraphic ranges of the fauna. Investigation of the faunas of the *Prolobites*-Stufe began more than fifty years ago (Wedekind, 1908; Lange, 1929), and all important data come from just one locality, the Enkenberg (Fig. 1; NE Rhenish Massif, sheet 4518 Madfeld). The section described by Wedekind (1908) is very finely subdivided, but there are unfortunately many discrepancies between his text and his faunal range and stratigraphic summary diagrams. For example, it is very unlikely that *Cymaclymenia "costata"* (= *C. costellata* Münster), recorded from the *delphinus* Zone, really occurs that early. Lange (1929) published a less detailed review of the same section, which did not improve our understanding. An often overlooked description of the Enkenberg section is given by Paeckelmann & Kühne (1936 : 28-31), including a list of the fossils which were identified by Schindewolf. This list shows a clear tripartite subdivision of the *Prolobites* Stufe : from bottom to top the *sandbergeri, delphinus* and *annulata* Zones (see Table 1).

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Table 1. - Cephalopod and conodont zones of the (upper) Famennian and (lower) Dinantian.
Cephalopod zones see Luppold & Korn, in prep.; conodont zones (a) Ziegler, 1962, 1971; Sandberg & Ziegler, 1973; Voges, 1960; (b) Sandberg *et al.*, 1978; Ziegler & Sandberg, 1984b. Ch. : *Cheiloceras.*

	Stufen	CEPHALOPOD ZONES	CONODONT ZONES (a)	CONODONT ZONES (b)
DINANTIAN (pars)	Gattendorfia	?	lower crenulata	lower crenulata
		patens	triangulus triangulus	sandbergi
		westfalicus	triangulus inaequalis	upper duplicata
		dorsoplanus		lower duplicata
		acutum	kockeli-dentilineatus	sulcata
		prorsum	upper Protognathodus	
			lower Protognathodus	upper praesulcata
	Wocklumeria	upper paradoxa	upper costatus	middle praesulcata
		lower paradoxa		lower praesulcata
		upper subarmata	middle costatus	
		lower subarmata		upper expansa
FAMENNIAN (pars)	Clymenia	piriformis	lower costatus	middle expansa
		ornata		
		acuticostata	upper styriacus	lower expansa
		serpentina		
	Prolobites	annulata	middle styriacus	upper postera
			lower styriacus	lower postera
		delphinus	upper velifer	upper trachytera
			middle velifer	lower trachytera
		sandbergeri	lower velifer	uppermost marginifera
	Ch.		upper marginifera	upper marginifera

