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Morphological pathways in the evolution of Early and Middle Devonian ammonoids

Dieter Korn and Christian Klug

Abstract.—The principal conch parameters—whorl expansion rate, whorl overlap rate, umbilical width, and whorl thickness—of Early and Middle Devonian ammonoids have been extensively investigated. Stratophenetic analyses show long-term trends in the transformations of these characters over long periods of time, but sudden and rapid reversals can also be observed. On the basis of these four quantifiable conch parameters and supplementary qualitative characters, ten ammonoid morphs were distinguished. Reconstruction of the evolutionary history of these morphs reflects the existence of two major phylogenetic lineages, both already visible in Early Devonian faunas. The agoniatitid lineage is characterized by slow character development and leads to the Frasnian gephuroceratids; the anarcestid lineage displays rapid morphological evolution that leads to the late Givetian pharciceratids as well as the Middle and Late Devonian tornoceratids. Morphological evolution is interpreted as partly limited by geometrical and physical constraints.

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Introduction

The mathematically calculable geometry of spirally coiled ammonoid conchs has long attracted the attention of scientists. Robert Hooke, one of the most ingenious philosophers of science of the seventeenth century, was fascinated by the logarithmic coil of ammonite shells with their regularly arranged septa (posthumously published 1705): "That the Shell is of a true Conical Figure from the *Base* to the *Apex*. . . That this Cone is turned into a *Voluta* or Spiral Cone. . . That this Spiral being a true proportional Spiral, is continually at certain distances intercepted by Diaphragmes; so that those Diaphragmes being taken as Bases of several Cones, the Cones shall be found to diminish in a series Geometrically Proportional."

The first mathematical analyses of Recent *Nautilus* conchs and of ammonites were achieved in the middle of the nineteenth century by Moseley (1838), Müller (1850), and Sandberger (1855). Surprisingly, these pioneering studies were not continued by subsequent researchers and more than 100 years passed before David Raup, in three innovative articles (Raup and Michelson 1965; Raup 1966, 1967), outlined the theoretical framework for further investigation. Raup analyzed different types of mollusk conchs in terms of their geometrical properties. He defined principal morphological conch parameters such as the whorl expansion rate, i.e., the opening rate of the whorl spiral.

Mathematical investigations were furthered by Kullmann and Scheuch (1970, 1972), and by Kant, who in a series of articles (1973a,b, 1975, 1977; Kant and Kullmann 1980, 1988) concentrated his efforts on the basic parameters conch radius, whorl width, whorl height, and umbilical width as well as their development throughout ontogeny. According to these studies, allometric growth is particularly common in Carboniferous and Permian ammonoids.

Application of the former largely theoretical studies on Carboniferous ammonoids was initiated by Saunders and Swan (1984), Saunders and Shapiro (1986), Swan and Saunders (1987), and Saunders and Work (1995, 1996, 1997). Saunders and Swan (1984) demonstrated that eight different morphotypes can be discriminated for the Namurian Stage. They

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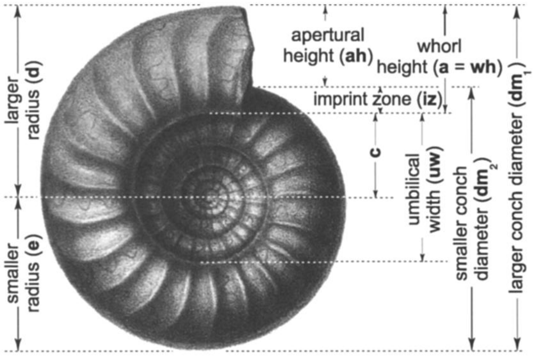
GIVETIAN	LATE	*Petteroceras errans*	6
		Pharciceras tridens	
	EARLY	*Maenioceras terebratum*	5
		Sellagoniatites waldschmidti	
		Agoniatites obliquus	
EIFELIAN		*Agoniatites expansus*	4
		Cabrieroceras plebeiforme	
		Subanarcestes macrocephalus	
		Pinacites jugleri	
		Foordites veniens	
EMSIAN	DALEJAN	*Anarcestes lateseptatus*	3
		Sellanarcestes wenkenbachi	
		Latanarcestes noeggerathi	
	ZLICHO-VIAN	*Mimagoniatites fecundus*	2
		Erbenoceras advolvens	1

FIGURE 1. Emsian to Givetian ammonoid biostratigraphic units (Units 1 to 6), based on investigations of Moroccan outcrops, after Klug 2002.



RAUP 1967	$W = \left(\frac{d}{e}\right)^2$	
KORN 2000	$WER = \left(\frac{dm_1}{dm_2}\right)^2$	$dm_2 = dm_1 - ah$
RAUP 1967	$D = \left(\frac{c}{d}\right)$	
this paper	$UWI = \left(\frac{uw}{dm}\right)$	
RAUP 1967	$S = \left(\frac{b}{a}\right)$	whorl width = b
this paper	$WWI = \left(\frac{ww}{wh}\right)$	whorl width = ww
this paper	$IZR = \left(\frac{wh - ah}{wh}\right)$	

FIGURE 2. The principal conch characters whorl expansion rate (WER), as proposed by Raup (1967) and the modified equation as introduced by Korn (2000); umbilical width index (UWI); whorl width index (WWI); and whorl imprint zone (IZR) in ammonoids.

are distinguished mainly by the ratio of whorl expansion rate to umbilical width.

Morphological transformations and morphospace occupation of successive ammonoid faunas across the Devonian/Carboniferous boundary were documented by Korn (2000). Detailed inquiries into the whorl expansion rate and umbilical width refuted the common assumption, proposed by Nikolaeva and Barskov (1994), that the earliest Carboniferous goniatites rapidly occupied the morphospace abandoned by the clymeniid ammonoids after their demise.

In this paper, changes in conch morphology of Early and Middle Devonian ammonoids through time are portrayed and interpreted in terms of phylogeny.

Materials and Methods

The evolutionary history of Early and Middle Devonian ammonoids is remarkable in light of several morphological trends and encourages a stratophenetic analysis of some of the conch parameters. The period under examination can be subdivided into six time units from the basal Zlíchovian (Unit 1) to the late Givetian (Unit 6), numbered 1 to 6 in the subsequent text and figures (Fig. 1). Further subdivision would be possible but is not useful for the present study because the exact stratigraphic occurrences of many of the species are not sufficiently known.

For the stratophenetic analysis, morphometric data of almost all currently known Early and Middle Devonian ammonoid species were gathered from our own material and from published illustrations (see Appendices 1 and 2). These analyses show that four quantifiable aspects of conch geometry (1–4 below; Fig. 2) and a number of additional characters (5–18) underwent significant modifications during the time units 1 to 6:

1. The whorl expansion rate (WER = the opening rate of the whorl spiral, which is

regarded here as the primary coiling parameter). This parameter is the most important because it correlates with the length of the body chamber and the life orientation of the aperture in regularly coiled ammonoids (Raup 1967; Saunders and Shapiro 1986; Swan and Saunders 1987; Klug 2001b).

2. The umbilical width index (UWI = umbilical width/conch diameter ratio). The size of the umbilicus has an effect on the drag of the ammonoid conch (Swan and Saunders 1987; see Jacobs 1992 or Jacobs and Chamberlain 1996 for specific references).
3. The whorl width index (WWI = whorl width/ whorl height ratio). This parameter had a strong effect on the drag of the ammonoid conchs (Jacobs 1992; Jacobs and Chamberlain 1996).
4. The imprint zone rate (IZR = whorl overlap rate) is important because it determines the whorl cross-section and thus the space for the soft body. A low IZR allows a compact body and a large buccal apparatus, and a high IZR leads to semilunatic whorls in which the distribution of the soft body is different.
5. The general coiling of the conch. In the early ammonoids, it can be described as gyroconic (when the whorls do not touch), advolute (when the whorls touch each other), and embracing.
6. The size of the umbilical window. From very large in the earliest forms, this window is continuously closed in all subsequent lineages (see Erben 1964 and Korn 2001).
7. The shape of the venter (rounded, acute, or flattened).
8. The shape of the umbilical margin (rounded or angular).
9. The general septal form (synclastic, i.e., simply domed; or anticlastic, i.e., with distinct corrugation).
10. The form of the external lobe (simple or subdivided by a median saddle).
11. The form of the lateral lobe (broadly rounded, narrowly rounded, or acute).
12. The number of umbilical lobes.
13. The direction of the growth lines (rursiradiate, rectiradiate, or prorsiradiate).
14. The course of the growth lines (linear, convex, concavo-convex, or biconvex).
15. The height of the ventrolateral projection of the growth lines.
16. The depth of the external sinus of the growth lines.
17. The presence of ribs.
18. The presence of ventrolateral furrows.

New equations (Fig. 2) for the first three of these parameters were introduced (Korn 2000; Korn and Klug 2002; this paper); they differ from those established earlier by Raup and Michelson (1965) and Raup (1966, 1967). Raup's equations were modified, because these were part of a theoretical model that could not be applied to ammonoids with an umbilical window. Either the studied material is incompletely preserved or we had to take measurements from illustrations in the literature. Consequently, it was often impossible to identify the position of the protoconch, which is needed to measure the radii, which in turn are required for Raup's W and D variables. The modified equations, however, can be computed even if the umbilicus is obscured by matrix.

The use of real ammonoids (including taxa with gyroconic conchs) and of the modified equations results in certain consequences that need to be taken into account: In the case of gyroconic conchs, a modified equation was used to determine the WER:

$$\mathrm{WER} = [\mathrm{dm}_1/(\mathrm{dm}_1 - \mathrm{wh})]^2$$

Furthermore, because of allometric growth in many ammonoids, the whorl expansion rates and the values of the umbilical width index plot on both sides of the D = 1/W curve (see Fig. 4), although never far below this curve. This occurs when the WER is increasing during ontogeny, as happens in the D-morph, but also to a lesser degree in other morphs.

