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Morphospace occupation of ammonoids over the Devonian-Carboniferous boundary

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With 7 figures

Kurzfassung: In einer Fallstudie wird eine stratophänetische Analyse der aufeinanderfolgenden Ammonoideen-Faunen aus den Cephalopodenkalken des höchsten Devon und untersten Karbon im Rheinischen Schiefergebirge durchgeführt. Die Untersuchung konzentrierte sich auf die Entwicklung der Windungsexpansionsrate (WER), einem wichtigen Merkmal bei Ammonoideen; es beeinflußt die Länge der Wohnkammer und somit die Orientierung des Tieres in der Wassersäule sowie seine Mobilität. Die Studie führt zu dem Ergebnis, daß der Hangenberg-Event einen vollständigen Wechsel in der Ammonoideen-Geometrie verursachte. Alle Clymenien und Tornoceraten starben am oder unmittelbar nach dem Hangenberg-Event aus; der von diesen devonischen Gruppen zurückgelassene Morphospace wurde durch die überlebenden Prionoceraten nur unvollständig neu besetzt.

Abstract: In a case study, a stratophenetic analysis of the succeeding ammonoid faunas of the latest Devonian and earliest Carboniferous cephalopod limestones of the Rhenish Massif has been made. This investigation concentrated on the development of the whorl expansion rate (WER), a character very important for ammonoids since it indicates the body chamber length and hence the orientation in the water column as well as mobility. The study leads to the conclusion that the Hangenberg Event caused an almost complete change in the morphospace adopted by ammonoids. All clymeniids as well as tornoceratids became extinct at or immediately after the Hangenberg Event, and the morphospace left behind by these Devonian groups was reoccupied only incompletely by the surviving prionoceratid ammonoids.

Introduction

The transition from the Devonian to the Carboniferous (Fig. 1) is marked by an almost complete changeover of ammonoid faunas, caused by the anoxic Hangenberg Event (PRICE & HOUSE 1984; KORN 1986, 1991; BECKER 1993; BECKER & KORN 1997; KORN & BECKER 1997). The entire order Clymeniida, which is the dominant latest Devonian ammonoid group, became extinct during or shortly after the Hangenberg Event, and no descendants continued into the Carboniferous. The same happened to the last remnants of the family Sporadoceratidae and also the tornoceratids, of which during the late Famennian only the monophyletic family Posttornoceratidae and long-ranging genera of the family Tornoceratidae were represented by few species.

The only surviving ammonoids were the prionoceratids, of which also most species did not survive the Hangenberg Event, but which immediately after that event were the only ammonoids remaining and gave rise to all Carboniferous, Permian, and Mesozoic ammonoids. In contrast, a few short-term surviving clymeniids became extinct during the *prorsum* Zone, immediately before the Devonian-Carboniferous Boundary.

It was commonly assumed that during the basal Carboniferous *Gattendorfia* Stufe the prionoceratid ammonoids replaced the morphological range of the died-out clymeniids; e.g. NIKOLAEVA & BARSKOV (1994) stated that morphological diversity was restored in the earliest Carboniferous. However, the present investigations do not confirm this statement.

Detailed stratophenetic analyses of Palaeozoic ammonoid faunas with respect to fine-scaled biostratigraphical discrimination have only rarely been attempted (see SWAN 1988, for example). Most of these studies are based on sutural and ornament features, and considered the mode of coiling of the planispiral conch to a lesser degree.

Investigations of Late Carboniferous ammonoid morphospace occupation have been published by SAUNDERS & SWAN (1984) and SAUNDERS & WORK (1996), who recognised eight different morphotypes, mainly based on the two morphological characters of whorl expansion rate and ratio of umbilical width and conch diameter. In their review of the latest Devonian and Carboniferous ammonoids, NIKOLAEVA & BARSKOV (1994) discriminated, on the basis of whorl expansion rate and umbilical width, five morphotypes which were defined by the conch geometries of the Namurian genera *Anthracoceras*, *Schartymites*, *Isohomoceras*, *Prolecanites*, and *Syngastrioceras*.

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<tr><td rowspan="4">Zone of Para-wocklumeria paradoxa</td><td rowspan="2">Subzone of Wocklumeria sphaeroides</td><td rowspan="2">HBS
Upper paradoxa Zone</td><td>Cymaclymenia nigra Zone</td></tr>
<tr><td>Wocklumeria sphaeroides Zone</td></tr>
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Fig. 1. Revised biostratigraphical scheme of the latest Devonian and earliest Carboniferous rocks and their correlation with older subdivisions.- HBS = Hangenberg Black Shale.

Methods

Among the characters comprising ammonoid morphospace, e.g. conch parameters (whorl expansion rate, umbilical width, apertural height, whorl width), sutural and ornament details, the whorl expansion rate was chosen as the cardinal character for the present study. The opening rate of the coil appears to be one of the most important characters of the ammonoid conch, because it controls the length of the body chamber, the location of centres of mass and gravity, and therefore the position of the aperture in the living animal. The umbilical width as the second character regarded here is important because it controls the outline of the aperture and the whorl cross section. Both characters undergo rapid fluctuations during the evolution of Palaeozoic ammonoids, and hence are suitable for a detailed stratophenetic study with discrimination of short time intervals.

Basic theoretical questions of geometrical shell analysis were discussed in the pioneering studies by MOSELEY (1838) and NAUMANN (1840a, 1840b, 1845, 1849), and were applied for investigations in Devonian ammonoids by MÜLLER (1850, 1853) and SANDBERGER (1855). It was MÜLLER (1850, also presented in SANDBERGER & SANDBERGER 1850) who showed that ammonoid conchs, in his case conchs of *Prolobites delphinus* (SANDBERGER & SANDBERGER 1850), can consist of two ontogenetic coiling stages with different geometrical properties. Such modifications in growth of ammonoids were later exemplified in a large number of Palaeozoic ammonoids (KULLMANN & SCHEUCH 1970, 1972).

A method for description of the geometrical conch parameters was introduced by RAUP & MICHELSON (1965) and RAUP (1966, 1967), using the four principal parameters W (whorl expansion rate), D (relative distance of the whorl from the coiling axis), S (shape of the whorl), and T (rate of whorl translation). RAUP and later authors (SAUNDERS & SWAN 1984, 1996; NIKOLAEVA & BARSKOV 1994) focused on the significance of the two parameters W (whorl expansion rate) and D (umbilical diameter),

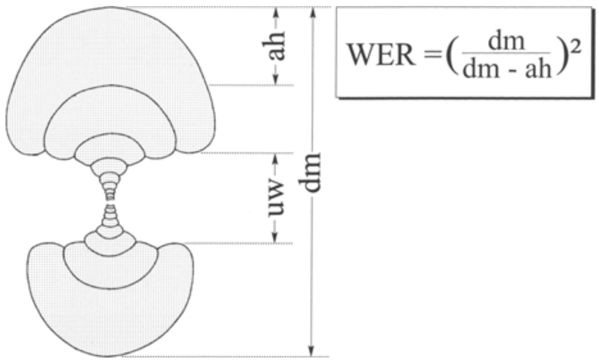

Fig. 2. Explanation of the morphological parameters whorl expansion rate (WER) and umbilical width (uw/dm) as used in the text.

using these parameters as the basis for functional and ecological interpretation of ammonoid shells.

