

ANALYSIS OF AMMONOID PALAEOBIOGEOGRAPHY IN RELATION TO THE GLOBAL HANGENBERG (TERMINAL DEVONIAN) AND LOWER ALUM SHALE (MIDDLE TOURNAISIAN) EVENTS

by

R. Thomas BECKER¹

(2 figures and 5 tables)

ABSTRACT.- The global ammonoid record of the latest Famennian (Wocklumian) to Upper Tournaisian is reviewed in order to analyze patterns of the palaeogeographical distribution, developments in time and to elucidate the influence of the international Hangenberg and Lower Alum Shale Events. Occurrences of 77 genus-level taxa in 61 sedimentary provinces are summarized. The terminal Devonian Hangenberg Event caused a major ammonoid extinction but had little lasting influence on their palaeobiogeography. However, there was an unusual very short-timed spreading of ammonoid facies in formerly uninhabited areas of North America, Europe and NE-Siberia. The Lower Alum Shale Event at the base of the classical Middle Tournaisian, by contrast, marks a major palaeobiogeographical turning point associated with a medium scale extinction. Centres of evolution shifted from the Europe-Ural area to the west (North American interior) and east (Kazakhstan) and globally there is no significant faunal sequence crossing the event level. Endemism and faunal dispersal continue in the Upper Tournaisian with some evidence for the separation of two faunal provinces. The increasing spread of goniatite biofacies (enlargement of species-areas) as sign of sealevel highstand and wide overflowing of epicratonic areas curiously is not paralleled by an increase of global diversity. This may reflect non-palaeogeographic factors such as global climatic change. In a taxonomic chapter potential subdivisions of the genera *Acutimitoceras*, *Imitoceras* and *Eocanites* are discussed. The *Prodromitidae* are assigned to the *Prionocerataceae*.

KEY-WORDS.- Ammonoids, Devonian, Carboniferous, Palaeobiogeography, Mass extinction, Hangenberg Event, Lower Alum Shale Event.

1.- INTRODUCTION

1.1.- TERMINAL DEVONIAN AND MIDDLE TOURNAISIAN GLOBAL EVENTS

The major change between ammonoid faunas of the latest Devonian and earliest Carboniferous has been recognized for a long time and became especially evident after the detailed investigation of the Wocklum-Stufen faunas by Schindewolf (1937). Clymenids disappeared completely with the end of the Devonian and goniatites became almost extinct. Other fossil groups such as trilobites, conodonts,

miospores and stromatoporoids were also much affected. This mass extinction has been named the "Hangenberg Event" after the Middle and South European Hangenberg Shale that immediately postdates the main ammonoid extinction level. It represents a short-period interruption of cephalopod limestone sequences by hypoxic shales just below the Devonian-Carboniferous boundary. The event interval frequently encompasses also paraconformities or coarser detrital facies such as sandstone (Hangenberg Sandstone), bioclastic limestone with neritic fauna and calcareous oolites. This suggests a couplet of initial transgression and subsequent major sea-

1. Paläontologisches Institut, Freie Universität Berlin, Schwendener Str. 8, 1000 Berlin 33, Deutschland.

level fall. Equivalents of the event marker horizon occur in a vast area from North America (e.g. parts of the Exshaw Shale, ?Conchostracan Shale in the Pilot Shale, Leatham Formation; Bakken Formation and Sappington Member of the Three Fork Formation; see Gutschick & Rodriguez, 1977) to the Montagne Noire (Southern France; Feist & Flajs, 1987), Eastern Iran (Walliser, 1984), Southern China (e.g. Hou *et al.*, 1985) and perhaps Australia.

The significance of the terminal Devonian ammonoid extinction is well illustrated in the diversity analysis of Kullmann (1983) and Korn (1986) or in the compilations of generic ranges in Price & House (1984) and House (1985). House (1981) and Teichert (1986) already emphasized that the Hangenberg extinction event is in the scale of the Upper Kellwasser Event at the Frasnian-Famennian boundary and comparable to the end-Permian, end-Triassic and Cretaceous-Tertiary boundary events. According to present knowledge only two imitoceratid lineages ("*Imitoceras*" *lineare* group and *Mimimitoceras*) occur both in strata of the *Wocklumeria* and *Gattendorfia* Limestones. *Cymaclymenia* survived the main extinction only for a very brief period (Korn, 1989). The claimed survival of *Epitornoceras* in Teichert (1986) is based on an erroneous quotation of an oxyconic tornoceratid genus that occurs in the early Famennian (not early Carboniferous) of Novaya Zemlya and that is homoeomorphic to the true late Givetian *Epitornoceras*.

The faunal change between the Lower and Middle Tournaisian (of classical Belgian definition) or between the Lower and Upper Hastarian has attracted less attention so far although the major break and gap between faunas of the *Gattendorfia*- and *Pericyclus*-*Stufen* in Europe was already realized by Matthews (1970). Indeed there is not a single section or succession described in the world with a continuous goniatite record crossing the Lower/Middle Tournaisian boundary. An intriguing range chart of all Tournaisian goniatite genera that needs updating was published by Weyer (1972a), who also emphasized the lack of any ammonoid zonation in the Middle and early Upper Tournaisian (Upper Hastarian and Lower Ivorian). He predicted the future insertion of several zones between the European cu I and the cu IIa. North American authors gave more and more evidence that faunas with co-occurrences of *Gattendorfia* and relatives, *Muensteroceras* and early pericyclids fill the gap (e.g. Manger, 1979; Gordon, 1986). The globally best succession is obviously developed in Missouri and some other neighbouring states, where the entry of *Eoprodromites* and *Per.*

(*Goniocyclus*), *Prodromites* and *Protocanites* and muensteroceratids (*medium*; *pfefferae/esbaughi* or preferably *oweni/parallelum*) could serve for the introduction of a zonal scheme. Kullmann *et al.* (1991) recently separated similarly Middle Tournaisian faunas with *Per.* (*Goniocyclus*) and *Protocanites* from early Upper Tournaisian *Muensteroceras*-*Pericyclus* assemblages. Their genozone-concept could be further developed.

In Europe (e.g. Rhenish Slate Mountains, Thuringia, Moravia, Poland, Montagne Noire, SW England) the disappearance of goniatite faunas at the end of the *Gattendorfia*-*Stufe* (cu I) is linked with the transgressive black Lower Alum Shale of the *Siphonodella crenulata* Zone that terminated cephalopod limestone formation and finally drowned Schwellen areas such as extinct Frasnian reef structures (e.g. Stritzke, 1990). A contemporaneous major sea-level rise is reported in North America (Event 15 of Sandberg *et al.*, 1983) and obviously also changed fundamentally the facies configuration in Asia and China (*crenulata*-transgression e.g. reported in Guangxi; Bai & Ning, 1989). The term **Lower Alum Shale Event** is introduced for the regionally varying and short-termed sedimentary and palaeoceanographic perturbations that led to the global disruption of pelagic biota. Its significance for nearshore benthic communities still has to be elucidated. Kalvoda (1989) observed a foraminiferan radiation associated with the global eustatic rise and in South China there is a significant negative shift of $\delta^{13}\text{C}_{\text{org}}$ at the base of the *crenulata* Zone (base of the Muhua Formation/Guizhou; Xu *et al.*, 1989). In condensed Schwellen sections such as Drewer (Warstein area/Rhenish Slate Mountains; Clausen *et al.*, 1989) the Hangenberg and Lower Alum Shale may be remarkably similar pointing to similar palaeoceanographic conditions. The sedimentary event is associated with a medium-scale extinction among goniatites. More than 50 % (7) of genus-level taxa of the latest *Gattendorfia*-*Stufe* (*patens* Subzone) do not range into the Middle Tournaisian. Two of these victim groups (N. Gen. I aff. *Karagandoceras* Bartsch & Weyer, 1988 and *Qiannanites*), however, represent low diversity lineages that have post-event descendants (*Karagandoceras*, *Eoprodromites*) and they are therefore cases of pseudo-extinction, at least at the genus-level.

The condensed time-resolution used in diversity analysis of longer periods by Kullmann (1983) or House (1989a) did not allow the recognition of the Lower Alum Shale extinction but it was briefly noted by Becker (1990).

1.2.- AMMONOID PALAEOBIOGEOGRAPHY

Palaeobiogeographical aspects of Devonian and Lower Carboniferous ammonoids have neither been the matter of hot debate nor have they been the subject of extensive publication. This comes as little surprise since the open marine pelagic life-style of the group would always have allowed fast and cosmopolitic distribution of most taxa. It has been long known that Paleozoic ammonoids are confined both to tropical/subtropical warm-water areas and to moderately deep epicontinental seas rather than true bathyal facies. Patterns of distribution therefore may reveal information about climatic factors and barriers formed by either oceanic deep-sea basins or too shallow neritic marine seaways. Additionally the overall distribution of pelagic ammonoid biofacies reflects stages in the developments of regional sedimentary basins or of global eustatic conditions. The global faunal structure (degrees of endemism, cosmopolitism and taxonomic dispersal) mirrors the general rate of faunal exchange.

Upper Devonian ammonoid palaeobiogeography was studied by House in a series of papers (1964, 1973a,b, 1981) and he established three main links of faunal migration and exchange: **Trans-Arctic**, **Afro-Appalachian** and **Prototethys**. The North African-European-Urals realm was identified as the major evolutionary centre. The Lower Carboniferous goniatite distribution was summarized by Hodson & Ramsbottom (1973) and some aspects concerning the Tournaisian were recently discussed again by Gordon (1986). Of special importance is the supposed diachroneity of faunas with *Gattendorfia* in Europe and North America that was explained by a migration of the genus with time. Such a behaviour would fundamentally conflict with the usual fast spreading pattern of abundant and wide-spread goniatite groups that makes them so extraordinary suitable tools for high-resolution biostratigraphy and interbasinal correlation.