Analyses of these four quantifiable characters (WER, UWI, WWI, and IZR) demonstrate that several Early and Middle Devonian ammonoid morphs can be distinguished more or less clearly, and this is supplemented by a set

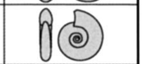
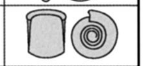
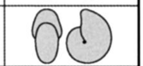
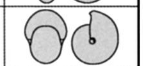
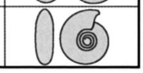
morph name		WER	UWI	WWI	IZR	typical genera	time units	example
A	erbenoceratid	1.50	0.60	0.60	0	*Erbenoceras* *Anetoceras*	1 - 4	
B	mimosphinctid	2.25	0.45	0.60	0	*Mimosphinctes* *Gyroceratites*	1 - 3	
C	convoluticeratid	3.00	0.30	0.70	0.05	*Convoluticeras* *Teicherticeras*	2 - 3	
D	mimagoniatitid	3.75	0.20	0.80	0.05	*Mimagoniatites* *Archanarcestes*	2 - 3	
E	agoniatitid	2.75	0.15	0.80	0.25	*Agoniatites* *Fidelites*	3 - 5	
F	ponticeratid	2.25	0.30	0.80	0.25	*Ponticeras* *Mzerrebites*	6	
G	anarcestid	1.50	0.50	1.40	0.35	*Anarcestes* *Cabrieroceras*	3 - 4	
H	tornoceratid	2.25	0.05	0.80	0.45	*Tornoceras* *Parodiceras*	4 - 6	
I	holzapfeloceratid	1.60	0.10	1.40	0.55	*Holzapfeloceras* *Sobolewia*	4 - 5	
K	pharciceratid	1.75	0.30	1.20	0.45	*Pharciceras* *Triainoceras*	6	

FIGURE 3. Characterization of the ten discriminated Early and Middle Devonian ammonoid morphs, together with typical representative genera as well as stratigraphic range. WER = whorl expansion rate, UWI = umbilicus/conch diameter ratio, IZR = imprint zone rate, WWI = whorl width/whorl height ratio; median values of WER, UWI, WWI, and IZR are shown.

of additional qualitative characters (see Appendix 2). Because evolution was gradual, these ammonoid morphs form statistically definable groups, sometimes without sharp limits. They largely correspond to distinct phylogenetic units and are specified in Figure 3.

In the studied faunas, complex morphological trends can be observed and graphed on Cartesian coordinate diagrams (Figs. 4, 5). We computed density contour lines to provide a clear visual presentation of the WER/UWI morphospace occupied by the ammonoids.

Statistical analyses of the morphological diversity of ammonoids in the six time units were carried out to demonstrate the character distribution over time. The median value is regarded as the average, because rare extreme morphologies influence the arithmetic mean. For the same reason, the range of the middle two quartiles within a data matrix was preferable to the standard deviation to express the variability within each time unit.

Morphological Trends

Four principal characters (Fig. 2) were investigated and analyzed in detail, because they were the crucial parameters for hydrodynamic and thus ecological properties of the ammonoid conchs. The stratophenetic analysis reveals remarkable fluctuations within the six discriminated time units (Figs. 4, 6).

Whorl Expansion Rate (WER).—From the early Zlíchovian to the Dalejan (Units 1 to 3), the development of ammonoid conch morphologies exhibits a wide range of coiling values, whereas the morphological evolution of this character was considerably reduced in the Middle Devonian (Units 4 to 6). Figure 6A demonstrates that the average coiling rates of ammonoids did not change as significantly after Unit 3 as they did before. The Early Devonian can thus be regarded as an innovative phase, in which rapid character evolution took place. Half of all Early Devonian species range between 1.75 and 2.8.

In Unit 1, the WER has a relatively wide range (from 1.3 to 3.3), though it lies between 1.7 and 2.3 in 50% of the species. In Unit 2, the situation is completely different in that the species occupy a larger morphospace. An almost exact match of the data to the best-fit normal distribution results from a symmetri-

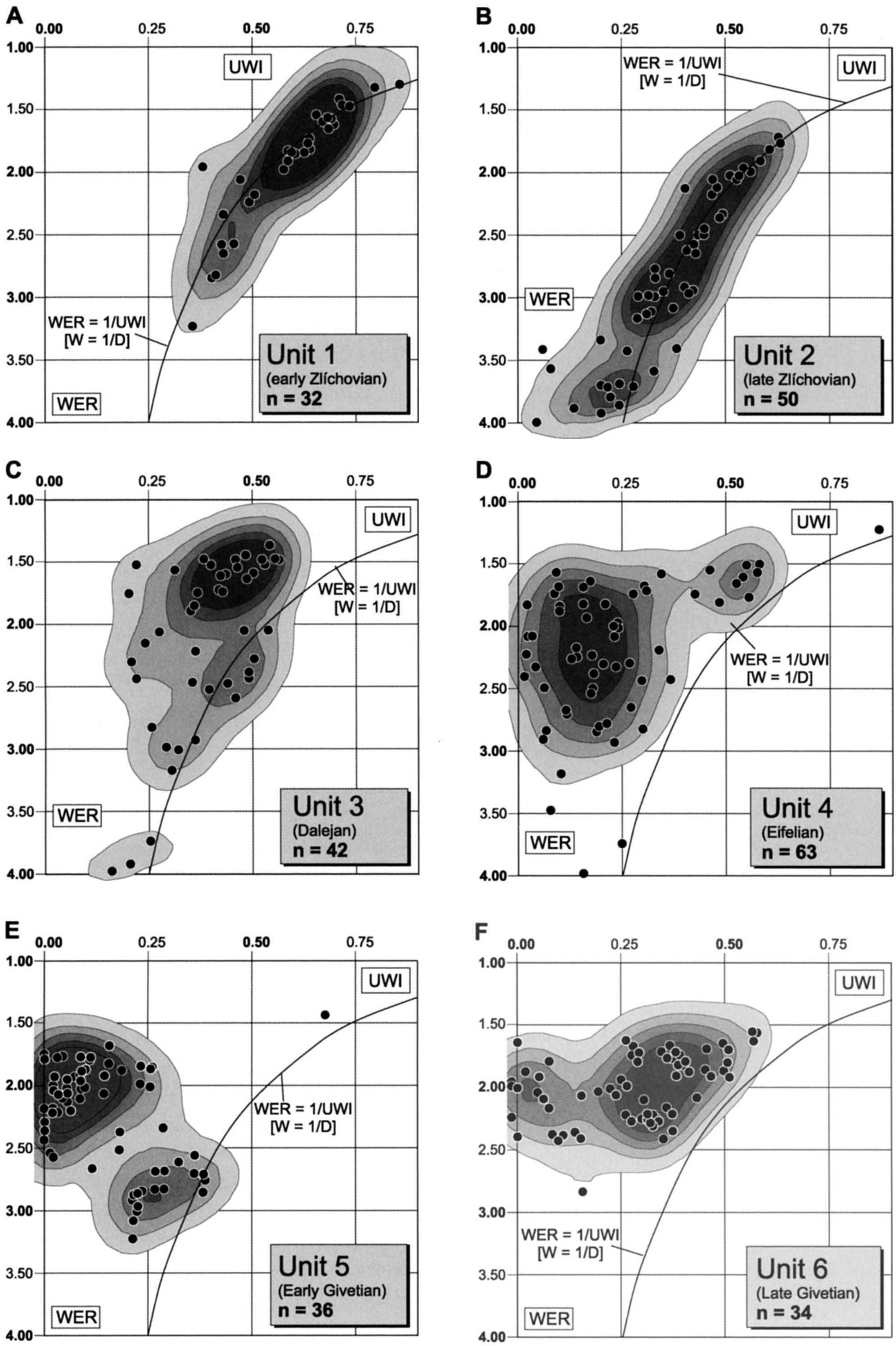


FIGURE 4. Bivariate diagrams of whorl expansion rate (WER)/umbilical width index (UWI) of Early and Middle Devonian ammonoid species during the six separated time units. Each species is represented by one dot. Because of the covariance of WER and WWI and of UWI and IZR respectively, the above parameters (WER, UWI) were selected for the graphs. An increase in the diversity of conch morphology from Unit 1 (4A) to Unit 4 (4D) is followed by a decrease during Units 5 and 6 (4E, F). This is evident from the size of the area occupied by ammonoid taxa. It is mainly caused by the rise and fall of the D-morph and E-morph, which produced conchs with high WERs. WERs and UWIs vary the most among ammonoid taxa from Unit 3 (4C) and Unit 4 (4D), whereas the earliest ammonoid associations (Unit 1, 4A) are the least diverse in WWI and IZR values.

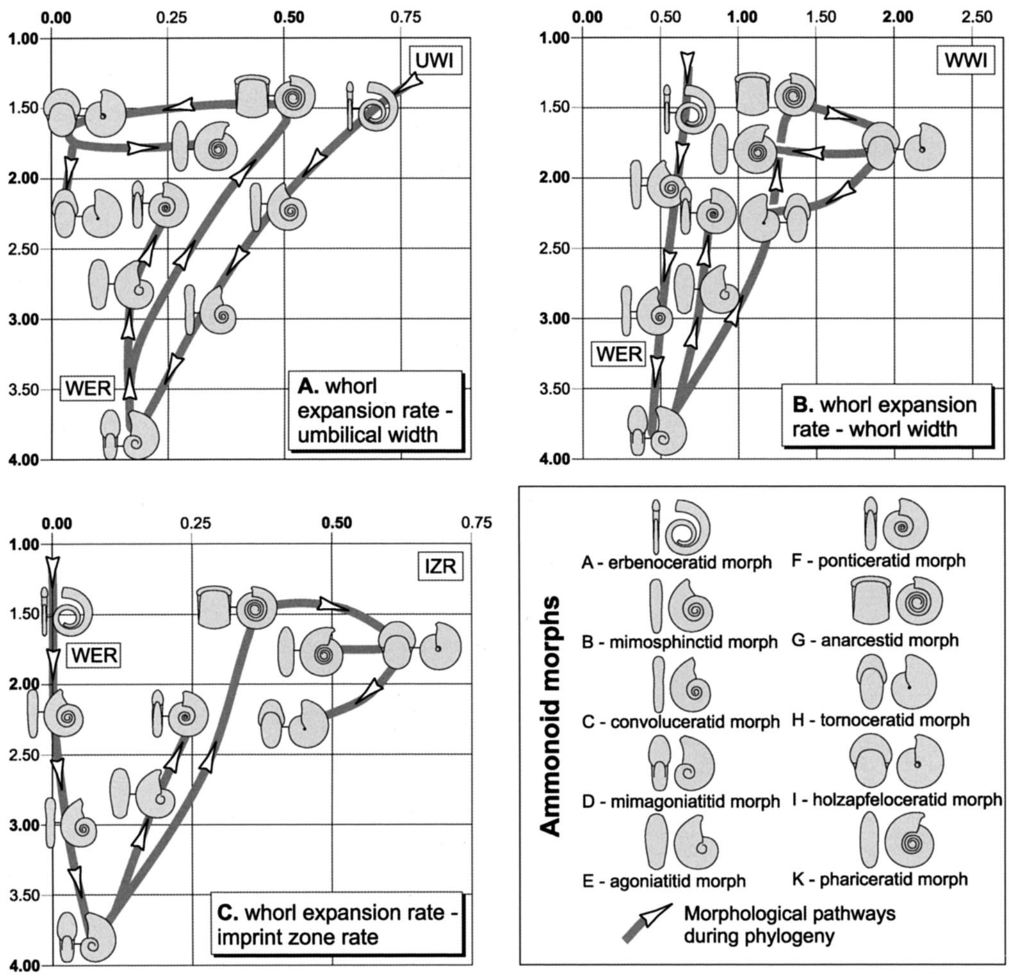


FIGURE 5. Morphological pathways of the ten Early and Middle Devonian ammonoid morphs (mean values indicated by sketched representatives) in bivariate coordinate diagrams. A, Whorl expansion rate (WER)/umbilical width index (UWI). B, Whorl expansion rate (WER)/whorl width index (WWI). C, Whorl expansion rate (WER)/imprint zone rate (IZR).