The whorl expansion rate (WER) as calculated by these authors is the squared quotient of the larger radius and the smaller radius of the coil [$(d/e)^2$], and the umbilical diameter is the quotient of the umbilical width and the conch diameter [uw/dm]. A problem in application of the whorl expansion rate as calculated by these authors is the absolute necessity to investigate exact cross sections for determination of the coiling axis, since otherwise major errors can easily occur. However, for most of the species discussed here no cross sections are available for study and thus calculation of an exact whorl expansion rate is impossible.

A much simpler way to calculate a whorl expansion rate (Fig. 2) is the division of the conch diameter by the conch diameter minus aperture height [$(dm/dm\text{-}ah)^2$]. In an exact logarithmic spiral, values gained by this method lead to the same results as in the traditional approach: differences may occur only for those whorls in which the spiral angle changes. Use of this simpler method leads to exact values for most of the ammonoid species, and measurements can be obtained from carefully photographed specimens as well as cross sections of those specimens in which the inner whorls are not preserved. This is the reason why in the following the value of the whorl expansion rate (WER) is calculated in a slightly different way to that used by RAUP (1966) and subsequent authors.

For the study presented here, one well preserved representative specimen of each species was measured (appendix 2). If possible, an adult specimen was chosen, and of better known species, several individuals were taken into account to check the intraspecific variability which is extremely low in all the investigated species.

It is astonishing that the WER values gained by this method are much more stable, within certain taxa of higher rank, than the values given by SAUNDERS & SWAN (1984, appendix). For example, values of species of *Mimimitoceras* range between 1.47 and 1.58, and values of kosmoclymeniids between 1.87 and 2.02, whereas SAUNDERS & SWAN proposed for the Namurian genus *Cancelloceras* a range between 1.44 and 2.50, and for *Phillipsoceras* even between 1.19 and 2.66, despite the fact that conchs of the different species within these genera are rather similar to each other. These extremely wide ranges require further explanation.

Figures of the bivariate plots and density contours presented below have been produced using version 2.0 of the program Spheristat for Windows (©1995 Pangaea Scientific), for which the data were transformed. For each data set, four contour lines were calculated for the bivariate plots. The mode chosen for creating these contour lines results in separation of different morphologies, but causes the effect that remote morphologies in the occupied morphospace were not embraced within a contour line (see bivariate plot for the *Balvia lens* Zone, for example). Diagrams are edited using CorelDraw Version 8.0.

The stratigraphical subdivision is based on the schemes provided by SCHINDEWOLF (1937), VÖHRINGER (1960), and KORN (1995), but a new zonal terminology is introduced here (Fig. 1; for definition of the zones see Appendix 1).

Morphological diversity in latest Devonian and earliest Carboniferous ammonoid shells

Wocklumeria Stufe before the Hangenberg Event

At the base of the *Wocklumeria* Stufe, five morphological groups (which are not sharply separated but are connected with intermediate forms) of ammonoids can be recognised, of which the first four maintain up to the Hangenberg Event (Fig. 3):

(1) *Mimimitoceras* morph: involute goniatites with very low (1.45-1.60) WER (*Mimimitoceras*, *Balvia*, but also *Epiwocklumeria*);
(2) *Discoclymenia* morph: involute goniatites with high (2.40-2.90) WER (*Discoclymenia*, *Gundolficeras*, *Posttornoceras*);
(3) *Cymaclymenia* morph: narrowly umbilicated clymeniids with moderate (1.95-2.40) WER (*Cymaclymenia*, *Cyrtoclymenia*, etc.);
(4) *Kosmoclymenia* morph: widely umbilicated clymeniids with low (1.75-2.05) WER (*Kosmoclymenia*, *Kalloclymenia*);
(5) *Sphenoclymenia* morph: medium umbilicated clymeniids with high (2.30-2.50) WER (*Sphenoclymenia*).

The diversity plots for the *Muessenbiaergia sublaevis* Zone and *M. parundulata* Zone (Fig. 5) demonstrate only minor faunal modifications. The *Balvia lens* Zone differs from these in possessing only a few new entries, e.g. the occurrence of *Balvia*, which leads to emphasis of the first morphological group. Additionally, the first two representatives (*Glatziella*, *Soliclymenia*) of a sixth group appear:

(6) *Kamptoclymenia* morph: wocklumeriid and glatziellid clymeniids with very low WER (1.35-1.60) and variable umbilical width.

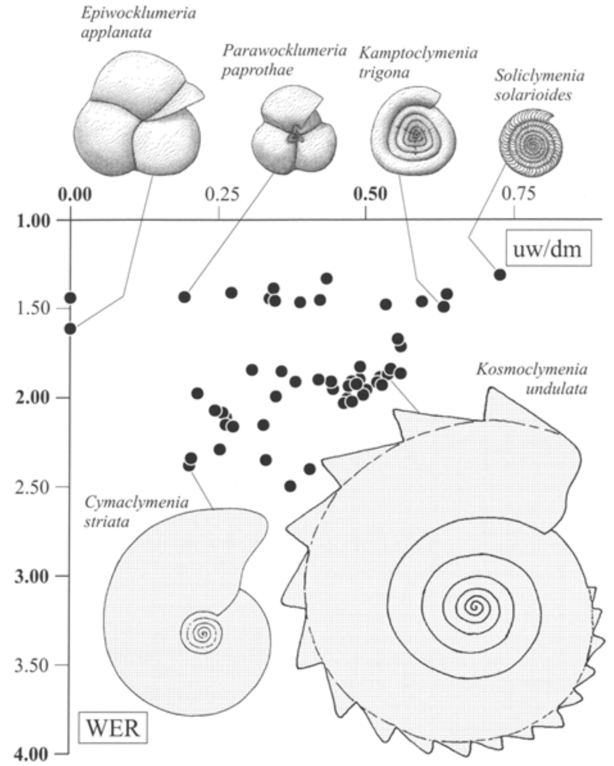

Fig. 3. Bivariate plots showing the distribution of data points [characters whorl expansion rate (WER) and umbilical width (uw/dm)] in clymeniids of the Late Devonian *Wocklumeria* Stufe of the Rhenish Massif, together with the conch morphology of some representative species.– Drawings after KORN (1995).

