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Morphometric evolution and phylogeny of Palaeozoic ammonoids. Early and Middle Devonian

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ABSTRACT:

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A combination of methods from cladistics and stratophenetic analyses is used for a reconstruction of Early and Middle Devonian ammonoid phylogeny. The analyses are based mainly on principal characters such as conch geometry (coiling form, whorl expansion rate, whorl cross-section shape), septal geometry (form of septa, number, position, and shapes of lobes), and ornament (growth lines and ribs); a new classification scheme of the ancient ammonoid order Agoniatitida is proposed. It is subdivided into four suborders: Agoniatitina (paraphyletic), Gephuroceratina (monophyletic), Anarcestina (paraphyletic), and Pharciceratina (monophyletic). Morphometric analysis shows the unfolding of several morphological trends, such as the modification of coiling parameters, among the Early and Middle Devonian ammonoids. Two major independent lineages can be recognised in the phylogeny of the Middle Devonian ammonoids, the first represents the agoniatids in which the Gephuroceratina is nested, the second are the anarcestids which gave rise to the Pharciceratina. The new families Latanarcestidae, Tamaritidae, Atlantoceratidae, and Taouzitidae, as well as the new genera *Taouzites*, *Croyites* and *Meragoniatites* are introduced.

Key Words: Ammonoids, Evolution, Phylogeny, Palaeozoic, Devonian.

INTRODUCTION

Much of the knowledge of diversity and phylogeny of the earliest ammonoids was developed by Heinrich Karl ERBEN, who, in a series of papers (ERBEN 1953, 1960, 1962a, 1964, 1965) attempted to determine the origin and early phylogeny of these cephalopods. He based his conclusions (ERBEN 1965) on his own significant investigations of informative material as well as incorporating the classical studies of BARRANDE (1865, 1866, 1867, 1877), SCHINDEWOLF (1933), BOGOSLOVSKY (1958, 1961, 1963, 1969), and others.

ERBEN's interpretations recognised several morphological transitions that occurred during the evolutionary history of earliest ammonoids which are as follows:

The conch was transformed from an orthocone shape in the Bactritida, passing through "gyrocone", "advolute", and "perforate" stages (i.e. with an umbilical window), towards a coiled and involute form. [In this study, only the coiled forms are regarded as ammonoids, in contrast to HOUSE (1980), who included the bactritids within the Ammonoidea.]

The whorl cross section is compressed in the earliest ammonoids and was successively converted into circular or depressed shapes in early ontogenetic stages and extending towards the adults in more derived forms.

The outline of the aperture was also modified during phylogeny; the rursiradiate course of the growth lines at the beginning of ammonoid evolution was altered towards a prorsiradiate form in phylogenetically later stages.

The simple ribs from the beginning of ammonoid phylogeny were either transformed into more complex sculptures or were abandoned.

GIVETIAN	LATE	*Petteroceras errans*
		Pharciceras tridens
	EARLY	*Maenioceras terebratum*
		Sellagoniatites discoides
		Agoniatites obliquus
EIFELIAN		*Agoniatites vanuxemi*
		Cabrieroceras plebeiforme
		Subanarcestes macrocephalus
		Pinacites jugleri
		Foordites veniens
EMSIAN	DALEJAN	*Anarcestes lateseptatus*
		Sellanarcestes wenkenbachi
		Latanarcestes noeggerathi
	ZLICHOVIAN	*Mimagoniatites fecundus*
		Erbenoceras advolvens

Fig. 1. Emsian to Givetian ammonoid biostratigraphical zones, based on investigations of Moroccan outcrops, after KLUG & KORN (1999)

Practically all subsequent authors based the classification of Early Devonian ammonoids mainly on ERBEN'S studies, but the new discoveries and methodologies now justify a critical reevaluation of the classification of Devonian ammonoids.