cal arrangement of the species within the WER morphospace (Fig. 7), with both mean and median values around 2.8, at the center of the distribution range. This means that the average WER increased by 1.0 in the time from Unit 1 to Unit 2.

In Unit 3, the total range of the WER increased, and, in contrast to the preceding time unit, the distribution of the species is here strikingly asymmetric. Half of the species are located between 1.7 and 2.5, with the median value at 2.1. The asymmetry shown in the long tail (deviating from the best-fit normal curve) is due to the predominance of the G-morph with low apertures on the left side. The few species belonging to the D-morph with an extremely high WER of 3.0 and more are located on the right side.

The transition from Unit 3 to 4 is not accompanied by any remarkable shift in the WER values. Thus, the expected normal curve is as symmetric as it is for Unit 3. The column diagram shows two peaks of distribution, one wide peak at 1.6 (anarcestids), and a narrower one at 2.5 (agoniatitids), which is separated by a saddle near 2.0. The middle two quartiles range between 1.8 and 2.4.

Distribution of the WER values in Unit 5 does not differ significantly from Unit 4. The best-fit normal curve is symmetric, but the column diagram demonstrates that two peaks, one at about 1.8 and the second at 2.5,

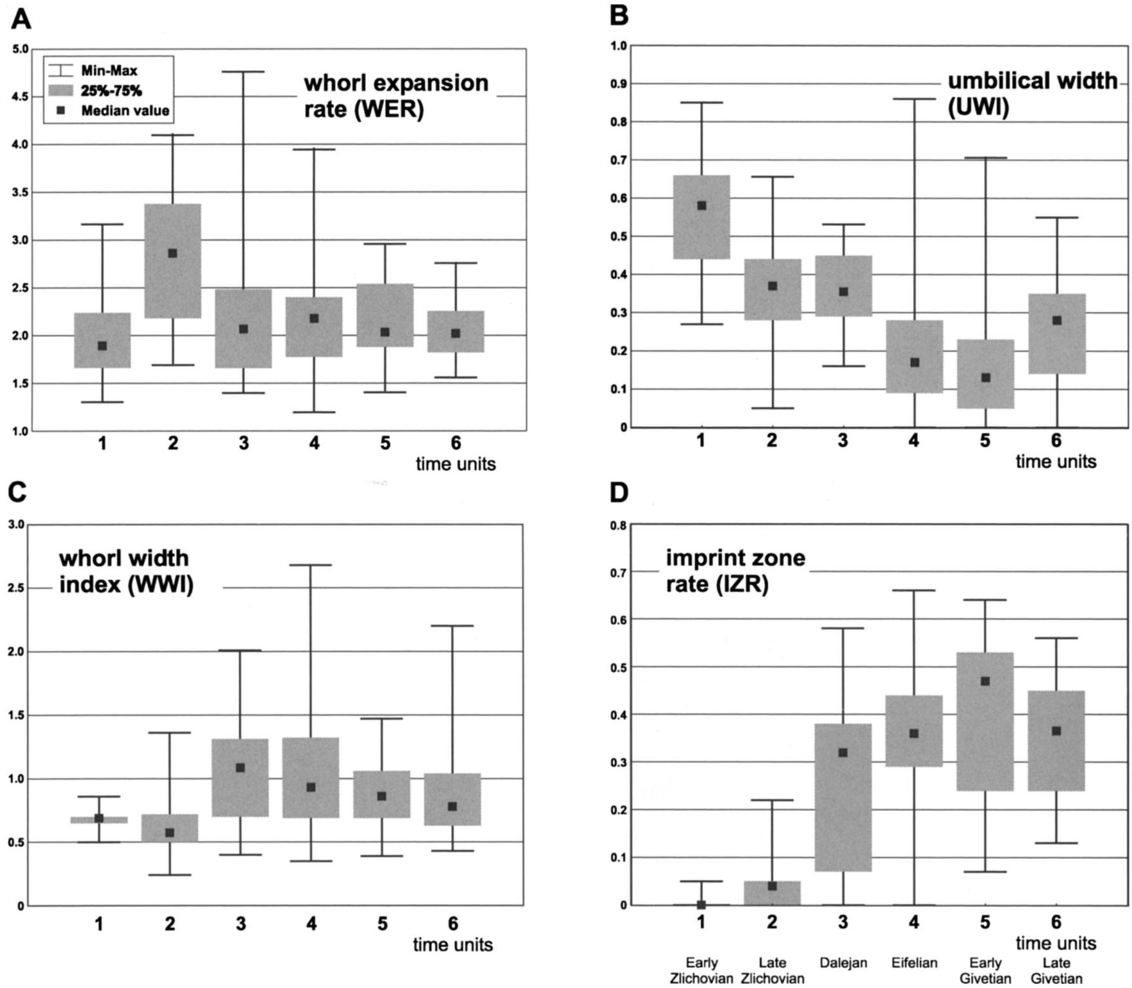


FIGURE 6. Whiskers diagrams showing the distribution and fluctuations of ammonoid conch morphology within the six discriminated time units (whiskers outline = range of morphology, gray boxes = middle two quartiles, dots = median value). An increase in the range of conch morphology from Unit 1 to Unit 4 is followed by a decrease during Units 5 and 6. Nearly all parameters vary the most among ammonoid taxa of Units 3 and 4, whereas the earliest ammonoid associations (Unit 1) are the least variable in WWI and IZR.

are separated by a deep saddle near 2.1 (Fig. 7). This two-fold distribution coincides with the almost equal presence of the two major lineages, i.e., the branches represented by the E- and G-morphs.

The occupied morphospace decreases in Unit 6. This is visible in the limited range of WERs from 1.6 to 2.8, and especially in the fact that half of the species range between 1.8 and 2.2. Such a narrow field of morphospace occupation is unique among the investigated Early and Middle Devonian time units. Figure 7 displays the striking fact that the peak caused by the E-morph completely disappeared. This is due to the very few agoniatitid descendants (E-morph) in Unit 6.

Umbilical Width Index (UWI).—In addition to having gyroconic coiling, many ammonoids of Unit 1 have very wide umbilici. A long-term trend toward narrowly umbilicate conchs can be observed in the subsequent units (Fig. 6B). This means that the average (median) value decreases from almost 0.6 in Unit 1 down to 0.13 in Unit 5. A leap in the median value to 0.28, caused by the radiation of the evolute K-morph, does not occur until Unit 6. It is notable that the variability within the faunas, which is expressed by the range of

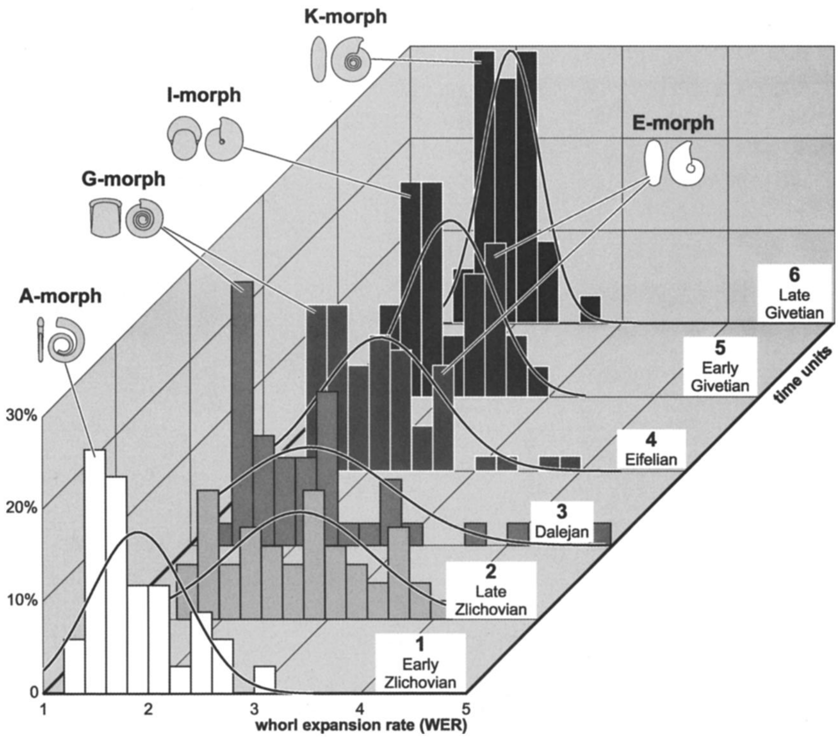


FIGURE 7. Frequency distribution and changes of the WERs of Early and Middle Devonian ammonoid species. Note the shift in the distribution of WER through time. In Unit 1, the values of this parameter are concentrated around 1.6. During Unit 2 and 3, two peaks are present at WER values of 1.8 and 2.8. Additionally, the total range of WER is extended toward high values of over 4. From Unit 2 to 6, one main trend can be seen in the diagrams: the range of WERs is reduced with a concentration on relatively low values.

the middle two quartiles, is stable during the Early and Middle Devonian. Extreme morphologies occur rarely, and they barely influence this picture.