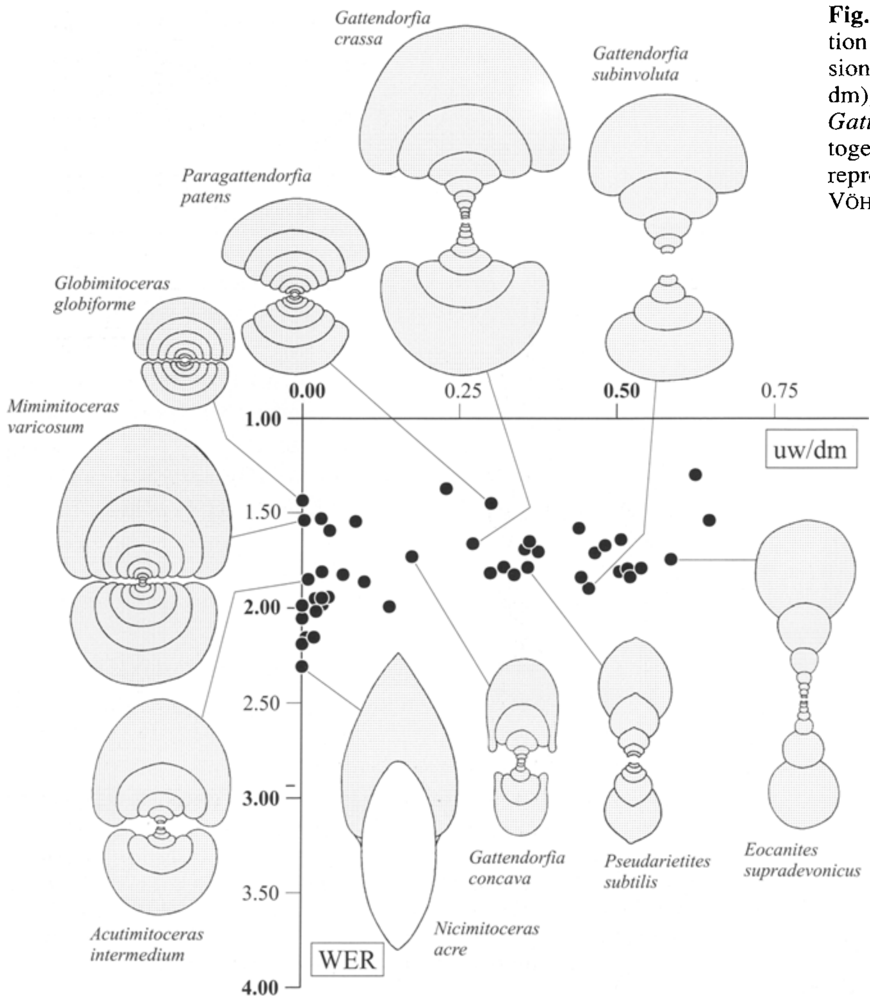

Fig. 4. Bivariate plots showing the distribution of data points [characters whorl expansion rate (WER) and umbilical width (uw/dm)] in goniatites of the Early Carboniferous *Gattendorfia* Stufe of the Rhenish Massif, together with the conch morphology of some representative species.– Cross sections after VÖHRINGER (1960).

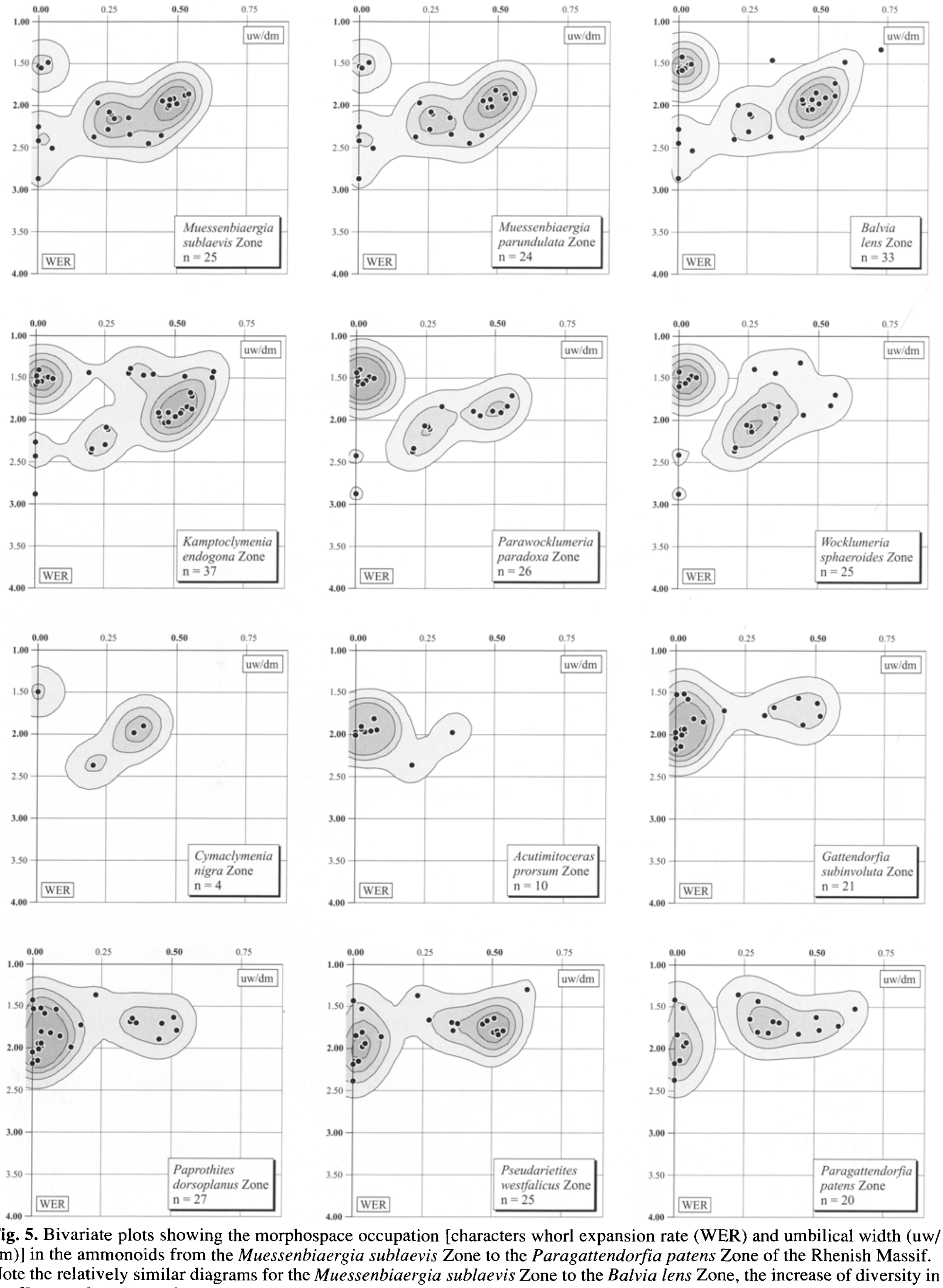

Fig. 5. Bivariate plots showing the morphospace occupation [characters whorl expansion rate (WER) and umbilical width (uw/dm)] in the ammonoids from the *Muessenbiaergia sublaevis* Zone to the *Paragattendorfia patens* Zone of the Rhenish Massif. Note the relatively similar diagrams for the *Muessenbiaergia sublaevis* Zone to the *Balvia lens* Zone, the increase of diversity in the *Kamptoclymenia endogona* Zone, the almost stable diversity in the *Parawocklumeria paradoxa* Zone and the *Wocklumeria sphaeroides* Zone, and the drastic reduction of diversity in the *Cymaclymenia nigra* Zone, caused by the Hangenberg Black Shale Event. In the *Acutimitoceras prorsum* Zone, diversity is still limited with predominating involute goniatites, but in the following *Gattendorfia subinvoluta* to *Paragattendorfia patens* Zones, widely umbilicated goniatites evolve and occupy a distinct field in morphospace.