Since the compilation of House (1973) and Hodson & Ramsbottom (1973) much progress has been made on taxonomy and the exact dating of classical ammonoid bearing beds. Many additional records, often hidden in local journals or conference field guides, have been added from various regions of the world. The aim of the present paper is to review all these data and to provide an overview of the distribution of genus-level taxa in all known areas with latest Famennian to early Upper Tournaisian records. Emphasize is laid on developments in time and an attempt is made to elucidate the influence of the Hangenberg and Lower Alum Shale Events on the global distribution pattern and overall assemblage

structures. Observed palaeobiogeographical trends again allow conclusions about the nature of the events themselves.

2.- METHODS

The principle methods used are an intensive literature survey and consequent taxonomic revisions. Material from the Rhenish Slate Mountains and unpublished collections from South Devon, the Montagne Noire, Maider (South Marocco), Canadian Rocky Mountains and Chile (material given to M.R. House) prevent a too theoretical approach to the subject and add to the known records. Descriptions of these faunas are planned for the future. Sixty sedimentary areas have been separated that are either isolated occurrences (e.g. Tibet, Eastern Australia) or part of larger basins (Variscan Geosyncline, Ural, South China) and intra- to epicratonic provinces (North American interior, North Africa).

Five biostratigraphic intervals have been distinguished (tab. 1-4): the Wocklumian (do VI), the Hangenberg Event interval (level of Hangenberg shale and Stockum Limestone = *evoluta* and *prorsum* Zones), the *Gattendorfia*-Stufe (cu l s.str.), the Middle Tournaisian (Upper Hastarian, late Kinderhookian) and Upper Tournaisian (Lower Ivorian, early Osagean; only pre-*anchoralis* records = level 5 of Kullmann *et al*, 1991). Although there are more refined zonations available their use for the present study is very limited because of their so far restricted global recognition, especially in epicontinental low-diversity assemblages.

The compilation not only lists well established genera but also subgenera and species-groups that require future taxonomic distinction on the genus-level. New taxonomic concepts are outlined in section 5, but the introduction of genera will be left for future description and revision of material. Many records were not accompanied by adequate description or illustrations. For the purpose of this study correct identifications are presumed, but future revisions well may change some former generic assignments. The potential confusion of closely related taxa such as subgenera within *Kosmoclymenia* or certain Gonio-clymeniidae, however, could only slightly alter the total number of taxa within one area. The great majority of ammonoid genera has been rarely confused by authors.

The global record is transformed into simple numerical parameters (tab. 5) that allow an analysis of the overall faunal structure. The total and relative amount of highly (more than 50 % of all genera of

the time interval) or moderately (more than 33 % of all genera) diverse faunas is used to recognize evolutionary centres and the degree of faunal dispersal. Endemism and cosmopolitanism are measured by the total and relative amount of genera with representation in more than 50 %, more than 33 % and in only about 10 % of all regions. Genera/subgenera with endemic distribution (e.g. rare occurrence in two widely separated areas), however, have to be distinguished from true endemics which may occur commonly in restricted provinces.

3.- DATA SETS

The data sets are given in table 1 to 4. As outlined by Hodson & Ramsbottom (1973) the compilation of course will never be complete. It is assumed that each of the time interval is equally investigated and therefore observed trends should not be too much affected by the still unsatisfying knowledge of faunas from isolated regions such as North Africa, parts of Russia and Siberia, South America and Northern China. The fact that only few completely new and rich assemblages have been discovered in the last decades illustrates the acceptable quality of the database for general interpretation. Sparse records from insufficiently investigated regions, however, are still currently being added. Surprisingly newly discovered localities rarely yielded new genera (with the exception of *Eoprodromites*) and the most abundant and cosmopolitan forms tend to be found at more and more sampling spots. An increase of knowledge rather can be expected from Southern China, Ireland, Algeria and the Carnic Alps, where the potential of moderately rich assemblages has not been fully exploited yet.

The recognized regions abbreviated in table 1 to 5 are as follows (in approximative geographical order following migration routes from west to east) : Chi = Chile, Nme = New Mexico, Nev = Nevada, Ut = Utah, Id = Idaho, Alb = Alberta, Mon = Montana, NDa = North Dakota, Io = Iowa, Ark = Arkansas, Mis = Missouri, Ill = Illinois, Ten = Tennessee, Ken = Kentucky, Ind = Indiana, Mig = Michigan, Oh = Ohio, Vir = Virginia, Dra = Dra Valley/South Morocco, Moy = Mouydir/S. Algeria, Ahn = Ahnet/S. Algeria, Lib = Libya, Gou = Gourara/Algeria, Sao = Saoura Valley/S. Algeria, Mai = Maider/S. Morocco, Taf = Tafilalt/S. Morocco, Mes = Moroccan Meseta, Por = Portugal, Can = Cantabrian Mountains/Northern Spain, MN = Montagne Noire/S. France, BIF = Black Forest/SW Germany, ArM = Armorican Massif, Ire = S. Ireland, Cor = Cornwall, Ard = Ardenne/Belgium and N. France, RhS = Rhenish Slate Mountains, Thu = Thuringia and Fichtel Mountains, Sil = Silesia/Poland, Car = Carpathian Foreland, Mor = Moravia/CSFR, Alp = Carnic Alps, Lub = Lublin Basin/Poland, HCM = Holy Cross Mountains, RP = Russian Platform, Tim = Timan/N. Russia, Koz = Kozhim/Arctic Ural, Ur = Ural and Mugodzhur Mountains, Dn = Dniepr-Donetz depression, Kau = Caucasus, Kaz = Kazakhstan, MA = Middle Asia, Tib = Tibet (Xingzang), Xin = Xinjiang/NW China, Gan = Gansu/N. China, Kol = Kolyma Basin/NE Siberia, Gua = Guangxi/S. China, Gui = Guizhou/S. China, CB = Canning Basin/NW Australia, Que = Queensland.

3.2.- COMMENTS ON INDIVIDUAL RECORDS

Faunas of the Wocklum-Stufe are easy to identify because of the dominance of marker genera such as *Kalloclymenia*, *Parawocklumeria* and *Wocklumeria*. Faunas with non-diagnostic forms (e.g. *Cymaclymenia*, *Cyrtoclymenia*, *Kosmoclymenia*) can be ascribed to the do VI with the help of conodont stratigraphy; the base of the Wocklumian coincided with the base of the former *M. costatus* Zone (Korn & Luppold, 1987). Isolated occurrences of *Cyrtoclymenia* in North America (New Mexico : House, 1962; Ohio : together with *Cymaclymenia* and "*Imitoceras*" : House, 1962; Alaska : Sable & Dutro, 1961) were referred either to the do IV, V or do VI (House, 1962, 1964). A specimen from Utah (Peterson & Stokes, 1983) came from the *styriacus* Zone (upper do IV to lower do V). All records mentioned above are probably earlier than do VI and are omitted from table 1.

Beside undoubted faunas of the event interval there are North American imitoceratid records in the Middle Pilot Shale, Leatham Formation, Sappington Member of the Trident Formation and Bakken Formation of Utah, Montana, SE Nevada and the North Dakota subsurface (House, 1965; Johnson & Reso, 1966; Gutschick & Rodriguez, 1979; Thrasher, 1987). Following a lag sandstone marking a significant regional unconformity, goniatites occur in a conchostracan shale marker horizon and an overlying widespread oncolithic alga-brachiopod biostromal limestone (Gutschick & Rodriguez, 1979). From the viewpoint of event- and sequence-stratigraphy it is tempting to correlate the conchostracan shale with the lower part of the Hangenberg Shale of Germany and the Montagne Noire (Southern France), which yielded "posidoniids" that display conchostracan-type shell-structures (Flajs & Feist, 1988). Similar forms also have been reported from the Changshun Shale (Bai & Ning, 1989) of South China (e.g. Muhua section). The oncolithic limestone with rich neritic fauna could be correlated with the oolites within the Hangenberg Shale of the Montagne Noire (La Serre Stratotype; Flajs & Feist, 1989). Oolites of similar stratigraphic position seem to be much more widely distributed : e.g. topmost Etroeungt (probably upper part of *M. praesulcata* Zone) of the Bergisches Land (Michels, 1986); basal Hastiere Limestone (probably *U. praesulcata* Zone) of Belgium (van Steenwinkel, 1984).