Whorl Width Index (WWI).—Among the four investigated conch parameters, the WWI is the most stable (Fig. 6C). The variability is low in Units 1 and 2, and increases in Unit 3. From Units 3 to 6, the median value continuously decreases from 1.1 to 0.7.

Imprint Zone Rate (IZR).—Ammonoid phylogeny started with gyroconic and advolute conchs, and hence an overlap of whorls is an apomorphic character of stratigraphically later (Unit 3 and younger) species. Figure 6D shows that highly overlapping whorls became common in Unit 3. The middle two quartiles occupied a range between 0.08 and 0.38, representing an enormous disparity. Although the total range became even wider during Unit 4, the middle quartiles occupied a much smaller field. The median IZR increased until Unit 5 (0.47) and decreased in Unit 6 (0.36).

Morphological Pathways

Unit 1 (Early Zlíchovian).—At the beginning of recorded ammonoid existence in Unit 1, ammonoids occupied only a limited area of morphospace (Figs. 4A, 6). Species from Unit 1 belong only to the A- and B-morphs, of which the A-morph represents the most plesiomorphic ammonoid group. The B-morph derived from the A-morph as a result of an increase in WER (1.50 → 2.25) and a narrowing of the umbilicus (0.60 → 0.45). This is mainly caused by the shift from a gyroconic toward an advolute (i.e., with whorls touching the preceding) coiling mode of the conch. As in the A-morph, the whorls may slightly embrace each other in the B-morph, and hence the IZR remained very low. There was no significant modification of the whorl cross-section. In both morphs, the whorl cross-section remained compressed and oval.

Unit 2 (Late Zlíchovian).—In Unit 2, a successive heightening of the aperture caused an increase in WER in many species. Four morphs (A-, B-, C-, and D-morphs) existed, all of them of approximately equal abundance (Figs. 4B, 5). These four morphs represent a more or less continuous morphological series from widely umbilicate conch shapes (UWI 0.60) with low aperture (WER 1.50) to conch geometries with a narrow umbilicus (UWI 0.20) and high aperture (WER 3.75). A phylogenetic succession of the following morphs is proposed: erbenoceratid (A-morph) → mimosphinctid (B-morph) → convoluticeratid (C-morph) → mimagoniatitid morph (D-morph).

The C-morph is a novelty in Unit 2 because it displays slender conchs with a high aperture and insignificantly overlapping whorls. Within the morphospace occupied by the C-morph, the WWI is a plastic character: there are discus-shaped forms and also forms with circular whorl cross-sections.

Among the Early and Middle Devonian ammonoids, the D-morph is the group that includes the species that possesses the highest WER of all Devonian ammonoids. This reflects a wide opening angle of the whorl spiral (Klug 2001b). The D-morph first appeared in Unit 2 but persisted into Unit 4.

Unit 3 (Dalejan).—A significant faunal changeover occurred from the Unit 2 to Unit 3, mainly characterized by the demise of most of the plesiomorphic ammonoids (i.e., the superfamily Mimosphinctaceae). The A-, B-, and C-morphs are only present by a few relicts, and the D-morph is less important than in Unit 2 (Fig. 4C).

In contrast to the preceding faunas of Units 1 and 2, where only one general morphological trend can be traced, two independent and successful lineages were established in Unit 3 (Fig. 5). The two novelties were the E-morph (agoniatids) and the G-morph (anarcestids). Both derived from the D-morph, which can be proven by a cladistic analysis (Korn 2001) and which is supported by stratigraphic data.

The E-morph is not significantly different from the ancestral D-morph, but displays a lowering of the WER (from almost 4 to approximately 3 and less). Simultaneously, the IZR increased from 0.05 to 0.25.

The G-morph is dominant in Unit 3, where some genera are diverse in species and almost globally distributed. In contrast to the agoniatitid lineage (E-morph), the anarcestid branch (G-morph) undergoes rapid character transformation, leading to new ammonoid morphologies. Representatives of the G-morph display a very low WER of approximately 1.50, which is nearly as low as in the earliest ammonoids of the basal Unit 1, and a wide umbilicus. This means that the morphological trend that led to higher WERs during Unit 1 and 2 was reversed in the anarcestid lineage (G-morph) within Unit 3. It does not imply that Unit 1 and late Unit 3 ammonoids (especially the A- and G-morphs) display similar conchs. The anarcestids (G-morph) have, in contrast to the erbenoceratids (A-morph), circular or semilunate whorl cross-sections that embrace the preceding ones with an IZR of 0.35 or more.

Unit 4 (Eifelian).—The bivariate plot of WER and UWI, characteristic of the ammonoid morphospace of Unit 4, presents a markedly modified image when compared with that of Unit 3 (Fig. 4D): The B- and C-morphs are no longer existent, the D-morph has almost completely disappeared, and the anarcestids (G-morph) have also lost importance. Predominant are the agoniatitid morph (E-morph) and the new holzapfeloceratid (I-morph) and tornoceratid (H) morphs, the latter two being anarcestid descendants.

In the Eifelian, the morphologically rather conservative agoniatitids (E-morph) are important and diverse. Only in conch thickness do they show a relatively wide variability, ranging from pachyconic conchs with moderately wide umbilici to extremely slender, oxyconic conchs with closed umbilici (Klug and Korn 2002). The WER of most of the species ranges from 2.50 to 3.00 but may be temporarily higher due to eccentric coiling during the ontogeny of some species (Klug 2001b). Similarly stable is the IZR, ranging from 0.20 to 0.30.

In Unit 4, the G-morph is represented by only a few genera, with extremely low WERs

(1.40 to 1.70) and wide semilunate whorl cross-sections.

It is again the anarcestid lineage that is remarkable for rapid morphological evolution in Unit 4. From the basal part of Unit 4, a trend from widely umbilicate to involute conchs can be observed. This is documented by intermediate forms (UWI = 0.1 to 0.3), leading to the I-morph with punctiform umbilicus (Fig. 5). At the same time, the IZR increased from 0.35 to 0.60, whereas the WER only insignificantly increased from 1.50 to 1.75. The umbilical window became closed in the transformation from the G- to the I-morph.

The second novelty in Unit 4 is the very narrowly umbilicate H-morph with a WER of approximately 2.25. It probably derived from the I-morph by narrowing the umbilicus and reducing the IZR to 0.40. As can be seen in Figure 4D, these two morphs cannot be clearly distinguished; they are connected by intermediates that do not allow unequivocal assignment. Representatives of the H-morph became extremely successful in the Late Devonian Famennian stage.

Unit 5 (Early Givetian).—Unit 5 is a low-diversity period, as can be seen in the bivariate plot of the WER and UWI. Almost no widely umbilicate species existed, and only three morphs (E-, H-, and I-morphs) occupied a comparatively small area of the morphospace. New morphs were not introduced.

The E-morph was still rather important (because of diversification of *Agoniatites*), but the predominant ammonoid morphs of Unit 5 were the narrowly umbilicate anarcestid descendants, the holzapfeloceratids (I-morph) and tornoceratids (H-morph). These two morphs together represent the maximum density in the bivariate plot (Fig. 4E).

Unit 6 (Late Givetian).—A faunal changeover from Unit 5 to Unit 6 is mainly documented by the entry of two new advanced ammonoid groups, the ponticeratids (F-morph) and the pharciceratids (K-morph). Only few of the ammonoids of Unit 6 belong to the H- and I-morphs which dominated the faunas of Unit 5.

The two novelties share morphological features of their ancestors: The F-morph upheld the comparatively high WER (2.25–2.50) and low IZR (0.25) of the E-morph, whereas the umbilicus became wider (0.25–0.35). This morph, which is represented by only a few Middle Devonian species (Unit 6), became important during the Late Devonian Frasnian stage.

The anarcestid lineage again displayed a more rapid character transformation, leading to the establishment of the K-morph, which originated in the I-morph in Unit 6 (Fig. 5). The following characters unfolded in the development of the I- and K-morphs: The umbilicus is shown to be the most plastic character. It became wider (0.10 $\rightarrow$ 0.40), but the width was reduced in the advanced multilobate pharciceratids (K-morph), which are almost involute. In conclusion, this means that within the lineage from the anarcestids (G-morph) to the advanced pharciceratids (K-morph), trends in UWI were reversed twice. Both WER and IZR are similar as in the I-morph and do not show significant modifications.

Discussion

When compared with the development of morphological diversity in the Namurian ammonoids (Saunders and Swan 1984), the Early and Middle Devonian character evolution displays both striking similarities and significant differences. The phylogeny of the early ammonoids shows two independent lineages, of which the agoniatitids (E-morph) resemble the Carboniferous prolecanitids in their slow morphological diversification. At the same time, the anarcestids (G-morph) evolved rapidly and are, in this behavior, similar to the Namurian goniatitids.

In contrast to the time units investigated by Saunders and Swan (1984), sudden radiations and reappearances of morphs play only a minor role in Early and Middle Devonian ammonoids, where the discriminated morphs largely coincide with phylogenetic units that are usually arranged in stratigraphic order. It is noteworthy that, even within the morphologically rather plastic anarcestid lineage (G-morph and descendants), character variability ranges within distinct limits; e.g., the WERs only rarely exceed a value of 2.25 to occupy part of the agoniatitid morphospace (E-morph). Additionally, all anarcestids (G-morph) as well as their Middle Devonian descendants maintain their deeply embracing whorls. Plasticity includes mainly the width of the umbilicus and the shape of the whorl cross-section.

Three major features can be detected in the evolutionary history of Early and Middle Devonian ammonoids; these trends can be discussed in terms of geometric constraints:

1. Long-term morphological trends (mainly expressed in the most ancestral ammonoids of Units 1 and 2; A- and B-morph).
2. Short-term morphological trends and character reversals (preferably expressed in the anarcestid lineage; G-morph).
3. Character stasis (expressed in the agoniatitid lineage; E-morph).

Long-term Morphological Trends.—Several long-term evolutionary trends are known from the Early and Middle Devonian ammonoids (Erben 1964; Korn 2001). One is the continuous closing of the umbilical window, which occur over a long period in the erbenoceratid → mimagoniatitid → anarcestid → holzapfeloceratid lineage (A-, D-, G-, I-morph) from Unit 1 to Unit 3. This trend is in part paralleled by an increase in WER (from 1.3 to maximally 4.75) and by a narrowing of the umbilicus from 0.85 to 0.20 of the conch diameter (in the lineage A- → B- → C- → D-morph). Another main trend is the increase of the whorl overlap; the IZR was continuously heightened from the B-morph (without whorl overlap) through the C-, D-, and G-morphs, reaching a maximum in the I-morph (with an IZR of 0.60 and more).