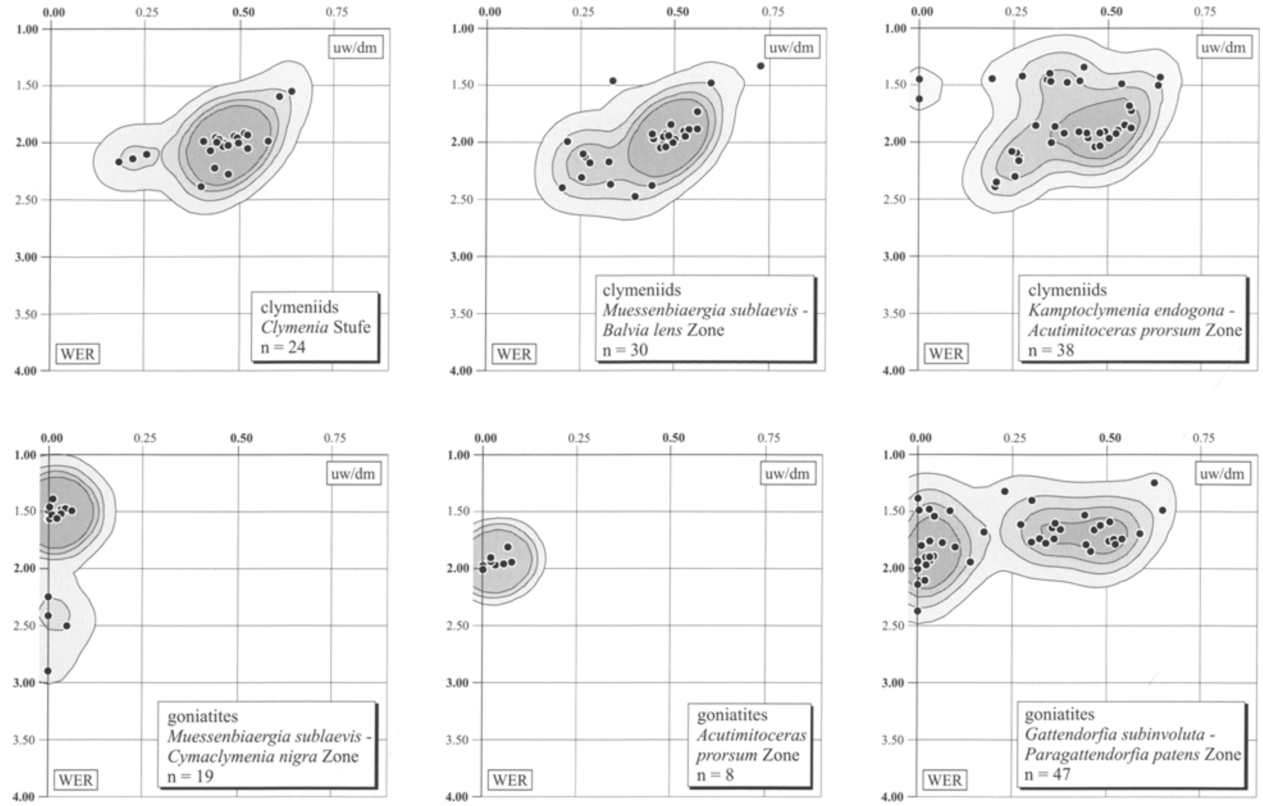

Fig. 6. Bivariate plots showing the morphospace occupation [characters whorl expansion rate (WER) and umbilical width (uw/dm)] in Late Devonian ammonoids of the Rhenish Massif: clymeniids of the *Clymenia* Stufe, clymeniids of the lower three zones of the *Wocklumeria* Stufe (*Muessenbiaergia sublaevis* Zone to *Balvia lens* Zone), clymeniids of the five upper zones within the *Wocklumeria* Stufe (*Kamptoclymenia endogona* Zone to *Acutimitoceras prorsum* Zone), and goniatites of the *Wocklumeria* Stufe (except for the *Acutimitoceras prorsum* Zone).

Note the similarity of clymeniid morphology of the *Clymenia* Stufe and early *Wocklumeria* Stufe, but the significant increase of morphological diversity that occurred in the middle to late *Wocklumeria* Stufe (*Kamptoclymenia endogona* Zone to *Acutimitoceras prorsum* Zone). Note also the reduced morphological diversity of the latest Devonian goniatites, in contrast to the early Carboniferous *Gattendorfia* Stufe.

The diversity maximum of conch geometry was reached in the *Kamptoclymenia endogona* Zone of the *Wocklumeria* Stufe, when the sixth morphological group is diverse with eight species of the genera *Kamptoclymenia*, *Parawocklumeria*, and *Glatziella*, and occupies the zone of clymeniids with low WER. Extinction of these species leads to an increase of clymeniid diversity during the *Parawocklumeria paradoxa* Zone (Fig. 5), but in the *Wocklumeria sphaeroides* Zone, the occurrence of the genus *Wocklumeria* induces a recovery of the morphospace formerly occupied by moderately umbilicated species of *Parawocklumeria*. The end-members of the wocklumeriid lineages, *Parawocklumeria paradoxa* (WEDEKIND 1918) and *Epiwocklumeria applanata* (WEDEKIND 1918) resemble, in their closed umbilicus and very low WER, the prionoceratid goniatites.

The diversity plots for these zones show that the morphs 3 and 4, which represent the long-ranging clymeniid lineages, continuously lost their predominance as seen in the plots for the *Clymenia* Stufe (Figs. 5, 6) and earliest zones of the *Wocklumeria* Stufe.

In the Hangenberg Black Shale, the diversity is extremely reduced, and only three species are known so far. Apart from a few short-term surviving species (*Cymaclymenia*, *Lissoclymenia*), all the morphological groups except for the first (*Mimimitoceras*) became extinct and were not present during the *Gattendorfia* Stufe.

Acutimitoceras prorsum Zone and *Gattendorfia* Stufe

Recovery after the Hangenberg Event was rapid, and already in the latest Devonian *Acutimitoceras prorsum* Zone, eight species of prionoceratids with open umbilicus in juvenile stages are known. *Acutimitoceras* and *Nicimitoceras* occur spontaneously with a new conch geometry that was probably developed already earlier. The lack of *Mimimitoceras*, the only genus so far known surviving the Hangenberg Event, in the *Ac. prorsum* Zone and its reappearance in the *Gattendorfia subinvoluta* Zone is regarded as migration effect.