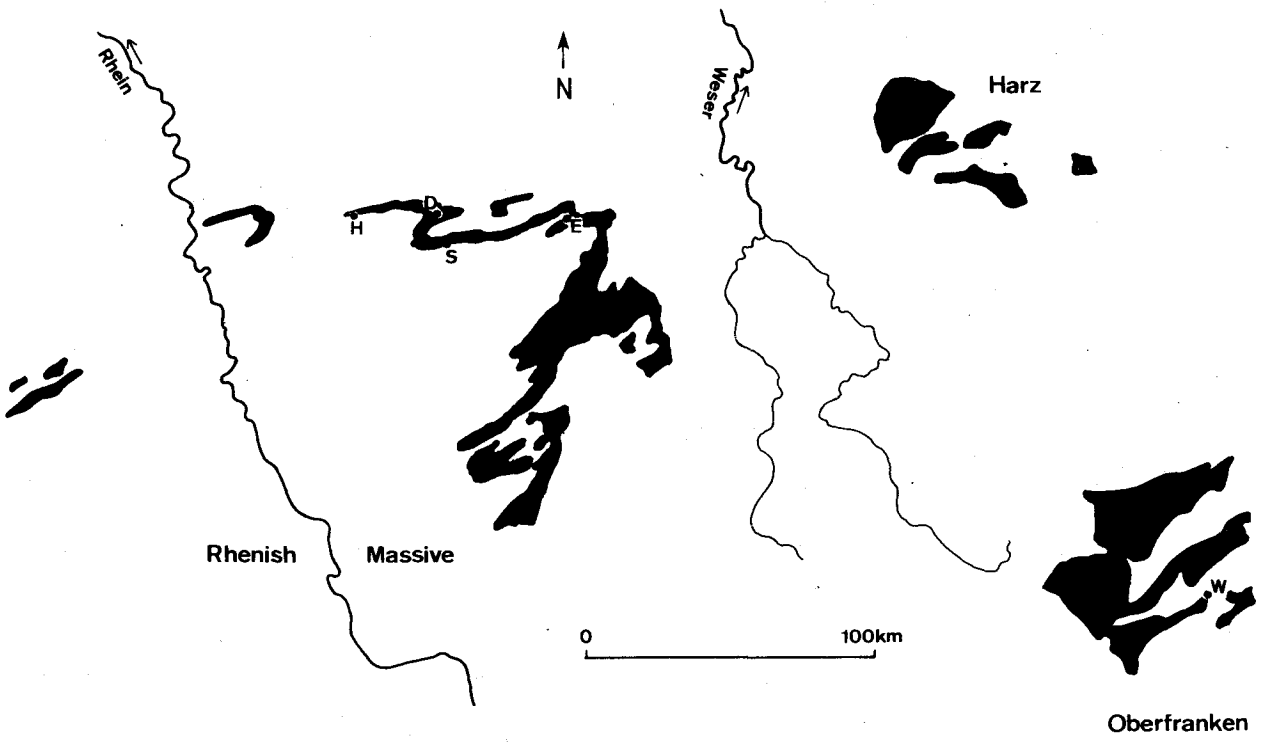

Figure 1. – Sketch map of the outcropping Dinantian (black colour) rocks in Germany, with localities mentioned in the text. H : Hasselbachtal north of Hohenlimburg; D : Dasberg, north of Sundern; S : Stockum, south of Sundern; E : Enkenberg, east of Brilon; W : Wäschholz, west of Hof.

The only exception seems to be "*Falciclymenia (?)* aff. *humboldti*" of Schindewolf's list which is marked already in the *sandbergeri* Zone, as the oldest and first clymeniid. However, this is generally thought to be a higher developed form. The inaccuracy of Schindewolf's determination is supposed to be based on questionable specimens, so that no important conclusions should be based on that reference.

A similarly detailed stratigraphic description of a section in the next younger *Clymenia* Stufe had long been lacking. A tripartite subdivision had been proposed by H. Schmidt (1924), but without a detailed analysis of faunal ranges to support this. The three-fold subdivision proposed by Lange (1929) seems to be incorrect. His zones Va-Vc are largely within the *acuticostata* Zone, one of the four zones proposed by Korn (1981a) which are based on several previously undescribed sections near the Dasberg (near Balve; sheet 4613).

The latest Devonian *Wocklumeria* Stufe, and the earliest Carboniferous *Gattendorfia* Stufe, were subject of extensive studies by Schindewolf (1937) and Vöhringer (1960). Therefore, this interval is now the best known part of the biostratigraphic column under discussion. Schindewolf's study concentrated on unusual clymeniids which however form a characteristic part of the ammonoid fauna. Recent examinations of hitherto undescribed jointly occurring species resulted in a new subdivision of Schindewolf's *subarmata* Zone. Faunas from near the Devonian-Carboniferous boundary were studied by Korn (1981b, 1984), considering particularly the question of whether the "Stockumer *Imitoceras*-Kalklinsen" should be referred to the Devonian or Carboniferous. The frequency of genera and subgenera of ammonoids occurring during the latest Devonian and earliest Carboniferous is shown in Fig. 2.

AMMONOID DEVELOPMENT

At the end of the *Cheiloceras* Stufe almost all characteristic genera became extinct, namely *Cheiloceras* and its relatives and a majority of the Tornoceratáceae. Only a few taxa continued into the *sandbergeri* Zone of the next younger *Prolobites* Stufe, especially *Protornoceras* and related forms, *Sporadoceras* and *Dimeroceras*. Clymeniids are not known from this zone (see above). Many new genera arose during the *delphinus* Zone, including *Postornoceras, Araneites, Praeglyphioceras* and *Prolobites* (the latter may have appeared during the *sandbergeri* Zone), and a number of remarkable clymeniids. Few of these genera (e.g. *Hexaclymenia* and *Araneites*) did not survive into the younger *annulata* Zone.

The *annulata* Zone undoubtedly represents a peak in the evolution of Paleozoic ammonoids. Almost all genera present in the *delphinus* Zone range up into the *annulata* Zone and also many new taxa have

their first appearance, such as *Prionoceras* and numerous clymeniids. The number of genera and subgenera exceeds 20, and such a number is not surpassed during the latest Devonian and earliest Carboniferous. Facies diversity, and therefore environmental diversity, is particularly marked in this zone. The well-known black *annulata* shale is present throughout the Rhenish Massif. The nodular and platy limestones of the *annulata* shale contain a fauna which is rich in individuals and poor in species : only *Platyclymenia, Protactoclymenia* and *Carinoclymenia* are present. A fossil-rich cephalopod limestone is developed in Oberfranken. Apart from genera present in the Rhenish Massif, rarely occurring genera such as *Sulcoclymenia, Aktuboclymenia* and *Protoxyclymenia* are represented, together with a number of as yet undescribed and unassigned forms. Further information for these genera might somewhat alter the picture conveyed in Fig. 2.