Such a correlation conflicts with published interpretations of conodont faunas. Sandberg *et al.* (1989) assign both the conchostracan shale and the lower part of the algal-brachiopod biostromal limestone to the *M. costatus* (*U. expansa* Zone). The upper part of the latter unit yielded the first specimens of *Siphonodella praesulcata* in Montana and Utah (Sandberg *et al.*, 1972) and these records were used to draw the *expansa*/

Table 3.- Global distribution of Middle Tournaisian (lower cu II) genus-level goniatite taxa

	NMe	Nev	Ut	Id	Alb	Mon	Io	Mis	■	Ind	Taf	Por	BLF	Thu	Kaz	Xin	Gan	Que
Imitoceras s. str.		?				x	x	x										
"Im." lineare gp.															?			
"Acut." prorsum gp.					x		x	x			x				x			
"Acut." multiulcatum gp.															x			
Gattendorfia	x	?	x			x	x	x		x	x				x	x		
Zadelsdorfia								x				x		?	x			
Kazakhstania				x											x	x	?	
Paralytoceras																		x
prodromitid gen. indet. SCHDW.					x													
Eoprodromites								x										
Prodromites							x	x	x	x								
Karagandoceras								?							x			
Intoceras								x										
"Muensteroceras"								x										
Protocanites		x	?	?				x			x	x	x	?		x		
"Proto." guryei gp.					x			x						?	?			x
Per. (Gonicyclus)	x	x	x	x		x		x			?	x				?		
Roto. (Rotopericyclus)		x		x														
Roto. (Hammatocyclus)			x			x												

Table 4.- Global distribution of Upper Tournaisian (pre-anchoralis time) genus-level goniatite taxa

	Nev	Ark	Mis	Ill	Ten	Ken	Ind	Mic	Oh	Vir	Dra	Moy	Ahn	Lib	Gou	Sao	Can	Ire	Dev	Cor	Ard	Thu	RP	Ur	Kaz	MA	CB	NSW
Imitoceras s.str.					x	x	x	x	x	x	x	x	x		x	x		x			x		x	?		?	x	x
"Im." lineare gp.		x																										
"Acut." werriense gp.		?																										x
Kazakhstania		x				x		x	x									x		x								
Zadelsdorfia								x	x													?		x		x		
Gen. II aff. Karagandoceras						x		x																				x
Protocanites	x	x			x	x	x	x	x	x	x		x		x				?		x	?		x		x		x
"Proto." gur'eyi gp.						x																						x
Acrocanites													x		x						x	x						
Prodromites							x																					
Muensteroceras		x	x	x		x	x	x	x	x		x	x	x	x	x	x			x	x			x		x		x
Eurites												x	x		x									x				
"Winchelloceras"							x																					
Intoceras																												
Per. (Pericyclus)		x													x				x	x	x	x	x	x	x			
Per. asiaticus gp.																				x	x							
Roto. (Rotopericyclus)												x	x									x		?		x		
Roto. (Hammatocyclus)																					x							
Gen. nov. A Matthews																				x								
Gen. nov. B Matthews																				x								

praesulcata Zone boundary within it (Sandberg *et al.*, 1989) suggesting time-equivalence with the European Wocklum Limestone. But *Protognathodus meischneri*, an index conodont of the middle to upper part of the Wocklum Limestone (Kürschner *et al.*, this volume), was already found in the lag sandstone below the conchostracan shale in the Middle Pilot Shale (Bactrian Mountains/Nevada; Sandberg *et al.*, 1972). *Protogn. meischneri* was also reported from bioclastic limestones of Unit 4 of the Leatham Formation in Utah preceding the oncolithic limestone, but the whole faunal association (Sandberg *et al.*, 1972) includes species of *Palmatolepis* (subspecies of *Pa. rugosa*) which normally do not range into the level of *Protogn. meischneri* in the Rhenish Slate Mountains. More precise documentation of conodont faunas is required to resolve current contradictions. German sections show that subtle changes in biofacies can result in the absence of *Siph. praesulcata* in sediments of *praesulcata* Zone age (e.g. Clausen *et al.*, 1989). It has to be considered whether this also could explain

the lack of *Siph. praesulcata* below the conchostracan shale (Nevada) or in limestone immediately above (Utah, Unit 4).

The imitoceratic findings are tentatively listed as event interval records. Johnson & Sandberg (1989) similarly correlated the algal-brachiopod biostromal limestone with the major terminal Devonian eustatic fall, which forms the upper part of the Hangenberg Event.

Black shales at the top of the Cleveland Shale in Ohio yielded pyritic faunas with *Cymaclymenia* and *Sporadoceras* (House *et al.*, 1986). This level perhaps

Table 5.- Simple numerical analysis of latest Devonian-Tournaisian ammonoid diversity and distribution indicating degrees of endemism, kosmopolitism and fauna dispersal

Table 5	regions total number	"genera" total number	regions with			distribution of "genera" in			
			> 50 % off all "genera"	> 33 %	ca. 10 %	> 50 %	> 33 %	ca. 10 %	
WOCKLUMIAN (percent)	28	33	5 18	8 29	12 43	3 9	9 26	10 29	
L. TOURNAISIAN (percent)	19	22	4 21	5 26	7 37	2 9	4 18	8 36	
M. TOURNAISIAN (percent)	18	19	1 5	2 11	7 37	1 5	3 16	10 53	
U. TOURNAISIAN (percent)	26	20	0 0	3 12	9 35	3 15	4 20	9 45	
interpretation			diversity centres				kosmop.		endemic

corresponds to the basal black shale (Wocklum Shale) of the German Hangenberg Shale. Miospore dating of the subsequent regressive Bedford Shale (LN Zone) are in agreement with such a correlation. This allows speculations about the representation of the global Hangenberg Event in eastern North America.

Earliest Middle Tournaisian ammonoid faunas globally seem to be exceedingly rare. The richest fauna is from the *cassini* Beds of Kazakhstan (Librovitch, 1940). Other sparse records are only from Queensland (revised in Campbell *et al.*, 1982), the Hannibal Shale of Missouri (Work *et al.*, 1988), perhaps from the Prospect Hill Sandstone of Iowa (Anderson, 1969 : *Siph. quadruplicata* is associated; Furnish & Manger, 1973) and from the Tafilaht of South Morocco (Hollard, 1970). From siltstones of the Exshaw Shale in Alberta Schindewolf (1959) described a fauna with "*Protocanites*" cf. *gurleyi*, Gen. aff. *Prodromites* and "*Acut.*" cf. *discoideale* that can only be assigned to the earliest Middle Tournaisian. McQueen & Sandberg (1970) reported *Siphonodella duplicata* that is most abundant in the cu I but that ranges up into the *Sulcata* Zone. The ammonoids suggest that the siltstone fauna is younger than those of the uppermost part of the black shale member of the Exshaw Shale at the type locality in Jura Creek, which has *Siph. cooperi* (McQueen & Sandberg, 1970) and flattened imitoceratids.

According to Gordon (1986) faunas with true *Muensteroceras* (especially *oweni* or *parallelum*) already fall into the early Upper Tournaisian (Osaegan). This is relevant for example for the Ohio fauna

with Gen. nov. II aff. *Karagandoceras bradfordi* (Manger, 1971). For a long time there have been arguments about the precise age of the Zadelisdorf fauna from Thuringia (Schindewolf, 1922, 1939). The assemblage from the "Geodenhorizont" contains species of Middle - early Upper Tournaisian (*Zadelsdorfia aperta*, *Protocanites quadratus*), Upper Tournaisian (*Acrocrites multilobatus*, *Pericyclus dilatatus*) and Lower Visean age (*Bollandites euryomphalus*, "*Goniatites*" *angustilobatus*). Under- and overlying beds leave this timespan open for the Rußschiefer Formation (Weyer, 1972b) that may have had ammonoids at different levels. *Stenocyclus carinatus* and *Caenocyclus perisphinctoides* seem to represent advanced and younger pericyclids, which are younger than the lower Ivorian. Both genera therefore are not included in table 4.

4.- TRENDS IN GLOBAL LATEST DEVONIAN-TOURNAISIAN AMMONOID DISTRIBUTION

4.1.- GENERAL OBSERVATIONS

Each individual record of hemipelagic to pelagic ammonoid facies in epicontinental areas can be taken as a signal of relative regional sea-level highstand and could serve as indicator for the degree of global cratonic overflowing. In geosynclinal basins, by contrast, transgression introduces quieter hydrodynamic conditions that allows the settling of the fine clay suspension. Consequently poorly fossiliferous basinal calcareous shales cover cephalopod limestones of local intrabasinal highs. Transgression