Starting from the acutimitoceratids, the basal Carboniferous diversification occurred, leading in the *G. sub-*

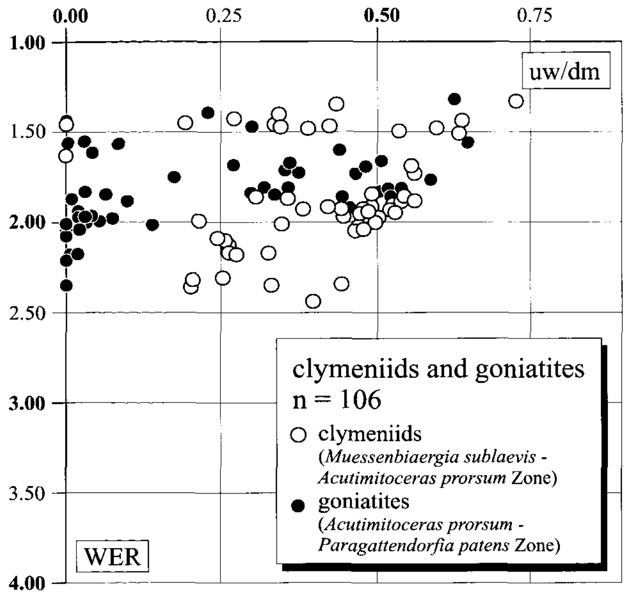

Fig. 7. Bivariate plots showing the distribution of data points [characters whorl expansion rate (WER) and umbilical width (uw/dm)] in Late Devonian and Early Carboniferous ammonoids of the Rhenish Massif, demonstrating the difference in morphospace occupied by clymeniids and goniatites. Note the insignificant overlap of data points that represent clymeniid and goniatite morphology.

involuta Zone to a relatively wide range of different conch morphologies. Within the *Gattendorfia* Stufe, four morphological groups are distinguishable (Fig. 4):

(1) *Mimimitoceras* morph: involute goniatites with very low (1.45-1.60) WER (*Mimimitoceras*, *Globimitoceras*);

(2) *Acutimitoceras* morph: involute goniatites with moderate to high (1.80-2.40) WER (*Acutimitoceras*, *Nicimitoceras*);

(3) *Paragattendorfia* morph: subinvolute goniatites with very low (1.35-1.60) WER (*Paragattendorfia*, partly *Acutimitoceras*);

(4) *Eocanites* morph: evolute goniatites with moderate (1.60-1.90) WER (*Gattendorfia*, *Eocanites*, *Pseudarietites*, etc.).

During the four earliest Carboniferous zones, from the *G. subinvoluta* Zone to the *Paragattendorfia patens* Zone, conch diversification did not increase remarkably, as can be seen from the very similar contour diagrams for these zones (Fig. 5). It can only be seen that a group of widely umbilicated goniatites became well established, and that intermediates became unimportant.

It is remarkable that the goniatites of the *Gattendorfia* Stufe differ so conspicuously in their WER values from the clymeniids of the Late Devonian *Wocklumeria* Stufe. The bivariate plot of the WER/uw values of all the clymeniids from the *Wocklumeria* Stufe and goniatites from the *Gattendorfia* Stufe demonstrates the significant differences in the position of the morphospace occupied by these groups. The clymeniids are almost exclusively subinvolute or evolute, and their WER values display two peaks in which most of the species are concentrated, one peak at WER = 1.46, and another, more dominant one at WER = 1.93, with a minimum zone between WER = 1.55 and 1.75. The prionoceratid goniatites of the *prorsum* Zone and *Gattendorfia* Stufe show two very closely arranged maxima at WER = 1.82 and 1.95. The first of these, composed by the genera *Gattendorfia*, *Paprothites*, *Pseudarietites*, and *Eocanites* lies in the morphospace which was hardly occupied by the clymeniids. The second peak, composed by *Acutimitoceras* and *Nicimitoceras*, coincides with the clymeniid maximum. Major differences in umbilical width, however, are the reason why the involute acutimitoceratids occupy a field in the morphospace diagram clearly separated from that of the subinvolute to evolute clymeniids (Fig. 7).

Among the ammonoids of the discussed timespan with very low whorl expansion rates, the goniatites are represented by the involute *Mimimitoceras* and narrowly umbilicated *Paragattendorfia* as well as the two species *Acutimitoceras sphaeroidale* (VÖHRINGER 1960) and *Acutimitoceras multisulcatum* (VÖHRINGER 1960). Clymeniids with WER resembling that of these goniatites are usually wider umbilicated, and thus separated in the bivariate plot. Only two clymeniid species, *Parawocklumeria paradoxa* (WEDEKIND 1918) and *Epiwocklumeria applanata* (WEDEKIND 1918), have a position in the morphospace that overlaps with that of goniatites.

There appears no obvious reason to explain this striking discordance. A possible reason that clymeniids could only, because of their dorsal siphuncle, occupy distinct morphospace is unlikely, because some stratigraphically older species of *Platyclymenia* show WER values which partly fill the morphospace gap of the forms investigated in this study. At the same time, goniatites from other stratigraphical intervals show clymeniid-like shell properties; e.g. *Agoniatites* and *Manticoceras* resemble *Cymaclymenia*, and *Anarcestes* resembles *Kamptoclymenia*.

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Appendices 1 and 2

Appendix 1 (page 255). Revised biostratigraphical scheme of the latest Devonian and earliest Carboniferous rocks with definition of the ammonoid zones. – FOD = first occurrence datum, LOD = last occurrence datum.

Appendix 2 (page 256-257). Latest Devonian and earliest Carboniferous ammonoid taxa used for the presented analyses and their morphometrical data. – Explanation for the abbreviations in the column "zones" is: *Ms* = *Muessenbiaergia sublaevis* Zone, *Mp* = *Muessenbiaergia parundulata* Zone, *Bl* = *Balvia lens* Zone, *Ke* = *Kamptoclymenia endogona* Zone, *Pp* = *Parawocklumeria paradoxa* Zone, *Ws* = *Wocklumeria sphaeroides* Zone, *Cn* = *Cymaclymenia nigra* Zone, *Ap* = *Acutimitoceras prorsum* Zone, *Gs* = *Gattendorfia subinvoluta* Zone, *Pd* = *Paprothites dorsoplanus* Zone, *Pw* = *Pseudarietites westfalicus* Zone, *Ps* = *Paragattendorfia patens* Zone, *Clym.* = *Clymenia* Stufe.