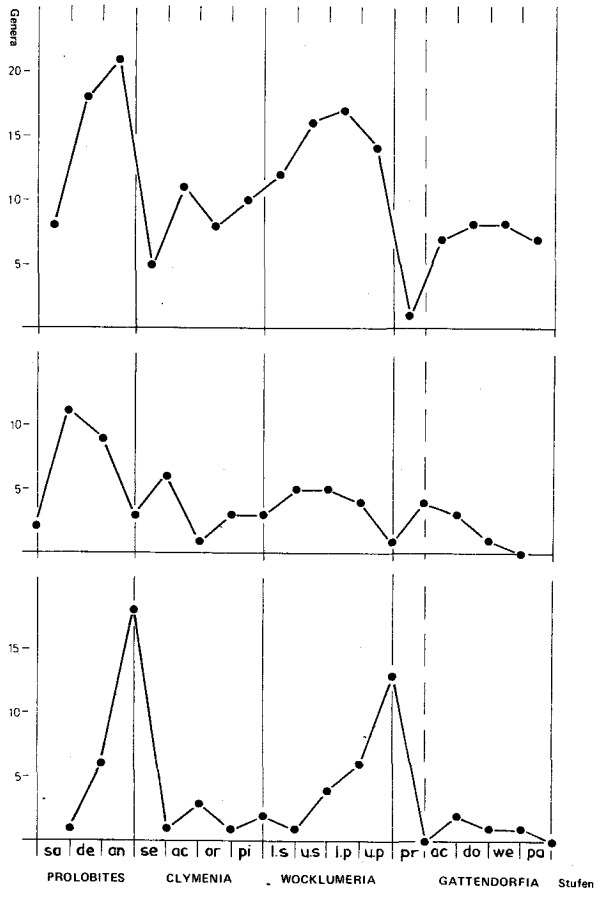

Figure 2. - Frequency diagrams
ordinate : number of genera and subgenera.
abscissa : cephalopod zones (left to right : from older to younger, see Tab. 1).
sandbergeri, delphinus, annulata zones (*Prolobites* Stufe); *serpentina, acuticostata, ornata, piriformis* zones (*Clymenia* Stufe); lower *subarmata,* upper *subarmata,* lower *paradoxa,* upper *paradoxa* zone (*Wocklumeria* Stufe); *prorsum* zone; *acutum, dorsoplanus, westfalicus, patens* zones (*Gattendorfia* Stufe).
The upper diagram shows frequency distribution of ammonoid genera and subgenera during the latest Devonian and earliest Carboniferous. The middle diagram shows the number of new genera appearing at the beginning of each zone, and the bottom figure shows the number of genera which have become extinct by the end of each zone.
Data are presented only for taxa which occur in the Rhenish Massif and Oberfranken, and whose stratigraphic ranges are known with certainty. Genera known only from other areas (e.g. *Uraloclymenia, Cteroclymenia*) could not be included, because their exact relative ages are not described.

The base of the *Clymenia* Stufe is marked by a striking poverty of both genera and species. Both *Sporadoceras* and *Prionoceras* survive from the *annulata* Zone and range into respectively the *Wocklumeria* Stufe and *Gattendorfia* Stufe, but it seems that *Cyrtoclymenia* is the only surviving clymeniid genus. However, it should be kept in mind that this genus has as yet not been the subject of intensive systematic study, and may therefore warrant further subdivision.

Also absent in the *serpentina* Zone are taxa intermediate in form between those occurring in the *annulata* Zone and those known from the younger *Clymenia* Stufe. This apparent absence is probably due to the extremely impoverished nature of the fauna seen in all sections examined so far.

Taxa very significant during the latest Famennian, such as *Kosmoclymenia, Gonioclymenia* and probably *Cymaclymenia* appear during the *acuticostata* Zone. From the *ornata* Zone to the lower *paradoxa* Zone the number of genera increased and there are almost 20 genera and subgenera known from the latter zone. The rate in which genera then became extinct increased from zone to zone during the *Wocklumeria* Stufe. Thus by the end of the upper *paradoxa* Zone no clymeniids and very few goniatites remained (Price & House, 1984). This cannot, however, be considered as a sharp extinction event, because almost all genera reach their acme in the upper *subarmata* Zone and lower *paradoxa* Zone. The decline of these forms is balanced by the blossoming of *Parawocklumeria, Wocklumeria* and *Balvia.* It is generally true that in the Rhenish Massif and Oberfranken a number of facies types prevail. However a major change occurred towards the top of the *Wocklumeria* Stufe. The uppermost part of the zone is represented by the lower part of the Hangenberg-Schichten. Their impoverished fauna (Schindewolf, 1937 : 14) comprises for the most part the same ammonoids which occur in the underlying part of the Wocklumer Kalk; *Cymaclymenia evoluta* (= *C. euryomphala* auct.) is the only species known to appear in this interval.