In contrast to Early Devonian ammonoids, phylogenetic relationships of Middle Devonian (Text-fig. 1) ammonoids have not been explored by studies comparable with those published by ERBEN. For example, it is commonly assumed that both the gephuroceratids and pharciceratids are derived from anarcestids, as proposed by RUZHENCEV (1957, 1960). Detailed studies of possible phylogenetic relationships have never been published. It is the aim of this study to present a phylogenetic reconstruction for both Early and Middle Devonian ammonoids.

The study presented here is the first cladistic analysis of Devonian ammonoids, and hence can be regarded as a test of this method when applied to this fossil group. Although results are probably biased by the current state of knowledge of ammonoid morphology, this study will at least form a basis for future investigations especially on the phylogenetic positions of some problematic genera.

DATA SOURCE

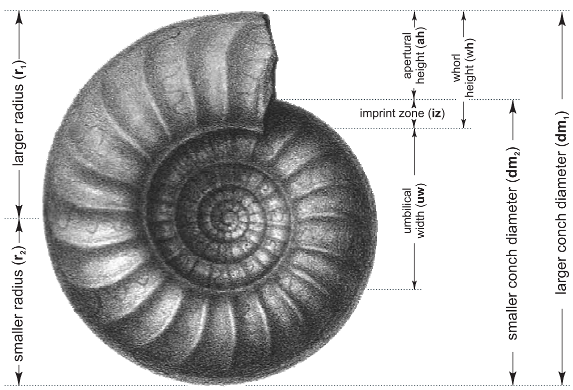
The principal data source for this study is the database GONIAT, Tübingen, version 2.8 (KORN & KULLMANN 1998), in which data from most of the published articles on Devonian ammonoids are assembled. Application of this database enabled a wide overview over the relevant literature, which had to be examined in detail. The most important publications from which data were obtained and which should be credited are listed in Appendix 1.

STRATOPHENETIC ANALYSIS

Methods

The Early and Middle Devonian ammonoids show a range of morphological trends, encouraging a stratophenetic analysis of certain conch parameters. In the following stratophenetic analysis, morphometrical data of most of the Early and Middle Devonian ammonoids were obtained from the literature, showing that four characters (Text-fig. 2), in particular, of conch geometry show significant modifications:

The whorl expansion rate (WER = coiling parameter).
The width of the imprint zone (IZW = whorl embracing rate).
The umbilical width index (umbilical width/conch diameter ratio, uw/dm).
The whorl width index (whorl width/whorl height ratio, ww/wh).



$WER = \left(\frac{r_1}{r_2}\right)^2$ $WER = \left(\frac{dm_1}{dm_2}\right)^2$ $dm_2 = dm_1 - ah$ $IZW = \left(\frac{wh - ah}{wh}\right)$

Fig. 2. The principal conch characters whorl expansion rate (WER), umbilical width, and whorl imprint zone (IZ) in ammonoids

Differences in the whorl expansion rate, the umbilical width, and the imprint zone width demonstrate the presence of distinctive ammonoid morphs (Text-figs 3, 4); these occur in varying abundancies in different time slices.

The whorl expansion rate and umbilical width could be calculated from most of the ammonoid species; the other parameters require well-figured material, especially of cross sections, which could not be gained from a statistically useful number of species. Therefore, the imprint zone width and whorl width/whorl height ratio were only obtained from representative species of each genus.

The parameters whorl expansion rate and umbilical width were plotted in a Cartesian co-ordinate diagram, and contour lines were drawn using the program Spheristat (©1995 Pangaea Scientific), a program usually used to plot and compute data in structural morphology. During the Emsian, Eifelian, and Givetian, complex morphological trends can be observed and figured in bivariate plots (Text-fig. 5).