		name of ammonoid zone	definition of lower boundary	definition of upper boundary	additional zonal characteristics
EARLY CARBONIFEROUS	*Gattendorfia* Stufe	*Paragattendorfia patens* Zone	FOD of *Paragattendorfia patens*	LOD of *Paragattendorfia patens*	FOD of *Eocanites aupradevonicus* and *Eoc. planus.* Top of the zone is marked by the Lower Alum Shale.
		Pseudarietites westfalicus Zone	FOD of *Pseudarietites westfalicus*	FOD of *Paragattendorfia patens*	FOD of *Acutimitoceras depressum*, *Pseudarietites subtilis*, *Nicimitoceras acre*, *Gattendorfia crassa*, *Eocanites brevis*, and *Eoc. spiratissimus.*
		Paprothites dorsoplanus Zone	FOD of *Paprothites dorsoplanus*	FOD of *Pseudarietites westfalicus*	FOD of *Acutimitoceras multisulcatum*, *Ac. exile*, *Costimitoceras ornatum*, *Globimitoceras globiforme*, and *Gattendorfia molaris.*
		Gattendorfia subinvoluta Zone	FOD of *Gattendorfia subinvoluta*	FOD of *Paprothites dorsoplanus*	FOD of *Acutimitoceras acutum, Ac. undulatum, and Gattendorfia reticulum*; *Eocanites nodosus* and *Gattendorfia tenuis* enter higher in this zone.
LATE DEVONIAN	*Wocklumeria* Stufe	*Acutimitoceras prorsum* Zone	FOD of *Acutimitoceras prorsum*	FOD of *Gattendorfia subinvoluta*	FOD of *Acutimitoceras subbilobatum*, *Ac. intermedium*, *Ac. kleinerae*, *Ac. stockumense*, *Nicimitoceras caesari*, and *Nic.* (?) *carinatum.*
		Cymaclymenia nigra Zone	FOD of *Cymaclymenia nigra*	FOD of *Acutimitoceras prorsum*	Range of the zone largely coincides with the Hangenberg Black Shale.
		Wocklumeria sphaeroides Zone	FOD of *Wocklumeria sphaeroides*	FOD of *Cymaclymenia nigra*	FOD of *Epiwocklumeria applanata*; top of the zone is marked by the Hangenberg Black Shale.
		Parawocklumeria paradoxa Zone	FOD of *Parawocklumeria paradoxa*	FOD of *Wocklumeria sphaeroides*	FOD of *Lissoclymenia wocklumeri*, *Balvia nucleus*, and *B. biforme*; *Fini-clymenia wocklumensis* and *Post-glatziella carinata* higher in this zone.
		Kamptoclymenia endogona Zone	FOD of *Kamptoclymenia endogona*	FOD of *Parawocklumeria paradoxa*	FOD of *Parawocklumeria paprothae*, *Paraw. distorta*, *Paraw. patens*, and *Balvia falx.*
		Balvia lens Zone	FAD of *Balvia lens*	FAD of *Kamptoclymenia endogona*	*Balvia minutula*, *Mimimitoceras trizonatum*, *Muessenbiaergia ademmeri*, and *Glatziella glaucopis* enter higher in this zone
		Muessenbiaergia parundulata Zone	FOD of *Muessenbiaergia parundulata*	FOD of *Balvia lens*	Probably FOD of *Muessenbiaergia bisulcata* and *Muessenbiaergia colubrina*; lack of the genus *Balvia*
		Muessenbiaergia sublaevis Zone	FOD of *Muessenbiaergia sublaevis*	FOD of *Muessenbiaergia parundulata*	FOD of *Kosmoclymenia undulata* and *Sphenoclymenia brevispina*; probably FOD of *Cymaclymenia striata and Cyrtoclymenia angustiseptata*
	Cl. St.	*Piriclymenia piriformis* Zone	FOD of *Piriclymenia piriformis*	FOD of *Muessenbiaergia sublaevis*	