The next ammonoid horizon is only known from two localities : Stockum and the Müssenberg (both near Sundern; see Fig. 1). Only *Acutimitoceras* occurs here, a genus which is not known from the *Wocklumeria* Stufe. The absence of *Prionoceras* and *Imitoceras* is noticeable, especially since these genera commonly occur in the adjacent *Wocklumeria* Stufe and *Gattendorfia* Stufe. However, latest Devonian representatives

of these genera need systematic revision, in order to clarify the relationships with forms occurring in the early Carboniferous.

The *Gattendorfia* Stufe is marked by the rapid development of an ammonoid fauna which largely descended from *Acutimitoceras*. New characters arose : evolute outer whorls *(Gattendorfia)*, median saddle in the ventral lobe *(Voehringerites)*, conspicuous sculpture *(Costimitoceras, Paralytoceras, Pseudarietites)*, but above all the development of the U-type sutural ontogeny *(Eocanites)*. Although these developments were significant ones only the appearance of *Eocanites* marks the start of a new phylogenetic suite, the order Prolecanitida.

PHYLOGENETIC TRENDS

Analogues for most of the trends in Paleozoic ammonoid evolution can be found in the short time span discussed here :

1. SHELL FORM

Generally, there is a transformation from involute to evolute shells. This transformation can be considered as an example of proterogenetic evolution. Transitional forms have evolute inner whorls, but gradually closing the umbilici in outer whorls. This trend can be observed both in successive genera (e.g. *Prionoceras - Acutimitoceras - Gattendorfia*), and within a single genus in successive species (*Cymaclymenia costellata - C. striata - C. evoluta*). It is generally the case in clymeniids that the end member of a phylogenetic series has a wider umbilicus than earlier members of that series. Exceptions to this are the Wocklumeriidae, Glatziellidae and Parawocklumeriidae, where the exact opposite is the case.

Triangularity is exhibited by four groups of ammonoids, all occurring during the *Wocklumeria* Stufe : *Wocklumeria, Soliclymenia, Parawocklumeria* and *Prionoceras.*

2. SUTURE LINE

Another, only slightly subordinate trend, is that towards the increase in the number of sutural lobes. This is seen for example in tornoceratids (*Posttornoceras - Discoclymenia - Alpinites*), and in gonioclymeniids (*Costaclymenia - Gonioclymenia - Sphenoclymenia*).

There are also three periods during which a median saddle was developed in the ventral lobe.

The appearance at the base of the *Gattendorfia* Stufe of taxa with an U-type ontogeny was an important step.

3. ORNAMENTATION

Ribbed sculpture occurred irregularly in various families. It seems generally the rule for clymeniids that weakly sculptured forms arose from those which were highly ornamented. Almost all end members of phylogenetic series are more or less smooth-shelled (*Sellaclymenia angulosa, Gonioclymenia wocklumensis, Cymaclymenia evoluta, Glatziella glaucopis, Clymenia laevigata, Kosmoclymenia wocklumeri*). Goniatites showing striking ornamentation first occur in the *Gattendorfia* Stufe (*Costimitoceras, Pseudarietites, Paralytoceras*).

Ventro-lateral and median spines are known only from clymeniids e.g. n. gen. aff. *Cyrtoclymenia* (*delphinus* Zone), *Platyclymenia (Trigonoclymenia)* and *Protoxyclymenia* (*annulata* Zone), and also *Platyclymenia (Spinoclymenia)* and *Falciclymenia excellens* (which are known only from the USSR), and the Gonioclymeniidae and *Kosmoclymenia* in the *Clymenia* Stufe and *Wocklumeria* Stufe.

Ventro-lateral furrows are known in *Lobotornoceras, Balvia* and *Pseudarietites,* but especially common only in clymeniids (*Glatziella, Sulcoclymenia, Piriclymenia, Ornatoclymenia* and *Kosmoclymenia*), and these occur in numerous zones.

RESULTS

Goniatite and clymeniid ammonoids reached an acme of evolutionary diversification in the Famennian. First appearances of species, genera, families and even an order (Clymeniida) can be traced in sequences of exactly limited, often a few centimetres or metres thick horizons. The appearances as well as the disappearances are scattered throughout the succession. These events seem to prove the absence of **direct** influences of one or more "global events". If global events influenced at all the phylogenetic evolution of ammonoids in the Famennian, it may have been an indirect influence causing geographic, sea currents, climatic and other changes. The general gradual decrease in the number of taxa and the following increase near the Devonian-Carboniferous boundary may reflect in an **indirect** way the influences of a "global event", but it seems difficult to fix a possible event exactly in a section or in time.

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