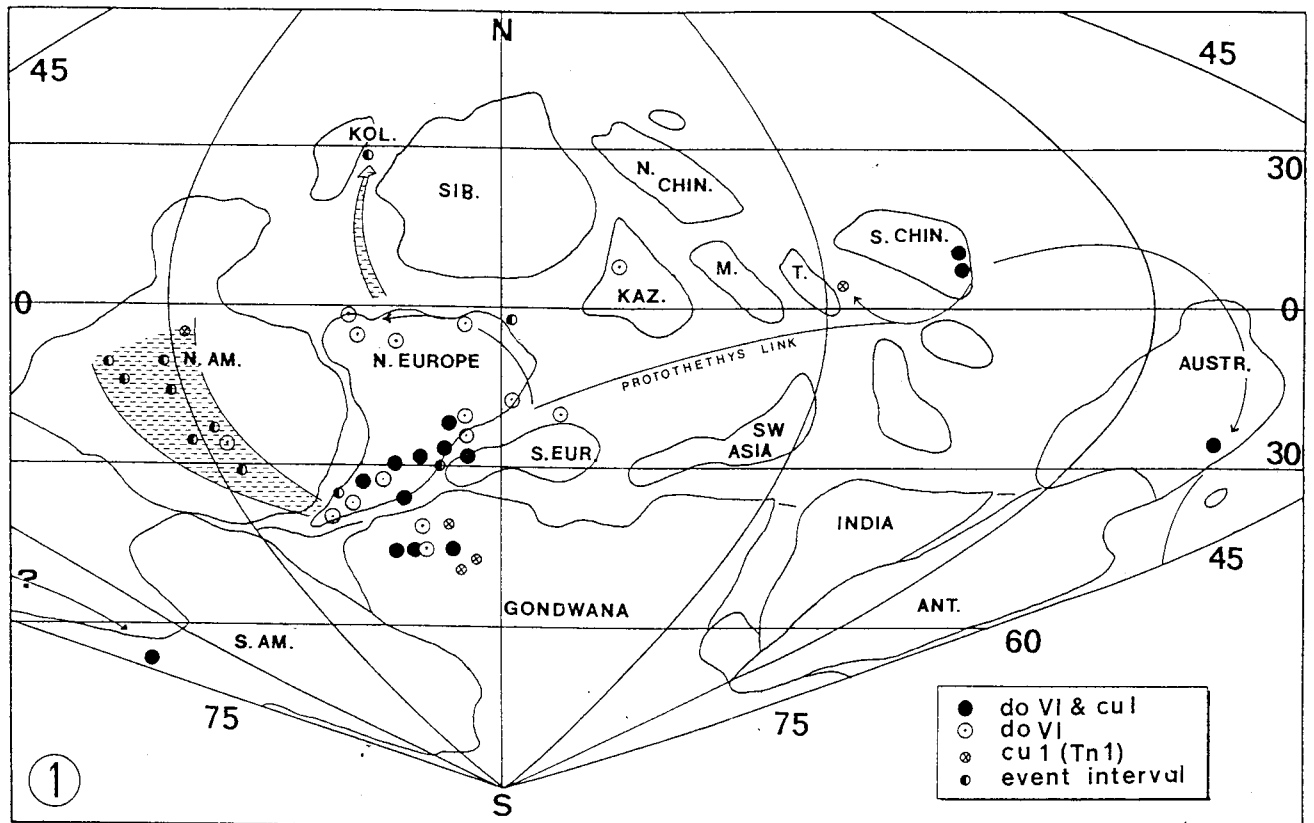


Fig. 1.- Palaeobiogeography of latest Devonian (do VI) to earliest Carboniferous (cu I, Tn 1B) ammonoids using the relevant part of the plate tectonic reconstruction of Heckel & Witzke (1979). Major routes of faunal migration and the event-related short-timed spreading of ammonoid biofacies are marked. [M. = Mongolia, T. = Tibet-West China plate, Ant = Antarctica, N.Am. = North America, Kol. = Kolyma River plate/NE Siberia, Kaz. = Kazakhstan].

therefore increases the number of pericratonic ammonoids regions and reduces basinal occurrences. The larger size of shallow marine continent margins still should normally cause an outnumbering of the basinal losses by epicontinental gains.

If this model is accepted one could deduce maximum sea-level highstands for the Wocklumian (27 areas), underlining the importance of the Strunian transgression, and later for the early Upper Tournaisian (26 areas), reflecting the global transgression of the *typicus* (or *cuneiformis*) Zone (Kalvoda, 1989). The drowning of more or less all Variscan basinal goniatite localities obviously prevents the recognition of the *crenulata* transgression in the number of ammonoid regions. The close relationships between eustasy and ammonoid diversity has been well established; transgression leads to diversification (House, 1989a) pointing to an important role for the "species-area-effect" (House, 1989b). Normally increasing ammonoid distribution thus should be parallel by increasing diversity and in the latest Devonian this seems to be the case (table 6; Korn, 1986 : fig. 2).

4.2.- DEVELOPMENTS IN TIME AND EVENT INFLUENCES

4.2.1.- Wocklumian (do VI)

The global distribution of do VI faunas follows the principle pattern described by House (1973a) but there are some further unnamed branches to areas with low-diversity faunas only (fig. 1). The poorly known Chile records cannot be connected with the Appalachian realm because the latter has no contemporaneous ammonoid facies. While similarities of late Givetian tornoceratids suggest an Appalachian-South American link the origin of the younger Andean fauna is still enigmatic. One should consider migration from the eastern Protothethys part via the "Protopacific" margin. Another problem is the palaeolatitude of Northern Chile in the timespan around the D-C-boundary. Most global palaeogeographic reconstructions (e.g. Heckel & Witzke, 1979; Scotese, 1986) would set the area into an almost south polar position and this is faunally obviously impossible. Terrane ("Chilenia") accretion (discussion summarized in Barrett & Isaacson, 1989) could offer an explanation.

The Afro-Appalachian and Trans-Arctic links were mostly out of function due to unsuitable facies in North America. The northward migrating faunas of the Ural Geosyncline reached only the Timan (Durkina & Avkimovitch, 1988) and Kozhim. New South Wales cannot be regarded as part of a continuous Protothetys route. The main and central part of Australia was not overflowed in Upper Devonian times and middle Famennian faunas of the Canning Basin and New South Wales are dissimilar. In late Famennian times ammonoids are completely lacking in NW Australia and therefore there is no intermediate link between southern China and the New South Wales occurrence of *Cymaclymenia*.

Faunas have a high degree of cosmopolitanism. Only about a quarter of all genus-level taxa have an endemic distribution (known from less than 10 % of all = max. two areas). There are six regions with high diversity (five with diversity >50 % of all taxa) : the Rhenish Slate Mountains, Thuringia, Silesia, Holy Cross Mountains, SW England and South China (especially Guizhou). In future the Carnic Alps may have to be added. Cosmopolitan genera are the "*Im.*" *lineare* group, *Cyrtoclymenia*, *Cymaclymenia* and to a lesser extent *Wocklumeria*, *Kalloclymenia* and *Kosmoclymenia*. Only *Kielcenisa* of Poland seems to be a true endemic form. *Triaclymenia* (Germany-Poland) and *Synwocklumeria* (Ural-Kaukasus) are moderately restricted in their distribution. There are some relict forms such as *Sellaclymenia*, the *Cyrtoclymenia stuckenbergi* group and last representatives of the Tornoceratidae. Records of *Protoxy-clymenia* and *Falcicyclomenia* in the do VI of the Holy Cross Mountains (Czarnocki, 1989) need further substantiation. The same applies to claimed occurrences of *Pachyclymenia* and *Progonioclymenia* in the Wocklum Stufe of South China (Yuan, 1988).

4.2.2.- Hangenberg Event-Interval

The event-interval is marked by a strange very short-timed spread of ammonoid biofacies into formerly uninhabited areas such as Moravia (Kalvoda & Kukal, 1987), S Ireland (Matthews, 1983) and North America (Ohio, Missouri, Illinois; probably also Montana, Nevada and Utah - see discussion above). Migration via the Afro-Appalachian link is probable. South of the Urals the Berchogur section of the Mugodzhur Mountains (Barskov *et al.*, 1984) is remarkable, because the same area otherwise has only a superb Hembergian fauna. A single unidentified ammonoid was even reported from the U. *praesulcata* Zone of the Kolyma region of NE Siberia (Gagiev & Kononova, 1990). The altered distribution pattern expresses the rapid and multiphase sea-level

changes leading to facies movements and opening new migration routes within the event-interval. The initial and hypoxic transgressive pulse of the "Wocklum Shale" is shortly followed by the major terminal Devonian eustatic fall that either caused hiatuses and paraconformities or the spreading of sandstone wedges and shallow-water carbonates. The significance of the Devonian-Carboniferous **sequence boundary** was emphasized by van Steenwinkel (1988). Pyritic faunas of the latest *praesulcata* Zone point to persisting low-oxygen conditions despite the shallowing and goniatites became part of mixed hemipelagic assemblages similar as in the upper part of the Upper Kellwasser Limestone at the Frasnian-Famennian boundary (Becker *et al.*, 1989). The opportunistic spread of *Protognathodus* in an important parallel to be icriodid-boom of the latest Frasnian (Sandberg *et al.*, 1988).

The only important and cosmopolitan goniatite "genus" of the event interval is the "*Acut.*" *prorsum* group. Relict genera are *Cymaclymenia* and perhaps *Sporadoceras* in the Bedford Shale of Ohio (House *et al.*, 1986). *Mimimitoceras* is a surviving "Lazarus-Taxon".

4.2.3.- Lower Tournaisian (cu I)

The long-term influence of the Hangenberg Event on the global ammonoid distribution is rather insignificant (fig. 1). More than 50 % of all regions have both good representation of the do VI and cu I. The event is judged as a relative brief period of sedimentary and faunal disruption but not as a major lasting turnover of global marine biosphere conditions. The onset of the early Carboniferous adaptive radiation did not fill the gaps left by the Hangenberg extinctions. Total ammonoid diversity of the whole cu I is a third below the do VI. Diversity centres, however, are the same as in the latest Devonian : Rhenish Slate Mountains, Thuringia, Silesia, Guizhou. Cosmopolitan genera are the "*Acut.*" *prorsum* group, *Gattendorfia* and to a slightly lesser degree *Eocanites*. Endemics according to current knowledge are *Qiannanites*, *Gattenpleura* and the *Imitoceras folliforme* group of South China. A strange feature is the complete lack of Soviet *Gattendorfia*-Stufen faunas. Two faunas are somewhat enigmatic. The Exshaw Shale fauna remains isolated because there are neither faunas from the Urals suggesting viability of the Trans-Arctic link nor are there faunas from the middle or eastern part of North America as proof for westward immigration. Similarities of constricted imitoceratids in the Exshaw and Bedford Shales suggest the survival of a part of the North American event-interval population and retraction to the