species	dm	WER	uw/dm	stratigr. distribution													main data source
				Clym.	*Ms*	*Mp*	*Bl*	*Ke*	*Pp*	*Ws*	*Cn*	*Ap*	*Gs*	*Pd*	*Pw*	*Ps*	
Gundolficeras sp.	12	2.50	0.05		x	x	x										Becker 1995
Discoclymenia cucullata (von Buch 1839)	17	2.89	0.00	x	x	x	x	x	x	x							Becker 1995
Posttornoceras posthumum (Wedekind 1918)	52	2.52	0.00	x													Wedekind 1918
Posttornoceras cf. *posthumum* (Wedekind 1918)	34	2.40	0.00		x	x	x	x	x	x							Becker 1995
Erfoudites spiralis	30	2.15	0.00	x													unpubl. data
Sporadoceras aff. *orbiculare* (Münster 1832)	36	2.22	0.00		x	x	x	x									unpubl. data
Mimimitoceras lineare (Münster 1832)	22	1.52	0.00	x													Korn 1994
Mimimitoceras pompeckji (Schindewolf 1923)	22	1.83	0.00	x													Korn 1994
Mimimitoceras disciforme (Schindewolf 1952)	25	1.95	0.00	x													Korn 1994
Mimimitoceras liratum (Schmidt 1924)	23	1.49	0.03	x	x	x	x	x									Korn 1994
Mimimitoceras alternum Korn 1992	23	1.54	0.00		x	x	x										Korn 1994
Mimimitoceras geminum Korn 1992	22	1.53	0.00		x	x	x	x	x								Korn 1994
Mimimitoceras trizonatum Korn 1988	18	1.47	0.04				x	x	x	x							Korn 1994
Mimimitoceras fuerstenbergi Korn 1992	25	1.54	0.02				x	x	x								Korn 1994
Mimimitoceras nageli Korn 1992	26	1.55	0.00				x	x									Korn 1994
Mimimitoceras lentum Korn 1992	24	1.58	0.00						x	x							Korn 1994
Mimimitoceras rotersi Korn 1992	24	1.52	0.03						x	x							Korn 1994
Mimimitoceras (?) *substriatum* (Münster 1840)	36	1.50	0.00								x						Korn 1994
Mimimitoceras varicosum (Schindewolf 1923)	18	1.54	0.03										x	x	x	x	Korn 1994
Mimimitoceras hoennense Korn 1994	16	1.57	0.00										x	x			Korn 1994
Balvia minutula Korn 1992	9	1.39	0.01				x	x	x								Korn 1994
Balvia lens Korn 1992	11	1.52	0.00				x	x	x								Korn 1994
Balvia falx Korn 1992	13	1.46	0.00					x	x								Korn 1994
Balvia globularis (Schmidt 1924)	10	1.51	0.06					x	x	x							Korn 1994
Balvia biforme (Schindewolf 1937)	9	1.53	0.03						x	x							Korn 1994
Balvia nucleus (Schmidt 1924)	11	1.56	0.02						x	x							Korn 1994
Globimitoceras globiforme (Vöhringer 1960)	24	1.45	0.00											x	x	x	Korn 1994
Paragattendorfia patens (Vöhringer 1960)	22	1.46	0.28													x	Korn 1994
Paragattendorfia sphaeroides Weyer 1972	25	1.38	0.21											x	x	x	Korn 1994
Acutimitoceras subbilobatum (Münster 1839)	32	1.96	0.03									x	x	x	x	x	Korn 1994
Acutimitoceras intermedium (Schindewolf 1923)	26	1.92	0.02									x	x	x			Korn 1994
Acutimitoceras kleinerae Korn 1984	27	1.80	0.06									x	x	x			Korn 1994
Acutimitoceras depressum (Vöhringer 1960)	24	1.94	0.04												x	x	Korn 1994
Acutimitoceras undulatum (Vöhringer 1960)	22	2.00	0.02										x	x			Korn 1994
Acutimitoceras convexum (Vöhringer 1960)	22	1.93	0.03										x	x			Korn 1994
Acutimitoceras antecedens (Vöhringer 1960)	19	1.84	0.09										x	x	x		Korn 1994
Acutimitoceras exile (Vöhringer 1960)	22	1.80	0.03											x	x		Korn 1994
Acutimitoceras simile (Vöhringer 1960)	16	1.83	0.01												x	x	Korn 1994
Acutimitoceras acutum (Schindewolf 1923)	22	2.02	0.00										x	x			Korn 1994
Acutimitoceras gracile (Vöhringer 1960)	16	1.97	0.13											x			Korn 1994
Acutimitoceras multisulcatum (Vöhringer 1960)	14	1.55	0.08											x			Korn 1994
Acutimitoceras sphaeroidale (Vöhringer 1960)	16	1.59	0.04										x	x			Korn 1994
Acutimitoceras prorsum (Schmidt 1925)	19	1.93	0.07									x					Korn 1994
Acutimitoceras stockumense Korn 1984	18	1.91	0.02									x					Korn 1994
Acutimitoceras procedens Korn 1984	22	1.95	0.05									x					Korn 1994
Nicimitoceras caesari (Korn 1984)	19	1.97	0.00									x					Korn 1994
Nicimitoceras subacre (Vöhringer 1960)	31	2.12	0.00										x	x	x		Korn 1994
Nicimitoceras trochiforme (Vöhringer 1960)	22	2.15	0.00										x	x	x	x	Korn 1994
Nicimitoceras acre (Vöhringer 1960)	46	2.39	0.00												x	x	Korn 1994
Nicimitoceras heterolobatum (Vöhringer 1960)	43	2.14	0.02										x	x	x	x	Korn 1994
Nicimitoceras (?) *carinatum* (Schmidt 1924)	19	2.01	0.00									x					Korn 1994
Costimitoceras ornatum Vöhringer 1960	27	1.94	0.03											x			Korn 1994
Voehringerites peracutus (Vöhringer 1960)	16	1.98	0.00										x				Korn 1994
Gattendorfia subinvoluta (Münster 1832)	29	1.90	0.43										x	x			Korn 1994
Gattendorfia crassa Schmidt 1924	38	1.64	0.25												x	x	Korn 1994
Gattendorfia tenuis Schindewolf 1952	24	1.65	0.48										x	x	x	x	Korn 1994
Gattendorfia costata Vöhringer 1960	28	1.68	0.33										x	x	x	x	Korn 1994
Gattendorfia reticulum Vöhringer 1960	15	1.59	0.41										x				Korn 1994
Gattendorfia molaris Vöhringer 1960	19	1.69	0.35											x	x	x	Korn 1994
Gattendorfia concava Vöhringer 1960	18	1.71	0.16										x	x			Korn 1994
Gattendorfia evoluta Vöhringer 1960	12	1.58	0.63													x	Korn 1994
Gattenpleura bartzschi Weyer 1976	40	1.77	0.30										x				unpubl. data
Paprothites dorsoplanus (Schmidt 1924)	20	1.70	0.44											x	x		Korn 1994
Paprothites raricostatus (Vöhringer 1960)	14	1.66	0.34											x			Korn 1994
Pseudarietites westfalicus Schmidt 1924	16	1.68	0.46												x		Korn 1994
Pseudarietites subtilis Vöhringer 1960	21	1.78	0.34												x		Korn 1994
Pseudarietites planissimus Vöhringer 1960	45	1.80	0.52												x		Korn 1994
Pseudarietites carinatus (Vöhringer 1960)	23	1.83	0.48												x		Korn 1994
Paralytoceras serratum (Vöhringer 1960)	16	1.80	0.28													x	Korn 1994
Paralytoceras crispum (Tietze 1871)	50	1.82	0.32													x	Weyer 1965
Eocanites nodosus (Schmidt 1925)	19	1.81	0.49										x	x	x	x	Korn 1994
Eocanites supradevonicus (Schindewolf 1926)	21	1.76	0.57													x	Korn 1994
Eocanites brevis (Vöhringer 1960)	19	1.85	0.50												x		Korn 1994
Eocanites planus (Schindewolf 1926)	42	1.83	0.42													x	Korn 1994
Eocanites tener (Vöhringer 1960)	14	1.81	0.52												x		Korn 1994
Eocanites spiratissimus (Vöhringer 1960)	7	1.30	0.60												x		Korn 1994