Short-term Morphological Trends and Character Reversals.—During the evolution of ammonoid morphology during the Early and Middle Devonian, three major turning points with subsequent character reversals can be traced:

1. D-morph (affecting the WER): The trend toward higher apertures (i.e., higher WER) had its climax in Units 2 and 3, when *Paraphyllites* and *Rherisites* reached 4.75, a value never again reached by Paleozoic ammonoids. The mimagoniatitids (D-morph) can be regarded as ancestral to the agoniatitids (E-morph) and anarcestid lineages (G-morph), both with a reduced WER. The reversal was insignificant in the E-morph (3.75 → 2.75), but was very striking in the G-morph (3.75 → 1.50).
2. G-morph (affecting the WER and UWI): The rapid decrease in the WER from the D- to the G-morph was paralleled by the development of widely umbilicate forms (*Anarcestes*, *Sellanarcestes*). The minimum WER lies around 1.45. Following this minimum, the WER slightly increased in the descendant anarcestids up to 1.75, and the umbilicus was closed almost perfectly.
3. I-morph (affecting the IZR and UWI): The I-morph displays the highest whorl overlap value with the IZR reaching 0.65. Such extreme semilunate whorls were not produced by later Middle Devonian anarcestids, in which the IZR lies between 0.45 and 0.60. Another reversing character is the umbilicus, which is very small in the I-morph and became wider in subsequent lineages.

Character Stasis.—It is striking that the two independent Middle Devonian lineages, the agoniatitid (E-morph) and the anarcestid branches (G-morph), are very dissimilar in their speed of unfolding conch morphologies. The agoniatitid lineage is much more conservative in the development of new conch geometries in contrast to the rapidly evolving anarcestid tree.

For example, the general conch morphology of early agoniatitids (i.e., *Fidelites* from the basal Eifelian) with WER = 2.75 and uw/dm = 0.25 can also be seen in the early Givetian *Agoniatites*, in the late Givetian *Mzerrebites*, and in the Frasnian *Manticoceras*. These genera also share common features such as the ontogenetic acceleration of the whorl expansion rate leading to eccentric coiling (Klug 2001b; Korn 2001).

Construction Constraints.—The geometrical limits of the four quantitative characters are as follows: The WER in coiled ammonoids cannot range below 1.30, because then the space in the body chamber would be too depressed to accommodate the animal. A WER higher than 5.00 was probably not reached by coiled ammonoids because of the extreme shortening of the body chamber in such forms (Raup 1967; Saunders and Shapiro 1986) and disadvantageous distribution of the soft body. The umbilical width (UWI) can range from zero (closed umbilicus) tp approximately 0.75. An extremely wide umbilicus can only be realized in conchs with very low WER (WER = 1/UWI line in Fig. 4). The IZR can range from zero (non-embracing whorls) to approximately 0.65. Such a high value can only be realized in conchs with very low WER and a small umbilicus. The limits of WWI are not very well defined; within the studied material, WWI ranges from 0.24 to 2.70.

It can be observed that these limits for the conch geometry were tested several times by the Early and Middle Devonian ammonoids: The D-Morph (mimagoniatitids) reached the upper limit of 4.75 in the WER; the G-Morph (anarcestids) reached the highest UWI (more than 0.50) together with low WER (1.50) and moderate IZR (0.35); and the I-Morph (holzapfeloceratids) reached the highest IZR (0.60).

Random or Nonrandom Processes?—At least some of the trends within the evolutionary history of the Early and Middle Devonian ammonoids can be explained by geometrical or physical limits of character unfolding. These trends appear to be random and display the characteristic pattern described as "left-wall effect" (Gould 1996). At the beginning of their evolution, and because of their origin from orthocone cephalopods with small opening angle of the cone (Schindewolf 1933; Erben 1964), ammonoids were at the "left wall" with their widely open spirals with low aperture (and thus wide umbilicus and low WER) of non-embracing whorls (and thus IZR = 0). Character unfolding could thus only include an opening of the aperture (toward higher WER), narrowing of the umbilicus, and increase in the embracing rate of the whorls (toward higher IZR).

However, the entire process of character unfolding in the Early and Middle Devonian ammonoids cannot be interpreted as random or passive. The geometrical constraints cannot explain the presence and course of morphological trends within the frame of geometric limits. As can be seen in Figures 4 and 6, a migration of the occupied morphospace occurs during time units 1 to 3, rather than an expansion of the morphological spectrum from a "left wall." Some patterns in the evolution of conch parameters are compatible with an nonrandom (active) system, but it remains unclear which agents biased this process. In conclusion it can be stated that the process of transformation of conch geometry in the Devonian ammonoids differs, in its expression of seemingly directed and also commonly reversed trends, from the picture outlined for the evolution of complexity in Paleozoic ammonoid sutures (Saunders et al. 1999).

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Appendix 1

Morphometric data of the 239 Early and Middle Devonian ammonoid species that were included in this study. Abbreviations: dm = conch diameter, WER = whorl expansion rate, UWI = umbilical width index, IZR = imprint zone rate, WWI = whorl width index, t unit = stratigraphic occurrence. Also shown are the morphs to which the species are attributed, and the source of the data.

Species	dm	WER	UWI	IZR	WWI	t unit	morph	Reference
Metabactrites formosus	42	1.32	0.77	0.00	0.60	1	A	Bogoslovsky 1972
Kokenia obliquecostata	36	1.19	0.86	0.00	0.83	4	A	Erben 1960
Anetoceras arduennense	84	1.76	0.55	0.00	0.65	1	A	Erben 1960
Anetoceras elegans	70	1.30	0.85	0.00	0.65	1	A	Yatskov 1990
Anetoceras elegantulum	41	1.86	0.55	0.00	0.80	1–2	A	Ruan 1981
Anetoceras hunsrueckianum	36	1.51	0.62	0.00	0.65	1	A	Erben 1960
Anetoceras medvezhense	28	1.57	0.64	0.00	0.64	1	A	Yatskov 1990
Anetoceras multicostatum	28	1.41	0.68	0.00	0.65	1	A	Ruan 1981
Ruanites cirratus	24	1.59	0.67	0.00	0.70	1	A	Ruan 1981
Ruanites luofuensis	50	1.56	0.66	0.00	0.70	1	A	Ruan 1981
Ruanites obliquecostatus	56	1.54	0.66	0.00	0.72	1	A	Ruan 1981
Ruanites oriens	57	1.77	0.61	0.00	0.70	1	A	Chlupàc and Turek 1983
Ruanites patulus	28	1.46	0.69	0.00	0.70	1	A	Ruan 1981
Ruanites rareplicatus	63	1.80	0.57	0.00	0.70	1	A	Ruan 1981
Ruanites serpentinus	66	1.61	0.65	0.00	0.70	1	A	Ruan 1981
Ruanites subtilis	51	1.47	0.71	0.00	0.71	1	A	Ruan 1981
Erbenoceras advolvens	119	1.77	0.57	0.00	0.59	2	A	Klug 2001a
Erbenoceras circum	43	1.80	0.56	0.00	0.55	1	A	Ruan 1981
Erbenoceras erbeni	72	1.70	0.60	0.00	0.80	1	A	House 1965
Erbenoceras khanakasuense	44	1.68	0.60	0.00	0.69	2	A	Yatskov 1990
Erbenoceras kimi	43	1.74	0.60	0.00	0.68	1–2	A	Bogoslovsky 1980
Erbenoceras sabolotuense	48	1.85	0.55	0.00	0.65	1	A	Yatskov 1990
Erbenoceras solitarium	101	1.80	0.59	0.00	0.66	1	A	Klug 2001a
Chebbites lissovi	40	2.25	0.40	0.00	0.53	1	B	Bogoslovsky 1969
Chebbites nantanense	32	2.17	0.46	0.00	0.70	1	B	Ruan 1981
Chebbites mattei	35	1.91	0.54	0.00	0.70	1	B	Feist 1970

Appendix 1. Continued.