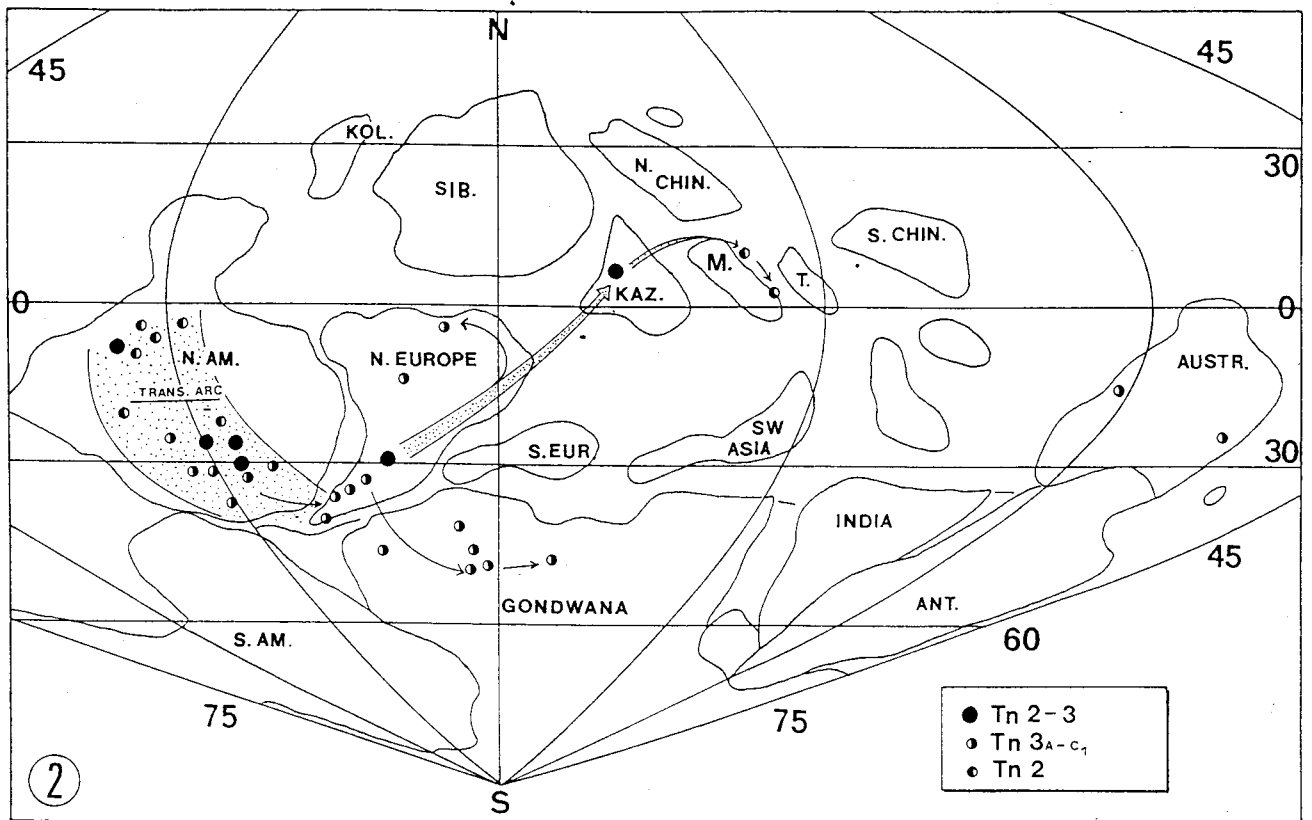


Fig. 2.- Middle to Upper Tournaisian (only pre-*anchoralis* records) ammonoid palaeobiogeography illustrating the major shift towards North America and Kazakhstan/NW China. The Upper Tournaisian return to Middle Europe, North Africa and the Ural is marked by small arrows. Australian faunas are isolated. Details of North American palaeobiogeography (e.g. significance of the transcontinental arc) see Gordon (1965).

Cordilleran refuge area. From South China there must have been a viable seaway around the SW periphery of the Yangtze craton to allow the occupation of the Tibet Trough (Liang, 1976; palaeogeography after Wang, 1987).

4.2.4.- Middle Tournaisian (early cu II)

The Lower Alum shale Event caused a fundamental and lasting shift of ammonoid distribution linked with the *crenulata* transgression and the drowning of the Variscan habitats. This, and not the Hangenberg Event (as assumed by Walliser, 1984), is the early Carboniferous palaeogeographical turning point of first order (Krebs, 1969). The associated discontinuity of ammonoid biostratigraphy is long known (e.g. discussion in Matthews, 1969). There are only three regions (13.5 %) known in the world with both Lower and Middle Tournaisian goniatites (Alberta, Black Forest/Germany, Thuringia) and many of these records are somewhat dubious. Despite the increase of data and discovery of new localities no continuous ammonoid sequence has been found anywhere. The evolutionary centre of N-Africa-

Europe-Ural divided and moved west- and eastwards (fig. 2). There are now only two new diversity centres : Missouri and to a lesser extent Kazakhstan. the more complicated palaeogeography of epicontinental areas is perhaps responsible for a significant increase of faunal dispersal. Only three regions (17 % of all) have moderately diverse (with more than 33 % of all genera) assemblages and only *Gattendorfia* is cosmopolitan, followed by *Protocanites* and *Per. (Goniocyclus)*. True endemics are the prodromitids of North America and the early *Intoceras osagense* of Missouri. *Paralytoceras* is a very rare relict genus in Queensland. The "prodromitid province" of North America is a strange feature because *Qiannanites* as the probable ancestor occurs only endemically in South China. Migration through a "Protopacific route" can be ruled out, because it is the area east of the transcontinental arc that has the prodromitid faunas (for North American palaeobiogeography see Gordon, 1986). With overlap in Missouri the western part of the United States can be characterized as an "early pericyclid province".

The claimed diachroneity of *Gattendorfia*-faunas (Hodson & Ramsbottom, 1973) expresses only the

fundamental global shift of the ammonoid biofacies distribution. Gordon (1986) still wondered about the absence of gattendorfiid-pericyclid associations outside North America. However they have been reported since from South Portugal (Oliveira *et al.*, 1985; Bordaleta Formation with *Protocanites*, *Zadelsdorfia* and *Per. (Goniocyclus) cf. blairi*) and Xinjiang (Zhang 1987; Liang & Wang, 1988; Lower Member of the Donggulubastau Formation with *Gattendorfia*, *Kazakhstania*, *Protocanites* and *Pericyclus* sp.). There is also an earlier record of a Tafilalt fauna with "*Acut.*" *subbilobatum*, *Gattendorfia*, *Protocanites* n. sp. aff. *algarbiensis* and *Pericyclus* gp. *princeps* (Hollard, 1970). The fauna of the Xinjiang-Mongolian Sea (Xinjiang and Gansu provinces; Liang & Wang, 1988; Liang, 1987) may have migrated from Kazakhstan along a route north of the platform and islands of West China (palaeogeography after Wang, 1987). With rising sea-level alternatively the crossing of the shallow area NW of the Tibet Trough may have been possible, but so far there are no Middle Tournaisian Tibet records.

4.2.5.- Upper Tournaisian (middle cu II)

In the early Upper Tournaisian endemism and faunal dispersal continued. There is no obvious centre of diversity although faunas are very widely distributed. The early Osagean is best represented in Ohio, Arkansas and Michigan. The famous lower Ivorian faunas of the Ardenne (Tn 3a-c = Cf2 = *Polygnathus comunis carina* Zone) may range slightly younger. Most associations are dominated by the cosmopolitan genera *Muensteroceras*, *Imitoceras* and *Protocanites*. *Eurites*, *Hammatocyclus*, Gen. nov. A and B Matthews and "*Winchelloceras*" sensu Gordon & Mason (1985) have endemic distribution. Restricted "relict genera" are late representatives of the "*Im.*" *lineare* group, the *Proto. gurleyi* group and *Prodromites* (Osagean range fide Manger, 1979). At present *Intoceras* is a "Lazarus-Taxon". In North America pericyclids are very rare and a *Kazakhstania-Karagandoceras* province could be distinguished from the pericyclid province of N-Africa-Europe-Russia. A mixed fauna with *Kazakhstania* occurs in SW England (Matthews, 1970).

In about a third of all regions there is a continuous record across the Middle/Upper Tournaisian boundary. The recognized global regression (Kalvoda, 1989) separating Kinderhookian and Osagean or Hastarian and Ivorian did not have a significant influence on ammonoid evolution. In China Ji (1987) reported a paraconformity associated with the

disappearance of *Siphonodella* conodont faunas and called it the "Mid-Aikuanian Event". Only the final extinction of *Gattendorfia* is remarkable, but *Zadelsdorfia* and *Kazakhstania* survived for some while. The re-settling of the N-Africa-Europe-Ural realm is more important. With the overflowing of northern Gondwana, ammonoids, for example, even reached parts of Libya (Conrad *et al.*, 1986).

The Middle and early Upper Tournaisian transgressions are curiously not paralleled by an expected increase of diversity. Cephalopod limestones of intrabasinal highs normally have the most diverse assemblages and the Middle Tournaisian drowning of these habitats not only accounts for the stagnation of the number of regions with ammonoid record despite sea-level highstand, but perhaps also explains the low total diversity. Similar eustatic rises in the Upper Devonian (e.g. *Annulata* Event) however do not show similar trends. The absence of a diversity gain in the early Upper Tournaisian is even more strange because the faunal distribution approaches almost the level of the latest Devonian. The durations of the lower half of the Ivorian and both halves of the Hastarian probably did not differ fundamentally and shortage of time for speciation cannot be assumed. The diversion of distribution and diversity therefore perhaps reflects non-palaeogeographic parameters delimiting ammonoid evolution.

The supposed Upper Devonian southern hemisphere glaciation (Caputo, 1985) now has been dated as terminal Devonian (about equivalent to the Hangenberg Event interval; Streel, 1992). This is in agreement with palaeotemperature measurements using oxygen isotope data (Brand, 1989), the lack of any gradient in latest Devonian Miospore-distribution (*lepidophytus*-floras; Streel, 1986) and middle Famennian warm-water sporocerotid occurrences in Bolivia (Babin *et al.*, 1991). Hünicken (1990) even suggested relationships between the disappearance of the Malvinokaffric cold-water province and the spreading of warm-water conodonts in the Upper Devonian of South America. According to Streel (1986) most glaciogenic sediments of South America fall in the Middle Tournaisian to Visean. This agrees well with Lower Visean tillites recently reported from Niger (Lang *et al.*, 1991). Playford (1991) drew attention to early Carboniferous floral regionalism in contrast to the global *lepidophytus* flora. Increasing global climatic cooling might have restricted the advantage offered to ammonoids by wide cratonic overflowing. Cool currents between continents may have cut migrational links and greater climatic gradients could have enhanced provincialism.