species	dm	WER	uw/dm	stratigr. distribution													main data source
				Clym.	*Ms*	*Mp*	*Bl*	*Ke*	*Pp*	*Ws*	*Cn*	*Ap*	*Gs*	*Pd*	*Pw*	*Ps*	
Cyrtoclymenia angustiseptata (MÜNSTER 1832)	55	2.10	0.25		x	x	x	x	x	x							unpubl. data
Cyrtoclymenia plicata (MÜNSTER 1832)	30	2.08	0.24	x	x	x	x	x	x	x							unpubl. data
Cyrtoclymenia tetragona (SCHMIDT 1924)	10	2.05	0.23						x	x							unpubl. data
Cymaclymenia cordata (WEDEKIND 1914)	37	2.43	0.22	x													KORN 1981
Cymaclymenia (?) *curvicosta* LANGE 1929	19	1.93	0.42	x													KORN 1981
Cymaclymenia striata (MÜNSTER 1832)	27	2.37	0.19		x	x	x	x	x	x	x	x					KORN 1981
Cymaclymenia costellata (MÜNSTER 1832)	26	2.26	0.24		x	x	x	x									KORN 1981
Cymaclymenia involvens LANGE 1929	42	2.31	0.19					x	x	x							KORN 1981
Cymaclymenia nephroides KORN 1981	31	2.14	0.25							x							KORN 1981
Cymaclymenia camerata SCHINDEWOLF 1923	27	2.13	0.31		x	x											KORN 1981
Cymaclymenia warsteinensis KORN 1979	16	2.34	0.31		x	x	x										KORN 1981
Cymaclymenia dorsocostata (MÜNSTER 1840)	36	2.16	0.26		x												KORN 1981
Cymaclymenia evoluta (SCHMIDT 1924)	22	1.99	0.33							x	x	x					KORN 1991
Cymaclymenia nigra KORN 1991	22	1.91	0.36								x						KORN 1991
Biloclymenia (?) sp.	18	2.11	0.21	x													unpubl. data
Kiaclymenia (?) sp.	42	1.97	0.20		x	x	x										unpubl. data
Progonioclymenia acuticostata (MÜNSTER 1842)	43	1.60	0.58	x													PRICE & KORN 1989
Progonioclymenia aegoceras (FRECH 1902)	19	1.56	0.62	x													PRICE & KORN 1989
Clymenia laevigata (MÜNSTER 1832)	43	2.04	0.50	x													unpubl. data
Ornatoclymenia ornata (MÜNSTER 1834)	22	1.95	0.38	x													KORN 1981
Piriclymenia piriformis (SCHMIDT 1924)	18	1.97	0.43	x													KORN 1981
Protoxyclymenia dunkeri (MÜNSTER 1839)	30	1.93	0.46	x													KORN & PRICE 1987
Franconiclymenia serpentina (MÜNSTER 1832)	92	1.94	0.47	x													KORN & PRICE 1987
Kosmoclymenia lamellosa (WEDEKIND 1914)	32	1.99	0.44	x													KORN & PRICE 1987
Kosmoclymenia inaequistriata (MÜNSTER 1832)	42	1.98	0.44	x													KORN & PRICE 1987
Kosmoclymenia effenbergensis KORN & PRICE 1987	67	1.92	0.49	x													KORN & PRICE 1987
Kosmoclymenia undulata (MÜNSTER 1832)	76	1.90	0.50		x	x	x	x									KORN & PRICE 1987
Kosmoclymenia ptychofera KORN & PRICE 1987	95	2.01	0.45				x										KORN & PRICE 1987
Kosmoclymenia callima KORN & PRICE 1987	38	1.88	0.52		x												KORN & PRICE 1987
Kosmoclymenia schindewolfi KORN & PRICE 1987	38	1.90	0.50					x	x								KORN & PRICE 1987
Kosmoclymenia n. sp.	56	1.93	0.45		x												unpubl. data
Lissoclymenia wocklumeri (WEDEKIND 1914)	74	1.83	0.52					x	x	x							KORN & PRICE 1987
Linguaclymenia similis (MÜNSTER 1839)	11	1.95	0.42	x	x	x	x	x	x	x							KORN & PRICE 1987
Linguaclymenia clauseni (KORN & PRICE 1987)	34	1.90	0.42				x	x									KORN & PRICE 1987
Linguaclymenia n. sp.	44	1.91	0.47						x								unpubl. data
Muessenbiaergia diversa (KORN & PRICE 1987)	43	1.97	0.42	x													KORN & PRICE 1987
Muessenbiaergia sublaevis (MÜNSTER 1832)	31	2.04	0.44		x	x	x	x									KORN & PRICE 1987
Muessenbiaergia galeata (WEDEKIND 1914)	56	1.91	0.46				x	x									KORN & PRICE 1987
Muessenbiaergia parundulata (KORN & PRICE 1987)	34	1.85	0.47			x	x										KORN & PRICE 1987
Muessenbiaergia bisulcata (MÜNSTER 1840)	44	1.94	0.45			x											KORN & PRICE 1987
Muessenbiaergia ademmeri (KORN & PRICE 1987)	47	1.96	0.48				x	x									KORN & PRICE 1987
Muessenbiaergia colubrina (LANGE 1929)	43	1.95	0.51			x											KORN & PRICE 1987
Muessenbiaergia xenostriata (KORN & PRICE 1987)	25	1.99	0.47		x												KORN & PRICE 1987
Muessenbiaergia n. sp.	45	1.93	0.46		x												unpubl. data
Glatziella glaucopis RENZ 1914	15	1.44	0.31				x	x									WEYER 1981
Glatziella tricincta SCHINDEWOLF 1937	12	1.46	0.57				x										SCHINDEWOLF 1937
Glatziella minervae RENZ 1914	20	1.47	0.36					x									unpubl. data
Postglatziella carinata SCHINDEWOLF 1937	11	1.83	0.29						x	x							SCHINDEWOLF 1937
Soliclymenia solarioides (VON BUCH 1839)	11	1.34	0.71				x										unpubl. data
Nodosoclymenia n. sp.	12	1.98	0.56	x													unpubl. data
Costaclymenia binodosa (MÜNSTER 1832)	27	1.94	0.50	x													unpubl. data
Costaclymenia kiliani (WEDEKIND 1914)	62	1.99	0.48	x													unpubl. data
Sellaclymenia plana (MÜNSTER 1832)	75	2.05	0.40	x													unpubl. data
Sellaclymenia torleyi (WEDEKIND 1914)	54	2.25	0.45	x													unpubl. data
Gonioclymenia speciosa (MÜNSTER 1832)	167	2.20	0.42	x													unpubl. data
Gonioclymenia subcarinata (MÜNSTER 1832)	108	2.38	0.38	x													unpubl. data
Kalloclymenia crassa (WEDEKIND 1914)	36	2.02	0.45	x													unpubl. data
Kalloclymenia subarmata (MÜNSTER 1832)	100	1.87	0.54		x	x	x	x									PRICE & KORN 1989
Kalloclymenia uhligi (FRECH 1902)	46	2.03	0.46			x	x	x									unpubl. data
Kalloclymenia pessoides (VON BUCH 1839)	31	1.72	0.54				x	x	x	x							unpubl. data
Kalloclymenia frechi (LANGE 1929)	75	1.69	0.53					x									SCHINDEWOLF 1937
Finiclymenia wocklumensis (LANGE 1929)	46	1.85	0.34							x							PRICE & KORN 1989
Finiclymenia n.sp.	52	1.90	0.40						x								unpubl. data
Sphenoclymenia brevispina (LANGE 1929)	36	2.36	0.42		x	x	x										PRICE & KORN 1989
Sphenoclymenia erinacea PRICE & KORN 1989	65	2.48	0.38		x	x											PRICE & KORN 1989
Kamptoclymenia endogona SCHINDEWOLF 1937	21	1.43	0.62					x									SCHINDEWOLF 1937
Kamptoclymenia trigona SCHINDEWOLF 1937	16	1.50	0.61					x									SCHINDEWOLF 1937
Kamptoclymenia trivaricata SCHINDEWOLF 1937	18	1.48	0.51					x									SCHINDEWOLF 1937
Parawocklumeria patens SCHINDEWOLF 1937	18	1.45	0.40					x									SCHINDEWOLF 1937
Parawocklumeria distorta (TIETZE 1871)	14	1.39	0.32					x									SCHINDEWOLF 1937
Parawocklumeria paprothae KORN 1990	12	1.44	0.18					x									CLAUSEN et al. 1990
Parawocklumeria paradoxa (WEDEKIND 1918)	17	1.46	0.00						x	x							SCHINDEWOLF 1937
Wocklumeria sphaeroides (RICHTER 1848)	19	1.40	0.25							x							SCHINDEWOLF 1937
Wocklumeria plana SCHINDEWOLF 1937	29	1.45	0.32							x							SCHINDEWOLF 1937
Wocklumeria aperta SCHINDEWOLF 1937	34	1.35	0.41							x							SCHINDEWOLF 1937
Epiwocklumeria applanata (WEDEKIND 1918)	14	1.61	0.00							x							SCHINDEWOLF 1937