Species	dm	WER	UWI	IZR	WWI	t unit	morph	Reference
Chebbites pyshmense	41	1.98	0.44	0.03	0.70	1	B	Bogoslovsky 1969
Chebbites reisdorfi	11	2.16	0.27	0.02	0.85	1	B	Klug 2001a
Mimosphinctes bipartitus	25	1.93	0.53	0.00	0.70	2	B	Erben 1953
Mimosphinctes cantabricus	46	2.10	0.44	0.00	0.66	2	B	Kullmann 1960
Mimosphinctes discordans	36	2.40	0.41	0.03	0.52	2	B	Erben 1965
Mimosphinctes erbeni	55	1.89	0.51	0.00	0.58	2	B	Bogoslovsky 1980
Mimosphinctes rotatile	48	2.11	0.48	0.00	0.67	1	B	Ruan 1981
Mimosphinctes rudicostatum	55	1.96	0.48	0.01	0.68	2	B	Bogoslovsky 1980
Mimosphinctes tenuicostatus	29	2.05	0.45	0.02	0.57	2	B	Bogoslovsky 1969
Mimosphinctes tripartitus	19	1.99	0.50	0.00	0.72	2	B	Erben 1953
Mimosphinctes zlichovensis	26	2.48	0.40	0.02	0.70	1–2	B	Chlupàc and Turek 1983
Talenticeras talenti	64	2.50	0.43	0.00	0.60	1	B	Erben 1965
Lenzites gesinae	71	2.75	0.38	0.01	0.50	1	B	Klug 2001a
Lenzites lenzi	55	2.56	0.41	0.00	0.72	1–2	B	House and Pedder 1963
Gyroceratites angulatus	22	2.40	0.37	0.00	0.56	2–3	B	Erben 1960
Gyroceratites armoricanus	30	2.25	0.47	0.00	0.53	2	B	Erben 1960
Gyroceratites circularis	10	2.41	0.42	0.00	0.55	2	B	Chlupàc and Turek 1983
Gyroceratites dorsolamellatus	30	2.18	0.47	0.00	0.53	3	B	Erben 1960
Gyroceratites glaber	27	2.30	0.46	0.00	0.50	2–3	B	Bogoslovsky 1969
Gyroceratites gracilis	63	2.37	0.41	0.00	0.58	3	B	Chlupàc and Turek 1983
Gyroceratites laevis	17	1.97	0.50	0.00	0.46	2–3	B	Erben 1953
Gyroceratites pallantianus	10	2.34	0.46	0.00	0.55	3	B	Montesinos and T-M 1986
Teicherticeras buluti	56	3.02	0.36	0.02	0.46	2	C	Erben 1965
Teicherticeras coskuni	37	1.99	0.44	0.02	0.56	2	C	Erben 1965
Teicherticeras discus	11	2.47	0.43	0.05	0.70	3	C	Erben 1953
Teicherticeras erbeni	16	2.83	0.39	0.04	0.68	2	C	Bogoslovsky 1969
Teicherticeras ilanense	43	2.36	0.42	0.02	0.70	2	C	Ruan 1981
Teicherticeras planum	21	2.54	0.39	0.05	0.54	2	C	Bogoslovsky 1980
Teicherticeras teicherti	51	2.72	0.39	0.04	0.57	1	C	Teichert 1948
Gracilites nevadensis	108	2.68	0.31	0.10	0.34	2	C	Miller 1938
Gracilites svetlanae	66	2.88	0.33	0.04	0.37	2	C	Bogoslovsky 1972
Gracilites talyndzhensis	43	2.72	0.35	0.05	0.24	2	C	Yatskov 1992
Palaeogoniatites lituus	63	2.85	0.41	0.00	0.96	2	C	Chlupàc and Turek 1983
Irdanites aphelum	32	3.03	0.31	0.02	0.54	2	C	Ruan 1981
Irdanites korni	55	3.17	0.34	0.05	0.86	1	C	Klug 2001a
Irdanites leptum	23	3.66	0.28	0.04	0.73	2	C	Ruan 1981
Convoluticeras flexuosum	19	3.35	0.38	0.03	0.57	2	C	Bogoslovsky 1984
Convoluticeras lardeuxi	10	2.89	0.28	0.05	0.44	2	C	Erben 1960
Convoluticeras nikolaevi	27	3.03	0.30	0.05	0.44	2	C	Bogoslovsky 1969
Convoluticeras tenue	32	2.75	0.31	0.13	0.40	2	C	Bogoslovsky 1969
Fasciculoceras uralense	35	2.82	0.34	0.07	0.56	3	C	Bogoslovsky 1969
Rherisites tuba	55	4.75	0.16	0.07	0.40	3	D	Chlupàc and Turek 1983
Mimagoniatites angulostriatus	27	3.25	0.19	0.06	0.52	2	D	Bogoslovsky 1969
Mimagoniatites bohemicus	77	3.69	0.24	0.07	0.73	3–4	D	Chlupàc and Turek 1983
Mimagoniatites erbeni	64	3.35	0.25	0.04	0.65	2	D	Kullmann 1960
Mimagoniatites fecundus	50	3.88	0.25	0.04	0.72	2	D	Chlupàc and Turek 1983
Mimagoniatites janus	11	2.89	0.39	0.04	0.98	2	D	Erben 1960
Mimagoniatites kolymensis	30	3.57	0.32	0.05	1.36	2	D	Bogoslovsky 1969
Mimagoniatites nearcticus	86	3.64	0.20	0.05	0.60	2	D	Prosh 1987
Mimagoniatites tabuliformis	44	3.65	0.24	0.05	0.50	2	D	Kullmann 1960
Archanarcestes boreus	43	2.68	0.30	0.08	1.22	2–3	D	Bogoslovsky 1972
Archanarcestes kakvensis	32	3.76	0.22	0.06	1.02	2	D	Bogoslovsky 1969
Archanarcestes obesus	68	3.07	0.28	0.04	1.03	2	D	Erben 1960
Archanarcestes pronini	19	2.89	0.31	0.11	1.17	2	D	Bogoslovsky 1969
Amoenophyllites amoenus	81	4.10	0.21	0.09	0.55	2–3	D	Chlupàc and Turek 1983
Amoenophyllites doeringi	34	3.84	0.28	0.01	0.54	3	D	Klug 2002
Chlupacites ? kayai	40	3.04	0.29	0.05	0.70	3	D	Kullmann 1973
Chlupacites praeceps	54	2.69	0.24	0.19	0.87	3	D	Chlupèc and Turek 1983
Chlupacites uralensis	48	2.85	0.27	0.13	0.94	3	D	Bogoslovsky 1969
Latanarcestes latisellatus	26	2.05	0.37	0.20	0.93	2	E	Erben 1953
Latanarcestes noeggerathi	20	2.34	0.33	0.25	1.11	3	E	Becker and House 1994

Appendix 1. Continued.

Species	dm	WER	UWI	IZR	WWI	t unit	morph	Reference
Latanarcestes ventroplanus	23	2.05	0.22	0.29	0.94	3	E	Bogoslovsky 1969
Mimanarcestes nalivkini	38	1.96	0.44	0.27	1.88	3	E	Bogoslovsky 1969
Parentites praecursor	25	3.85	0.14	0.08	0.48	2	D	Bogoslovsky 1969
Kimoceras lentiforme	30	3.68	0.22	0.04	0.51	2	D	Bogoslovsky 1980
Gaurites sperandus	35	3.47	0.08	0.22	0.26	2	D	Bogoslovsky 1984
Celaeceras mirandum	44	4.00	0.05	0.14	0.37	2	D	Bogoslovsky 1969
Achguigites tafilaltensis	84	2.29	0.20	0.31	0.49	3	E	Klug 2002
Paraphyllites tabuloides	55	3.95	0.16	0.07	0.40	4	D	Chlupàc and Turek 1983
Fidelites clariondi	51	2.71	0.18	0.28	0.70	4	E	Petter 1959
Fidelites fidelis	52	3.03	0.10	0.26	0.57	4	E	Chlupàc and Turek 1983
Fidelites kayseri	48	2.55	0.11	0.23	0.59	4	E	House 1978
Fidelites occultus	69	2.25	0.17	0.28	0.60	4	E	Chlupàc and Turek 1983
Fidelites pinguior	71	2.10	0.16	0.40	0.92	4	E	Chlupàc and Turek 1983
Fidelites ruppachense	21	2.31	0.34	0.36	1.32	4	E	House 1978
Fidelites verma	30	2.11	0.13	0.38	0.98	4	E	Chlupàc and Turek 1983
Fidelites termieri	46	2.21	0.22	0.26	0.70	4	E	Termier and Termier 1950
Parafidelites atrousensis	49	2.35	0.16	0.32	0.84	4	E	Klug 2002
Parafidelites vernarhenanus	31	2.40	0.16	0.29	0.50	4	E	Becker and House 1994
Pseudofidelites bockwinkeli	33	2.05	0.13	0.38	0.97	4	E	Klug 2002
Agoniatites annulatus	58	2.31	0.28	0.19	0.72	4	E	Chlupàc and Turek 1983
Agoniatites bicanaliculatus	44	2.62	0.20	0.26	0.91	4–5	E	Becker and House 1994
Agoniatites costulatus	49	2.46	0.34	0.19	0.85	5	E	Wedekind 1918
Agoniatites expansus	56	2.71	0.28	0.18	0.70	4	E	Miller 1938
Agoniatites floweri	105	2.78	0.22	0.19	0.68	4	E	Miller 1938
Agoniatites fulguralis	34	2.55	0.27	0.18	0.69	5	E	Wedekind 1918
Agoniatites holzapfeli	95	2.95	0.20	0.22	0.39	5	E	Wedekind 1918
Agoniatites nodiferus	124	2.66	0.18	0.27	0.70	4	E	Miller 1938
Agoniatites obliquus	41	2.54	0.25	0.21	0.63	5	E	Wedekind 1918
Agoniatites phillipsi	83	2.72	0.21	0.24	0.63	5	E	Wedekind 1918
Agoniatites ? tetrolcus	14	2.18	0.25	0.26	1.26	4	E	Ruan 1981
Agoniatites urfensis	36	2.53	0.25	0.20	0.81	4	E	Correns 1923
Sellagoniatites unilobatus	35	2.60	0.36	0.26	0.70	5	E	Miller 1938
Sellagoniatites waldschmidti	62	2.58	0.22	0.17	0.62	5	E	Holzapfel 1895
Foordites platypleurus	38	2.14	0.12	0.36	0.42	4	E	Petter 1959
Foordites succedens	51	2.20	0.04	0.34	0.54	4	E	Chulpàc and Turek 1983
Foordites veniens	68	2.34	0.06	0.30	0.40	4	E	Chulpàc and Turek 1983
Pseudofoordites hyperboreus	30	2.53	0.11	0.29	0.46	4	E	Bogoslovsky 1969
Mimotomoceras djemeli	26	1.98	0.02	0.38	0.68	4	H	Petter 1959
Pinacites eminens	44	3.35	0.07	0.31	0.35	4	E	Klug and Korn 2002
Pinacites jugleri	33	2.70	0.06	0.32	0.39	4	E	Bogoslovsky 1969
Exopinacites singularis	50	2.76	0.06	0.33	0.36	4	E	Klug and Korn 2002
Meragoniatites meridionalis	13	2.51	0.37	0.07	0.91	5	E	Bansaïd 1974
Atlantoceras tataense	8	1.85	0.48	0.18	1.04	6	?	Bansaïd 1974
Tamarites subitus	61	1.40	0.71	0.10	1.06	5	?	Bogoslovsky 1969
Pseudoprobeloceras nebechense	18	2.20	0.29	0.24	0.79	6	F	Bansaïd 1974
Pseudoprobeloceras pernai	33	2.11	0.34	0.22	1.04	6	F	Wedekind 1918
Ponticeras kayseri	48	2.05	0.42	0.16	0.80	6	F	Wedekind 1918
Ponticeras orientale	34	2.28	0.14	0.32	0.58	6	F	Bogoslovsky 1969
Ponticeras tschernyschewi	18	2.18	0.32	0.19	0.74	6	F	Bogoslovsky 1969
Mzerrebites bifurcatum	21	2.16	0.25	0.19	0.76	6	F	Korn and Wunderlich 1982
Mzarrebites erraticus	77	2.19	0.30	0.29	0.43	6	F	Petter 1959
Mzerrebites juvenicostatus	19	2.37	0.34	0.13	0.92	6	F	Bensaïd 1974
Mzerrebites killani	31	2.17	0.32	0.34	0.90	6	F	Frech 1902
Taouzites acutus	34	2.30	0.09	0.22	0.61	6	F	Matern 1931
Taouzites taouzense	23	2.75	0.16	0.20	0.58	6	F	Bensaïd 1974
Sellanarcestes certus	53	1.46	0.49	0.39	1.44	3	G	Chlupàc and Turek 1983
Sellanarcestes cognatus	53	1.39	0.45	0.42	1.26	3	G	Chlupàc and Turek 1983
Sellanarcestes crassior	43	1.67	0.34	0.35	1.16	3	G	Walliser 1965
Sellanarcestes ebbighauseni	52	1.33	0.50	0.53	1.18	3	G	Klug 2002
Sellanarcestes eos	37	1.64	0.38	0.39	1.11	3	G	Klug 2002
Sellanarcestes naglectus	36	1.46	0.36	0.39	0.71	3	G	Chlupàc and Turek 1983
Sellanarcestes perfectus	43	1.55	0.40	0.38	0.87	3	G	Chlupàc and Turek 1983

Appendix 1. Continued.