5.- TAXONOMIC NOTES

Taxa and species groups listed in tables 1 to 4 in open nomenclature need some explanation to follow the course of this analysis. Progress in the knowledge of latest Devonian and Lower Carboniferous prionoceratids allowed the distinction of phylogenetic lineages with specific stratigraphic ranges within the former "mega-genus" *Imitoceras* (overview in Becker, 1988). This process has not been completed yet and taxonomic separation of evolutionary branches that can be applied for dating and correlation is required. Already Price & House (1984) drew attention to the fact that the generotype of *Imitoceras*, *Im. ixion* (? = *rotatorium*) and other Carboniferous relatives (*brevilobatum*, *crassum*, *foliiforme*, *jessiae*), are characterized by a parallel-sided ventral lobes, that is slightly swollen and shortened at the pointed of flat (*pilatium*, *planolobatum*, *yangi*, *abundans*, *discoideale*) base. This Carboniferous group obviously can be distinguished from the "*Im.*" *lineare* group with narrow lanceolate ventral lobes, that dominates the late Famennian. By contrast to *Mimimitoceras*, adult representatives of the latter group do not have shell constrictions and internal shell thickenings do not cause a shell tripartition. In the lower Carboniferous there are only a few members of this lineage (*bertchogurense*, *trochiforme*) and their relationships with Upper Tournaisian - Visean species (*sinuatum*, *wurmi*) need clarification. The main imitoceratid stock also survived into the Visean (e.g. *Im. "cf. xizangense"* Liang & Zhu, 1988 from Yunnan) and gave rise to *Irinoceras* with stronger emphasis of the basal lobe widening.

In the *Gattendorfia*-Stufe an important side branch led to forms with fast expanding whorls, wide adventitious lobes on the flanks and short v-shaped external lobes. This group (*subacra*, *acra*) is phylogenetically relevant, because it seems to represent the ancestor of the Karagandoceratidae (Bartsch & Weyer, 1988). A large number of species with evolute inner whorls of the basal Carboniferous currently is referred to *Acutimitoceras*, a genus introduced for oxyconic species (at present including *acutum*, *carinatum*, *wangyuense*, n. sp. aff. *acutum* and sp. Kusina). As in the "*Im.*" *acra* group this rapidly evolving lineage led to a genus (*Voehringierites*) with a subdivided ventral lobe as in typical goniatites. True acutimitoceratids should be separated from the diverse "*Acut.*" *prorsum* group with rounded venter and ventral lobe as in the "*Im.*" *lineare* group. Several species are morphologically intermediate between the *prorsum* group and *Gattendorfia*, because the umbilicus is not completely closed in the adult and the lateral lobe has moved into a subumbilical position (*multisulcatum*, *gracilis*, *antecedens*, *convexum*, "*Gatt.*"

applanata, *kazakhstanica*, *reticulata*, *yaliana*). First members of this group appear slightly later than the *prorsum* group at the base of the *subinvoluta* Zone but contemporaneously with *Gattendorfia*. Kusina (1985), who also recognized the special morphology of this "*Acut.*" *multisulcatum* group, lumped them together with *Paragattendorfia*-species. Revisionary work will have to show whether the group is a true phylogenetic lineage. They may also have formed the root stock for the "*Gatt. molaris*" group that led to *Gattenpleura*, but that still lacks the ribbing of the latter genus. "*Acutim.*" *werriense* Campbell & Engel (1963) from the lower Upper Tournaisian of New South Wales differs from all other imitoceratids with evolute inner whorls by its *Zadelsdorfia*- and *Kazakhstania*-type ventral lobe. It probably represents a new genus that was derived from *Imitoceras* s. str., since there are no other "acutimitoceratids" in the middle and upper part of the Middle Tournaisian. A new terminal Devonian imitoceratid genus with funnel-shaped ventral lobe was announced by M.R. Petersen. There is no convincing evidence for a Tournaisian range of *Cunitoceras* Weyer (1972a). "*Gatt.*" *shumardiana* from Michigan is ventrally too poorly preserved for a certain identification and is best regarded as nomen dubium. The very small "*Im.*" *rugilobatum* is possibly a juvenile karagandoceratid.

After the description of many new species of *Eocanites* from South China a division of this taxon into smaller phylogenetic units is desirable. Species groups with rounded (*Eoc. supradevonicus* group), tabulate or bicarinate (*Eoc. nodosus* group) and oxyconic venter (monospecific *Eoc. carinatus* group) can be distinguished. They all share an asymmetric acute subumbilical lobe in contrast to *Protocanites* with two similarly bell-shaped lobes on the flank. Weyer (1972b) used the shape of the ventral lobe to distinguish subfamilies within the Prolecanitidae. Middle and Upper Tournaisian protocanitids with lanceolate ventral lobes were placed in *Eocanites* regardless of their advanced lobe on the inner flank. This is the second species group of Weyer (1965) and includes "*Proto.*" *australis*, *gurleyi*, *abnobensis*, *planorbiformis*, n. sp. A Weyer (1965) and perhaps *geigenensis* and "*lyoni*" Librovitch (1940). Their taxonomic distinction from *Eocanites* is strongly indicated and of great stratigraphic importance. There are no known Middle Tournaisian true *Eocanites*. Campbell *et al.* (1982) refused to refer *australis* and *planorbiformis* to *Eocanites* and drew attention to the fact that there is a continuum between juvenile bell-shaped/lanceolate and adult (>13 mm Wh) *Protocanites* s. str.-type diverging ventral lobes in "*Proto.*" *australis*. Material of ?*gurleyi* and *lyoni* from Tennessee described by Mason & Chaplin (1979), however, show that in the adult both lanceolate and

v-shaped ventral lobes characterizing either the Eocanitinae or Protocanitinae (Weyer, 1972b) may be developed in different species. This supports the idea of a generic distinction between true *Protocanites* (Protocanitinae) and the "*Proto.*" *gurleyi* group (Eocanitinae).

In contrast to Weyer (1972b) and Kullmann *et al.* (1991) the Prodromitidae are not regarded as a morphologically advanced prolecanitid family. They were probably derived via *Qiannanites* (see also Work *et al.*, 1988) from *Paralytoceras* and therefore have to be placed in the Prionocerataceae. *Acrocenites* is regarded as a multilobed offshoot from *Protocanites*.

When Price & Korn (1989) introduced *Finiclymenia* (as a subgenus of *Gonioclymenia*, but full generic status is preferred here), they did not state the taxonomic position of the large-sized *Kalloclymenia pachydisca* group (*pachydisca*, nom. corr.; *kozhimensis*, n. sp. Becker, 1988) that has asymmetric angular lateral lobes as *Finiclymenia wocklumensis*. All other kalloclymenids have a more or less symmetric sagittate lateral lobe and this morphological feature is used here to define *Kalloclymenia*. In contrast to Price & Korn (1989) the taxon therefore includes both species with parabolic ribs (*Kallo. subarmata* group) and more or less smooth species (*Kallo. glabra* group). The *pachydisca* group is preliminarily referred to *Finiclymenia* although typical representatives have very compressed flat shells. This conch-type however developed several times independently within the Gonioclymeniaceae (*Sellaclymenia*, *Sphenoclymenia*). *Dimeroclymenia* and *Liroclymenia* Czarnocki (1989) are regarded as synonymous with *Riphaeoclymenia* Bogoslovsky. *Sinoglatziella* Sun is not kept separate from the ribbed typical glatziellids (Becker, 1992, in prep.).

ACKNOWLEDGEMENTS

I am indebted to M.R. House (Univ. Southampton) for critical reading and improving the manuscript. D. Korn (Tübingen) discussed taxonomic details, M. Streepl the question of Devonian southern hemisphere glaciations. As every review this paper has to exploit the hard work and data of numerous other specialists and their efforts are acknowledged by quoting a large number of references.

BIBLIOGRAPHY

ANDERSON, W.I., 1969.- Lower Mississippian Conodonts from Northern Iowa. *J. Pal.*, 43 (4) : 916-928.

- BABIN, C., RACHEBOEUF, P.R., LE HERISSE, A. & SUAREZ RIGLOS, M., 1991.- Données nouvelles sur les goniatites du Dévonien de Bolivie. *Geobios*, 24 (6) : 719-724.
- BAI, D. & NING, Z., 1989.- Faunal change and events across the Devoian-Carboniferous boundary at Huangmao section, Guangxi, south China. *Mem. Can. Soc. Petr. Geol.*, 14 (III) : 147-157.
- BARRETT, S.F. & ISAACSON, P.E., 1989.- Devonian paleogeography of South America. *Mem. Can. Soc. Petr. Geol.*, 14 (1) : 655-667.
- BARSKOV, I.S., SIMAKOV, K.V., ALEKSEEV, A.S., BOGOSLOVSKY, B.I., BYVSHEVA, T.V., GAGIEV, M.H., KONONOVA, L.N., KOCHETKOVA, N.M., KUSINA, L.F. & REITLINGER, E.A., 1984.- Devonian-Carboniferous transitional deposits of the Berchogur section, Mugodzhary, USSR (preliminary report). *Cour. Forsch.-Inst. Senck.*, 67 : 207-230.
- BARTZSCH, K. & WEYER, D., 1988.- Die unterkarbonische Ammonoidea-Subfamilia Karagandoceratinae. *Freib. Forsch.-H.*, C419 : 130-142.
- BECKER, R.T., 1988.- Ammonoids from the Devonian-Carboniferous boundary in the Hasselbach Valley (Northern Rhenish Slate Mountains). *Cour. Forsch.-Inst. Senck.*, 100 : 193-213.
- BECKER, R.T., 1990.- Numerical analysis of Mid-Paleozoic evolutionary events in ammonoids. *Abstr. 3rd Int. Symp. Ceph.: Present and Past, Symp. F. Roman*, Lyon, 1990 : 15.
- BECKER, R.T., FEIST, R., FLAJS, G., HOUSE, M.R. & KLAPPER, G., 1989.- Frasnian-Famennian extinction events in the Devonian at Coumiac, Southern France. *C.R. Acad. Sci. Paris*, 309, ser. II : 259-266.
- BRAND, U., 1989.- Global climatic changes during the Devonian-Mississippian : stable isotope biogeochemistry of brachiopods. *Palaeogeogr., Palaeocl., Palaeoec., Global and Planet. Change Sect.*, 75 : 311-329.
- CAMPBELL, K.S.W. & ENGEL, B.A., 1963.- The faunas of the Tournaisian Tulumba Sandstone and its members in the Werrie and Belvue Synclines, New South Wales. *J. geol. Soc. Austr.*, 10 : 55-122.
- CAMPBELL, K.S.W., BROWN, D.A. & COLEMAN, A.R., 1983.- Ammonoids and the correlation of the Lower Carboniferous rocks of Eastern Australia. *Alcheringa*, 7 : 75-123.
- CAPUTO, M.V., 1985.- Late Devonian glaciation in South America. *Palaeogeogr., Palaeocl., Palaeoec.*, 51 : 291-317.
- CLAUSEN, C.D., LEUTERITZ, K. & ZIEGLER, W., 1989.- Ausgewählte Profile an der Devon/Karbon-Grenze im Sauerland (Rheinisches Schiefergebirge). *Fortschr. Geol. Rheinl. u. Westf.*, 35 : 161-226.
- CONRAD, J., MASSA, D. & WEYANT, M., 1986.- Late Devonian and early Carboniferous transgression on the northern African platform. *Ann. Soc. géol. Belg.*, 109 : 113-122.
- CZARNOCKI, J., 1989 (posthum).- Klimentie gór Swietokrzyskich. *Prace panstw. Inst. Geol.*, 127 : 91 p.
- DURKINA, A.V. & AVKHIMOVITCH, V.I., 1988.- The reference sections of the Devonian/Carboniferous boundary deposits in the Timan-Pechora Province. *In* : The Devonian-Carboniferous boundary at the territory of the USSR, Nauka i Technica, Minsk : 87-101.
- FEIST, R. & FLAJS, G., 1987.- La limite Dévonien-Carbonifère dans la Montagne Noire (France). *Biostratigraphie et environnement. C.R. Acad. Sci. Paris*, 305, ser. II : 1537-1544.
- FLAJS, G. & FEIST, R., 1988.- Index conodonts, trilobites and environment of the Devonian-Carboniferous boundary beds at La Serre (Montagne Noire, France). *Cour. Forsch.-Inst. Senck.*, 100 : 53-107.

- FOLLOT, J., 1952.- Ahnet et Mouydir. *XIXe Congr. Geol. Internat., Monogr. reg., 1re ser., Algerie*, n°1 80 p.
- FURNISH, W.M. & MANGER, W.L., 1973.- Type Kinderhook Ammonoids. *Proc. Iowa Acad. Sci.*, 80 (1) : 15-24.
- GAGIEV, M.H. & KONONOVA, L.I., 1990.- The Upper Devonian and Lower Carboniferous Sequences in the Kamenka River Section (Kolyma River Basin, the Soviet North-East). Stratigraphic Description. Conodonta. *Cour. Forsch.-Inst. Senck.*, 118 : 81-103.
- GORDON, M. jr., 1986.- Late Kinderhookian (early Mississippian) Ammonoids of the Western United States. *J. Pal., Mem.*, 19 : 36 p.
- GORDON, M. jr. & MASON, C.E., 1985.- Progradation of the Borden Formation in Kentucky, U.S.A., demonstrated by successive Early Mississippian (Osagean) ammonoid fauna s. *C.R. 10. Int. Congr. Strat. Geol. Carb.*, Madrid 1983 : 191-198.
- GUTSCHICK, R.L. & RODRIGUEZ, J., 1979.- Biostratigraphy of the Pilot Shale (Devonian-Mississippian) and contemporaneous strata in Utah, Nevada, and Montana. *Brigham Young Univ., Geol. Studies*, 26 (1) : 37-63.
- HECKEL, P.H. & WITZKE, B.J., 1979.- Devonian world palaeogeography determined from distribution of carbonates and related lithic palaeoclimatic indicators. *Spec. Pap. Paleont.*, 23 : 99-123.
- HODSON, F. & RAMSBOTTOM, W.H.C., 1973.- The distribution of Carboniferous goniatite faunas in relation to suggested continental reconstruction for the period. *Spec. Pap. Paleont.*, 12 : 321-329.
- HOLLARD, H., 1970.- Sur la transgression dinantienne au Maroc présaharien. *C.R. 6e Congr. Intern. Strat. Géol. Car b.*, Sheffield 1967, III : 923-936.
- HOLLARD, H. & JACQUEMONT, P., 1956.- Le Gothlandien, le Dévonien et le Carbonifère des régions du Dra et du Zemoul. *Notes Serv. géol. Maroc*, 15 (135) : 7-33.
- HOUSE, M.R., 1962.- Observations on the ammonoid succession of the North American Devonian. *J. Pal.*, 36 : 247-284.
- HOUSE, M.R., 1964.- Devonian northern hemisphere ammonoid distribution and marine links. In : Nairn, A.E.M. (ed.). *Problems in Paleoclimatology*, Interscience Publishers, London : 262-269, 299-301.
- HOUSE, M.R., 1965.- Devonian goniatites from Nevada. *N. Jb. Geol. Pal., Abh.*, 122 (3) : 337-342.
- HOUSE, M.R., 1973a.- An analysis of Devonian goniatite distribution : organisms and continents through time. *Spec. Pap. Paleont.*, 12 : 305-317.
- HOUSE, M.R., 1973b.- Devonian Goniatites. In : Hallam, A. (ed.). *Atlas of Paleobiogeography*, Elsevier, London : 99-104.
- HOUSE, M.R., 1981.- On the origin, classification and evolution of the early Ammonoidea. In : House, M.R. & Senior, J.R. (eds.). *The Ammonoidea*, Syst. Assoc., Academic Press, London, Spec. Vol. 18 : 3-36.
- HOUSE, M.R., 1985.- Correlation of Mid-Paleozoic ammonoid evolutionary events with global sedimentary perturbations. *Nature*, 313 (3) : 17-22.
- HOUSE, M.R., 1989a.- Ammonoid extinction events. *Phil. Trans. R. Soc. London*, 325 : 307-326.
- HOUSE, M.R., 1989b.- Analysis of Mid-Paleozoic extinctions. *Bull. Soc. belge Géol.*, 98 (2) : 99-107.
- HOUSE, M.R., GORDON, M. jr. & HLAVIN, W.J., 1986.- Late Devonian ammonoids from Ohio and adjacent states. *J. Pal.*, 60 (1) : 126-144.
- HÜNICKEN, M.A., 1990.- Some paleogeographical aspects of South American conodonts and related forms. *Cour. Forsch.-Inst. Senck.*, 117 : 29-49.
- Ji, Q., 1987.- Early Carboniferous Conodonts from Jianghua County of Hunan Province and their stratigraphic value - with a discussion on the Mid-Aikuanian Event. *Bull. Inst. Geol., Chin. Acad. Geol. Sci.*, 16 : 115-141.
- JOHNSON, J.G. & RESO, A., 1966.- Brachiopods from the Pilot Shale (Devonian) in south-eastern Nevada. *J. Pal.*, 40 (1) : 125-129.
- JOHNSON, J.G. & SANDBERG, C.A., 1989.- Devonian eustatic events in the Western United States and their biostratigraphic response. *Mem. Can. Soc. Petr. Geol.*, 14 (III) : 171-178.
- KALVODA, J., 1989.- Tournaisian events in Moravia (Czechoslovakia) and their significance. *Cour. Forsch.-Inst. Senck.*, 117 : 353-358.
- KALVODA, J. & KUKAL, Z., 1987.- Devonian-Carboniferous boundary in the Moravian Karst at Lesni Lom Quarry, Brno-Lisen, Czechoslovakia. *Cour. Forsch.-Inst. Senck.*, 98 : 95-117.
- KORN, D., 1986.- Ammonoid evolution in late Famennian and early Tournaisian. *Ann. Soc. géol. Belg.*, 109 : 49-54.
- KORN, D., 1989.- *Cymaclymenia* aus der *Acutimitoceras*-Fauna (prorsum-Zone) vom Müszenberg (Devon/Karbon-Grenze; Rheinisches Schiefergebirge). *Bull. Soc. belge Géol.*, 98 (3/4) : 371-372.
- KORN, D. & LUPPOLD, W., 1987.- Nach Clymenien und Conodonten gegliederte Profile des oberen Famenniums im Rheinischen Schiefergebirge. *Cour. Forsch.-Inst. Senck.*, 92 : 199-223.
- KREBS, W., 1969.- Über Schwarzschiefer und bitumöse Kalke im mitteleuropäischen Variscikum. *Erdöl und Kohle, Erdgas, Petroch.*, 27 : 2-6, 62-67.
- KUSINA, L.F., 1985.- K revizii roda *Imitoceras* (Ammonoidea). *Pal. Zh.*, 1985 (3) : 35-48.
- KULLMANN, J., 1983.- Maxima im Tempo der Evolution karbonischer Ammonoideen. *Pal. Z.*, 57 (3/4) : 231-240.
- LANG, J., YAHAYA, M., EL HAMET, M.O., BESOMBES, J.C. & CAZOULAT, V., 1991.- Dépôts glaciaires du Carbonifère inférieur à l'ouest de l'Air (Niger). *Geol. Rdschau*, 80 (3) : 611-622.
- LIANG, X., 1976.- Carboniferous and Permian ammonoids from the Mount Jolmo - Lungma Region. A report of scientific expedition in the Mount Jolmo Lungma Region, 1966-1968. *Paleont.*, fasc. III : 215-222. (in Chinese with engl. summ.).
- LIANG, X., 1987.- Carboniferous Ammonoids from Jingyuan, Gansu. *11th Internat. Congr. Strat. Geol. Carb., Abstr.*, sect. 1-8 : 73-74.
- LIANG, X. & WANG, M., 1988.- Carboniferous Cephalopods of Xinjiang, NW China. In : Wiedmann, J. & Kullmann, J. (eds.). *Cephalopods - Present and Past*, Schweizerbart, Stuttgart : 553-575.
- LIANG, X. & ZHU, K., 1988.- Early Carboniferous cephalopods of Baoshan, Yunnan. *Acta Pal. Sinica*, 27 (3) : 288-306. (in Chinese).
- LIBROVITCH, L.S., 1940.- Ammonoidea iz otlozhenii Karbona severnogo Kazakhstana. *Pal. SSSR*, 4 (9), vyp 1, 391 p.
- MANGER, W., 1971.- The Mississippian ammonoids *Karagan doceras* and *Kazakhstania* from Ohio. *J. Pal.*, 45 (1) : 33-39.
- MANGER, W., 1979.- Lower Carboniferous ammonoid assemblages from North America. *C.R. 7th Congr. Intern. Strat. Geol. Carb.*, 3 : 211-221.
- MASON, C.F. & CHAPLIN, J.R., 1979.- Nancy and Cowbell Members of the Borden Formation. In : Etensohn, F.R. & Dever, G.R. jr. (eds.). *Carboniferous geology from the Appalachian Basin to the Illinois Basin trough eastern Ohio and Kentucky*, 9th Intern. Congr. Strat. Geol. Carb., Guidebook Field Trip 4 : 147-151.