Species	dm	WER	UWI	IZR	WWI	t unit	morph	Reference
Sellanarcestes solus	29	2.10	0.33	0.40	1.33	3	G	Chlupàc and Turek 1983
Sellanarcestes tenuior	85	1.52	0.46	0.35	1.08	3	G	Walliser 1965
Sellanarcestes wenkenbachi	35	1.42	0.35	0.48	1.55	3	G	Klug 2002
Anarcestes applanatus	58	1.44	0.48	0.36	1.29	3	G	Chlupàc and Turek 1983
Anarcestes densistriatus	21	1.57	0.45	0.35	1.15	3	G	Chlupàc and Turek 1983
Anarcestes lateseptatus	61	1.42	0.52	0.35	1.73	3	G	Chlupàc and Turek 1983
Anarcestes latissimus	61	1.43	0.52	0.38	2.01	3	G	Chlupàc and Turek 1983
Anarcestes plebeius	51	1.66	0.39	0.36	1.15	3–4	G	Chlupàc and Turek 1983
Anarcestes simulans	26	1.49	0.43	0.32	1.41	3–4	G	Chlupàc and Turek 1983
Paranarcestes chalix	39	1.44	0.42	0.50	1.41	3	G	Klug 2002
Paranarcestes hollardi	38	1.50	0.28	0.44	1.45	3	G	Klug 2002
Paranarcestes pictus	23	1.54	0.39	0.40	1.31	3	G	Chlupàc and Turek 1983
Praewerneroceras suchomastense	37	1.96	0.25	0.39	1.33	3	G	Chlupàc and Turek 1983
Werneroceras bobrovkense	34	2.17	0.19	0.32	0.93	3–4	G	Bogoslovsky 1969
Werneroceras subnautilinum	63	1.96	0.21	0.38	0.90	4	G	Sandberger and Sandberger 1850
Werneroceras subumbonale	26	2.08	0.31	0.36	1.32	4	G	Wedekind 1918
Werneroceras uralicum	41	2.25	0.17	0.39	0.96	4–5	G	Bogoslovsky 1969
Crispoceras crispum	68	1.80	0.32	0.38	0.90	3	G	Chlupàc and Turek 1983
Crispoceras hanusi	55	1.78	0.33	0.35	1.27	3	G	Chlupàc and Turek 1983
Crispoceras tureki	70	1.51	0.31	0.52	1.27	4	G	Klug 2002
Wendtia devians	89	1.54	0.50	0.29	1.22	4	G	Chlupàc and Turek 1983
Wendtia ougarta	21	1.72	0.45	0.33	1.83	4	G	Petter 1959
Cabrieroceras crispiforme	41	1.46	0.54	0.34	2.68	4	G	Klug 2002
Cabrieroceras housei	59	1.52	0.54	0.25	1.88	4	G	Klug 2002
Cabrieroceras mardonesae	90	1.71	0.52	0.35	2.12	4	G	Montesinos 1987
Cabrieroceras plebeiforme	16	1.48	0.51	0.40	2.64	4	G	House 1978
Cabrieroceras rouvillei	37	1.59	0.49	0.38	1.39	4	G	House and Pedder 1963
Diallagites altaicus	54	1.46	0.20	0.58	1.09	3	I	Bogoslovsky 1969
Diallagites globosus	61	1.84	0.15	0.50	0.90	4	I	Klug 2002
Diallagites lenticulifer	52	1.74	0.19	0.49	0.77	4	I	Klug 2002
Diallagites simone	52	1.73	0.09	0.54	0.99	4	I	Klug 2002
Diallagites socolicum	38	1.66	0.18	0.53	1.12	3	I	Bogoslovsky 1969
Diallagites testatus	69	1.88	0.22	0.41	1.27	4	I	Klug 2002
Diallagites wenkenbachiformis	72	1.64	0.25	0.37	0.91	4	I	Bogoslovsky 1969
Subanarcestes bisulcatus	20	1.91	0.22	0.34	1.36	4	I	Bogoslovsky 1969
Subanarcestes coronatus	59	1.57	0.16	0.58	1.40	4	I	Klug 2002
Subanarcestes jahni	19	1.91	0.21	0.41	1.32	4	I	Chlupàc and Turek 1983
Subanarcestes macrocephalus	41	1.72	0.14	0.54	1.59	4	I	Klug 2002
Subanarcestes marhoumensis	65	1.60	0.28	0.47	2.00	4	I	Klug 2002
Subanarcestes sphaeroides	65	1.63	0.28	0.48	1.81	4	I	Klug 2002
Sobolewia cancellata	34	1.54	0.00	0.64	0.93	5	I	Holzapfel 1895
Sobolewia globulare	40	1.66	0.08	0.56	1.22	4	I	Petter 1959
Sobolewia inflata	41	1.77	0.09	0.53	1.40	4–5	I	Termier and Termier 1950
Sobolewia nuciformis	18	1.77	0.05	0.56	1.33	5	I	House 1962
Sobolewia rotella	24	1.78	0.02	0.50	0.97	5	I	House 1962
Sobolewia virginiana	26	1.54	0.04	0.63	1.16	5	I	House 1962
Holzapfeloceras angulatostriatus	14	1.97	0.03	0.34	0.69	4–5	I	Holzapfel 1895
Holzapfeloceras circumflexiferum	12	1.60	0.14	0.55	1.38	4–5	I	Becker and House 1994
Holzapfeloceras convolutum	15	1.61	0.09	0.58	1.06	4	I	Holzapfel 1895
Holzapfeloceras denckmanni	13	1.49	0.08	0.60	1.79	4	I	House 1962
Bensaidites crassus	23	1.74	0.21	0.54	1.47	5	K	Becker and House 1994
Bensaidites koeneni	23	1.71	0.07	0.56	0.70	5	K	Frech 1902
Bensaidites molarius	17	1.77	0.23	0.48	1.35	5	K	Becker and House 1994
Afromaenioceras sulcatostriatum	31	1.68	0.08	0.58	0.70	5	K	Göddertz 1987
Maenioceras terebratum	20	1.93	0.02	0.52	0.59	5	K	Holzapfel 1895
Maenioceras tenue	24	1.88	0.05	0.53	0.65	5	K	Becker and House 1994
Pharciceras amplexum	42	1.83	0.43	0.31	0.93	6	K	House 1962
Pharciceras bidentatum	36	1.63	0.47	0.32	1.43	6	K	Petter 1959
Pharciceras galeatum	76	1.65	0.35	0.45	0.76	6	K	Wedekind 1918
Pharciceras kayseri	45	1.75	0.36	0.35	1.06	6	K	Petter 1959
Pharciceras tridens	45	1.69	0.33	0.38	1.08	6	K	Petter 1959

Appendix 1. Continued.

Species	dm	WER	UWI	IZR	WWI	t unit	morph	Reference
Lunupharciceras applanatum	20	1.80	0.38	0.33	1.37	6	K	Bensaïd 1974
Lunupharciceras arenicum	36	1.96	0.22	0.39	0.94	6	K	Petter 1959
Lunupharciceras becheri	60	1.90	0.24	0.40	0.70	6	K	Petter 1959
Lunupharciceras lateseptatum	22	1.68	0.44	0.26	1.69	6	K	Korn and Wunderlich 1982
Lunupharciceras lunulicosta	51	1.66	0.27	0.47	0.77	6	K	Wedekind 1918
Lunupharciceras pargai	28	1.71	0.37	0.42	1.11	6	K	Montesinos and Henn 1986
Stenopharciceras kseirense	22	1.96	0.19	0.43	0.89	6	K	Göddertz 1987
Synpharciceras clavilobum	38	1.74	0.08	0.54	0.88	6	K	Bensaïd 1974
Synpharciceras plurilobatum	42	1.99	0.06	0.48	0.52	6	K	Petter 1959
Neopharciceras kurbatovi	61	1.82	0.03	0.56	0.49	6	K	Bogoslovsky 1969
Noepharciceras rotundolobatum	18	1.90	0.00	0.49	0.75	6	K	Bogoslovsky 1982
Petteroceras errans	55	1.71	0.26	0.42	0.63	6	K	Petter 1959
Meropharciceras disciforme	55	2.05	0.29	0.43	0.52	6	K	Bensaïd 1974
Altayites gerassimovi	53	1.56	0.55	0.20	1.11	6	K	Bogoslovsky 1969
Parodiceras brachystoma	19	1.74	0.02	0.54	1.22	4	H	Petter 1959
Parodiceras discoideum	26	2.25	0.01	0.45	1.08	4–5	H	House 1978
Croyites croyi	20	2.10	0.02	0.44	0.81	4	H	House 1978
Trevoneites assesi	9	1.82	0.13	0.55	0.83	5	H	Becker and House 1994
Trevoneites foxi	18	2.08	0.26	0.24	0.73	5	H	House 1963
Trevoneites westfalicum	39	2.09	0.08	0.45	0.73	6	H	Holzapfel 1895
Mithraxites eberlei	42	1.58	0.10	0.55	0.60	5	H	Sweet and Miller 1956
Mithraxites mithrax	92	1.57	0.03	0.66	0.50	5	H	Sweet and Miller 1956
Wedekindella brilouensis	29	1.87	0.04	0.50	0.82	5	H	Holzapfel 1895
Wedekindella clarkei	32	1.85	0.08	0.51	1.12	5	H	Holzapfel 1895
Wedekindella lata	23	1.79	0.08	0.52	1.00	5	H	Bensaïd 1974
Wedekindella psittacina	26	1.66	0.17	0.57	1.21	5	H	House 1963
Tornoceras arkonense	19	2.31	0.02	0.42	0.73	5	H	House 1965
Tornoceras typum	26	2.16	0.00	0.47	0.63	5–6	H	Bogoslovsky 1969
Tornoceras uniangulare	44	1.93	0.00	0.44	0.62	5–6	H	Miller 1938