- MATTHEWS, S.C., 1969.- Comments on palaeontological standards for the Dinantian. *C.R. 6e Congr. Intern. Strat. Geol. Carb., Sheffield 1967*, III : 1159-1164.
- MATTHEWS, S.C., 1970.- A new cephalopod fauna from the Lower Carboniferous of east Cornwall. *J. Pal.*, 13 (1) : 112-131.
- MATTHEWS, S.C., 1983.- An occurrence of Lower Carboniferous (*Gattendorfia*-Stufe) ammonoids in southwest Ireland. *N. Jb. Geol. Pal., Mh.*, 1983 (5) : 293-299.
- McQUEEN, R.W. & SANDBERG, C.A., 1970.- Stratigraphy, age and interregional correlation of the Exshaw Formation, Alberta, Rocky Mountains. *Bull. Can. Soc. Petr. Geol.*, 18 (1) : 32-66.
- MICHELS, D., 1986.- Ökologie und Fazies der jüngsten Ober-Devon von Velbert (Rheinisches Schiefergebirge). *Gött. Arb. Geol. Pal.*, 29 : 86 p.
- OLIVEIRA, J.T., HORN, L., KULLMANN, J. & PAPROTH, E., 1985.- The stratigraphy of the Upper Devonian and Carboniferous sediments of southwest Portugal. *C.R. 10th Congr. Intern. Strat. Geol. Carb., Madrid 1983* : 107-120.
- PAREYN, C., 1962.- Les Massifs Carbonifères du Sahara Sud-Oranais. *Publ. Centr. Rech. Sah., sér. géol.*, 1 (1) : 325 p.
- PETERSEN, M. & STOKES, W.L., 1983.- A clymenid ammonoid from the Pinyon Peak Limestone of Utah. *J. Pal.*, 57 (4) : 717-719.
- PLAYFORD, G., 1991.- Australian Lower Carboniferous miospores relevant to extra-gondwanic correlations : an evaluation. *Cour. Forsch.-Inst. Senck.*, 67 : 15-22.
- PRICE, J.D. & KORN, D., 1989.- Stratigraphically important clymeniids (Ammonoidea) from the Famennian (Late Devonian) of the Rhenish Massif, West Germany. *Cour. Forsch.-Inst. Senck.*, 110 : 257-294.
- SABLE, E.G. & DUTRO, J.T., 1961.- New Devonian and Mississippian formations in De Long Mountains, Northern Alaska. *Bull. Am. Ass. Petr. Geol.*, 45 : 585-593.
- SANDBERG, C.A., STREEL, M. & SCOTT, R.A., 1972.- Comparison between conodont zonation and spore assemblages at the Devonian Carboniferous boundary in the western and central United States and in Europe. *C.R. 7th cong. Intern. Strat. Geol. Carb.*, 1 : 179-203.
- SANDBERG, C.A., GUTSCHICK, R.C., JOHNSON, J.G., POOLE, F.G. & SANDO, W.J., 1983.- Middle Devonian to Late Mississippian geologic history of the Overthrust Belt region, western United States. *Rocky Mountain Ass. Geol., Geol. Studies of the Cord. Thrust Belt*, 2 : 691-719.
- SANDBERG, C.A., ZIEGLER, W., DREESEN, R. & BUTLER, J.L., 1988.- Late Frasnian Mass Extinction : Conodont Event Stratigraphy, Global Changes, and possible Causes. *Cour. Forsch.-Inst. Senck.*, 102 : 263-307.
- SANDBERG, C.A., POOLE, P.G. & JOHNSON, J.G., 1989.- Upper Devonian of western United States. *Mem. Can. Soc. Petr. Geol.*, 14 (1) : 183-220.
- SCHINDEWOLF, O.H., 1922.- Über eine Unterkarbonfauna aus Ostthüringen. *Senck.*, 4 8-20.
- SCHINDEWOLF, O.H., 1937.- Zur Stratigraphie und Paläontologie der Wocklumer Schichten. *Abh. preuss. geol. L.-Anst.*, N.F., 178 : 132 p.
- SCHINDEWOLF, O.H., 1939.- Bemerkungen zur Stratigraphie des oberfränkisch-ostthüringischen Unterkarbons. *Jb. Preuss. geol. L.-Anst. f.* 1938, 59 : 456-479.
- SCHINDEWOLF, O.H., 1959.- Adolescent cephalopods from the Exshaw Formation of Alberta. *J. Pal.*, 33 (6) : 971-976.
- SCOTESE, C.R., 1986.- Early Famennian (367 ma) equatorial world view. In : Roy, S. (ed.) *The Devonian; a portfolio of maps 1978-1986*. Anchorage, Alaska Pac. Univ., The Dev. Inst., Anchorage, 12 p.
- STREEL, M., 1986.- Miospore contribution to the Upper Famennian-Strunian event stratigraphy. *Ann. Soc. géol. Belg.*, 109 : 75-92.
- STRITZKE, R., 1990.- Die Karbonatsedimentation im Briloner Vorriffbereich. *Geol. Jb.*, D 95 : 253-315.
- TEICHERT, C., 1986.- Times of crisis in the evolution of the Cephalopoda. *Pal. Z.*, 60 (3/4) : 227-243.
- THRASHER, L.C., 1987.- Macrofossils and stratigraphic subdivision of the Bakken Formation (Devonian-Mississippian), Williston Basin, North Dakota. *5th Intern. Williston Basin Symp., spec. publ.*, 9 : 53-67.
- VAN STEENWINKEL, M., 1984.- The Devonian-Carboniferous boundary in the vicinity of Dinant, Belgium. *Cour. Forsch.-Inst. Senck.*, 67 : 57-69.
- VAN STEENWINKEL, L., 1988.- The sedimentary history of the Dinant Platform during the Devonian-Carboniferous transition. Ph. D. thesis Kath. Univ. Leuven, 173 p.
- WALLISER, O.H., 1984.- Pleading for a natural D/C-boundary. *Cour. Forsch.-Inst. Senck.*, 67 : 241-246.
- WANG, C., 1987.- Devonian-Carboniferous boundary in South China. *Contr. 11th Intern. Congr. Strat. Geol. Carb.*, Beijing 1987 : 1-10.
- WEYER, D., 1965.- Zur Ammonoideen-Fauna der *Gattendorfia*-Stufe von Dzikowiec (Ebersdorf) in Dolny Slask (Niederschlesien), Polen. *Ber. geol. Ges. DDR*, 10 (4) : 443-464.
- WEYER, D., 1972a.- Zum Alter der Ammonoideen-Faunen des Marshall-Sandsteins (Unterkarbon; Michigan, USA). *Ber. dt. Ges. geol. Wiss., A, Geol. Pal.*, 17 (3) : 325-350.
- WEYER, D., 1972b.- Trilobiten und Ammonoideen aus der *Entogonites nasutus*-Zone (Unter-Karbon) des Büchenbergsattels (Elbringeröder Komplex, Harz), Teil 2. Zur Phylogenie und Systematik der älteren Prolecanitina. *Geologie*, 21 (3) : 318-349.
- WORK, D.M., MAPES, R.H. & THOMPSON, L.T., 1988.- A new prodromitid ammonoid genus from the Hannibal Shale (Lower Mississippian) of Missouri. *J. Pal.*, 62 (5) : 772-778.
- XU, D., ZHANG, Q., SUN, Y., YAN, Z., CHAI, Z. & HE, J., 1989.- *Astrogeological Events in China*. Scottish Academic Press, Edinburgh.
- YUAN, J., 1988.- Proetiden aus dem jüngeren Oberdevon von Süd-China. *Paleontogr., Abt. A*, 201 (1/3) : 1-102.
- ZHANG, L., 1987 (ed.)- *Carboniferous Stratigraphy in China*. Science Press, Beijing.
- ZIEGLER, W. & SANDBERG, C.A., 1984.- *Palmatolepis*-based revision of upper part of standard Late Devonian conodont zonation. *Geol. Soc. Am., Spec. Pap.*, 196 : 179-194.