Appendix 2

Qualitative characters of the 74 Early and Middle Devonian ammonoid genera that were included in this study. Abbreviations: coil = coiling of the conch (gyroconic, advolute, or embracing); u wind = size of the umbilical window (large, small, or none); vent = shape of the venter (rounded, acute, slightly flattened, or flat); umb m = shape of the umbilical margin (rounded or angular); sept = general septal form (synclastic or anticlastic); E lobe = form of the external lobe (simple or subdivided by a median saddle); L lobe = form of the lateral lobe (broadly rounded, narrowly rounded, or acute); U lobes = number of umbilical lobes (none, one, two, three, four, or many); gl dir = direction of the growth lines (rursiradiate, rectiradiate, or prorsiradiate); gl cou = course of the growth lines (linear, convex, concavo-convex, or biconvex); VL pro = height of the ventrolateral projection of the growth lines (none, low, or high); E sin = depth of the external sinus of the growth lines (shallow, deep, or very deep); ribs = presence of ribs; VL fur = presence of ventrolateral furrows.

Genus	coll	u wind	vent	umb m	sept	E lobe	L lobe	U lobes	gl dir	gl cou	VL pro	E sin	ribs	VL fur	morph
Metabactrites	gyr	lar	round	round	syn	simp	b rou	none	rurs	conv	none	shal	yes	none	A
Kokenia	gyr	lar	round	round	syn	simp	b rou	none	rurs	conv	none	shal	yes	none	A
Anetoceras	gyr	lar	round	round	syn	simp	b rou	none	rurs	conv	none	deep	yes	none	A
Ruanites	gyr	lar	round	round	syn	simp	b rou	none	rurs	conv	none	deep	yes	none	A
Erbenoceras	adv	lar	round	round	syn	simp	b rou	none	rurs	conv	none	deep	yes	none	A
Chebbites	emb	lar	flat	round	syn	simp	b rou	none	rurs	conv	none	deep	yes	none	B
Mimosphincaes	adv	lar	round	round	syn	simp	b rou	none	rurs	conv	none	deep	yes	none	B
Talenticeras	adv	lar	round	round	syn	simp	b rou	none	rurs	conv	none	deep	yes	none	B
Lenzites	emb	?	flat	round	syn	simp	b rou	none	rurs	bicon	low	v deep	none	none	B
Gyroceratites	adv	sma	flat	round	syn	simp	b rou	none	prors	c–c	high	deep	none	none	B
Teicherticeras	emb	lar	round	round	syn	simp	b rou	none	rurs	bicon	low	deep	none	none	C
Gracilites	emb	lar	flat	round	syn	simp	b rou	none	rurs	bicon	low	deep	none	none	C
Palaeogoniatites	emb	lar	round	round	syn	simp	b rou	none	rurs	bicon	low	deep	yes	none	C
Irdanites	emb	lar	round	round	syn	simp	b rou	none	rurs	bicon	low	deep	yes	none	C
Convoluticeras	emb	lar	round	round	syn	simp	b rou	none	rect	bicon	low	deep	none	none	C
Fasciculoceras	emb	lar	round	round	syn	simp	b rou	none	rect	bicon	low	deep	yes	none	C
Rherisites	emb	sma	round	round	syn	simp	b rou	none	prors	bicon	low	deep	juv	juv	D
Mimagoniatites	emb	sma	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	juv	juv	D
Archanarcestes	emb	sma	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	juv	juv	D
Amoenophyllites	emb	none	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	juv	juv	D
Chlupacites	emb	none	round	round	syn	simp	b rou	none	prors	bicon	high	deep	none	none	D
Latanarcestes	emb	sma	round	round	syn	simp	b rou	none	prors	bicon	high	deep	none	none	E
Mimanarcestes	emb	sma	round	round	syn	simp	b rou	none	prors	bicon	high	deep	none	none	E
Parentites	emb	sma	acute	round	syn	subd	b rou	none	prors	bicon	high	deep	none	none	D
Kimoceras	emb	sma	acute	round	syn	subd	b rou	none	prors	bicon	high	deep	none	none	D
Gaurites	emb	sma	acute	round	syn	subd	b rou	none	prors	bicon	high	deep	none	none	D
Celaeceras	emb	sma	acute	round	syn	subd	b rou	none	prors	bicon	high	deep	none	none	D
Achguigites	emb	none	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	?	juv	E
Paraphyllites	emb	none	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	juv	juv	D
Fidelites	emb	none	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	juv	juv	E
Parafidelites	emb	none	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	juv	juv	E
Agoniatites	emb	none	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	juv	juv	E
Sellagoniatites	emb	none	sl flat	ang	syn	simp	b rou	none	prors	bicon	high	deep	?	juv	E
Foordites	emb	none	sl flat	round	syn	simp	b rou	none	prors	bicon	high	deep	none	juv	E

Appendix 2. Continued.

Genus	coll	u wind	vent	umb m	sept	E lobe	L lobe	U lobes	gl dir	gl cou	VL pro	E sin	ribs	VL fur	morph
Pseudofoordites	emb	none	round	round	syn	simp	b rou	two	prors	bicon	high	deep	none	juv	E
Mimotomoceras	emb	none	round	round	syn	simp	b rou	one	prors	bicon	high	deep	none	juv	H
Pinacites	emb	none	acute	round	syn	simp	b rou	one	prors	bicon	high	deep	none	juv	E
Exopinacites	emb	none	acute	round	syn	subd	b rou	one	prors	bicon	high	deep	none	juv	E
Meragoniatites	emb	none	sl flat	round	syn	subd	b rou	none	prors	bicon	high	deep	juv	juv	E
Atlantoceras	emb	none	sl flat	round	anti	subd	b rou	none	prors	bicon	high	deep	juv	juv	?
Tamarites	emb	none	round	round	?	subd	b rou	none	prors	?	high	deep	yes	?	?
Pseudoprobeloceras	emb	none	round	round	anti	subd	n rou	none	prors	bicon	high	deep	juv	juv	F
Ponticeras	emb	none	round	round	anti	subd	b rou	none	prors	bicon	high	deep	juv	juv	F
Mzerrebites	emb	none	round	round	anti	subd	b rou	none	prors	bicon	high	deep	juv	juv	F
Taouzites	emb	none	acute	round	anti	subd	b rou	none	prors	bicon	high	deep	none	juv	F
Sellanarcestes	emb	sma	round	round	syn	simp	b rou	none	prors	bicon	high	deep	none	none	G
Anarcestes	emb	sma	round	round	syn	simp	b rou	none	prors	bicon	high	deep	none	none	G
Paranarcestes	emb	sma	round	round	syn	simp	b rou	none	prors	bicon	high	deep	none	none	G
Praewemeroceras	emb	sma	round	ang	syn	simp	b rou	none	prors	bicon	high	deep	none	none	G
Werneroceras	emb	none	round	ang	syn	simp	b rou	none	prors	bicon	high	deep	none	none	G
Crispoceras	emb	none	round	ang	syn	simp	b rou	none	prors	bicon	high	deep	none	none	G
Wendtia	emb	none	round	round	syn	simp	b rou	none	prors	bicon	high	deep	none	none	G
Cabrieroceras	emb	none	round	ang	syn	simp	b rou	none	prors	bicon	high	deep	none	none	G
Diallagites	emb	none	round	ang	syn	simp	b rou	none	prors	bicon	high	deep	none	none	I
Subanarcestes	emb	none	round	ang	syn	simp	b rou	none	rurs	conv	low	deep	none	none	I
Sobolewia	emb	none	round	round	syn	simp	b rou	none	rect	bicon	low	deep	none	none	I
Holzapfeloceras	emb	none	round	round	syn	simp	b rou	none	prors	bicon	high	deep	none	none	I
Bensaidites	emb	none	round	round	anti	subd	n rou	one	prors	bicon	high	deep	none	none	K
Afromaenioceras	emb	none	flat	round	anti	subd	n rou	one	prors	bicon	high	deep	none	none	K
Maenioceras	emb	none	round	round	anti	subd	acute	one	prors	bicon	high	deep	none	none	K
Pharciceras	emb	none	round	round	anti	subd	n rou	two	prors	bicon	high	deep	none	none	K
Lunupharciceras	emb	none	sl flat	round	anti	subd	n rou	three	prors	bicon	high	deep	none	none	K
Stenopharciceras	emb	none	acute	round	anti	subd	n rou	three	prors	bicon	high	deep	none	none	K
Synpharciceras	emb	none	round	round	anti	subd	n rou	four	prors	bicon	high	deep	none	none	K
Neopharciceras	emb	none	round	round	anti	subd	n rou	many	prors	bicon	high	deep	none	none	K
Petteroceras	emb	none	round	round	anti	subd	n rou	many	prors	bicon	high	deep	none	none	K
Meropharciceras	emb	none	round	round	anti	subd	acute	many	prors	bicon	high	deep	none	none	K
Altayites	emb	none	acute	round	anti	subd	acute	two	prors	bicon	high	deep	yes	yes	K
Parodiceras	emb	none	round	round	syn	simp	n rou	one	prors	bicon	high	deep	none	none	H
Croyites	emb	none	round	round	syn	simp	n rou	one	prors	?	?	deep	none	none	H
Trevoneites	emb	none	round	round	syn	simp	n rou	one	prors	bicon	high	deep	none	none	H
Mithraxites	emb	none	round	round	syn	simp	n rou	one	prors	?	?	deep	none	none	H
Wedekindella	emb	none	round	round	syn	simp	n rou	one	prors	bicon	high	deep	none	none	H
Tornoceras	emb	none	round	round	syn	simp	n rou	one	prors	bicon	high	deep	none	none	H