Early Zlichovian

The occupied morphospace is relatively small in the early Zlichovian (Text-fig. 5A); early Zlichovian ammonoids belong to only two morphs, the erbenoceratid (ER) and mimosphinctid (MS) morphs, the first representing the most plesiomorphic ammonoid group. The mimosphinctid morph is derived from the ER morph by narrowing of the umbilicus, which, of course, is mainly caused by the change from a gyroconic towards an advolute coiling mode of the conch. As in the ER morph, the whorls do not embrace the preceding one, and hence the imprint zone width is zero. No modification of the whorl cross section took place, which remained stable in a compressed oval shape.

Late Zlichovian

In the late Zlichovian, because of continuous increase of the whorl expansion rate, four morphs (ER, MS, CO, and MA) are present, all of them in approximately equal significance (Text-fig. 5B). These four morphs represent a continuous morphological series, of which the mimosphinctid follows from the erbenoceratid, the convoluticeratid from the mimosphinctid, and the mimagoniatid from the convoluticeratid morph.

Morph CO is a novelty in the late Zlichovian; it can be seen as a consequence of a morphological trend towards narrower umbilicate forms with increasing whorl expansion rate. The typical genus *Convoluticeras*

	morph name	WER	uw/dm	IZW	ww/wh	typical genera	stratigraphical range
ER	erbenoceratid	1.50	0.60	0	0.60	*Erbenoceras Anetoceras*	early Zlichovian to Dalejan
MS	mimosphinctid	2.25	0.45	0	0.60	*Mimosphinctes Gyroceratites*	early Zlichovian to Dalejan
CO	convoluticeratid	3.00	0.30	0.05	0.60 - 1.00	*Convoluticeras Teicherticeras*	late Zlichovian to Dalejan
MA	mimagoniatitid	3.75	0.20	0.05	0.40 - 1.00	*Mimagoniatites Archanarcestes*	late Zlichovian to Dalejan
AG	agoniatitid	2.75	0.05 - 0.30	0.25	0.30 - 0.60	*Agoniatites Fidelites*	Dalejan to early Givetian
PT	ponticeratid	2.25	0.30	0.25	0.70 - 1.00	*Ponticeras Mzerrebites*	late Givetian to Frasnian
AN	anarcestid	1.50	0.50	0.35	1.00 - 2.80	*Anarcestes Cabrieroceras*	Dalejan to Eifelian
TO	tornoceratid	2.25	0.05	0.45	0.60 - 1.20	*Tornoceras Parodiceras*	Eifelian to Famennian
HO	holzapfeloceratid	1.60	0.10	0.55	1.00 - 2.00	*Holzapfeloceras Sobolewia*	Eifelian to early Givetian
PH	pharciceratid	1.75	0.10 - 0.55	0.40 -0.50	0.50 - 2.00	*Pharciceras Triainoceras*	late Givetian to Frasnian

Fig. 3. Characterisation of the 10 discriminated Early and Middle Devonian ammonoid morphs, together with typical representative genera as well as stratigraphical range [left column = coded morph names, WER = whorl expansion rate, uw/dm = umbilicus/conch diameter ratio, IZW = imprint zone width, ww/wh = whorl width/whorl height ratio]

displays a slender conch with high aperture and only slightly embracing whorls. Within the morphospace of the CO morph, the whorl width is seen as a plastic character, which contains discus-shaped forms (such as *Gracilites*) and thickly discoidal forms with circular whorl cross sections (*Palaeogoniatites*, *Irdanites*).

Among the Early and Middle Devonian ammonoids, the mimagoniatids (morph MA) is the group that possesses the highest whorl expansion rate, reflecting a rapid opening angle of the whorl spiral. Morph MA is derived from morph CO and first appears in the late Zlichovian, but remains into the Dalejan. Genera of the MA Morph such as *Mimagoniatites* and *Archanarcestes* show oval to subcircular whorls which embrace each other only to a small extent, and the genera of the family Auguritidae have discus-shaped conchs.

Dalejan

There occurred a significant faunal changeover between the late Zlichovian and the Dalejan (Text-fig. 5C), mainly characterised by the demise of the ple-

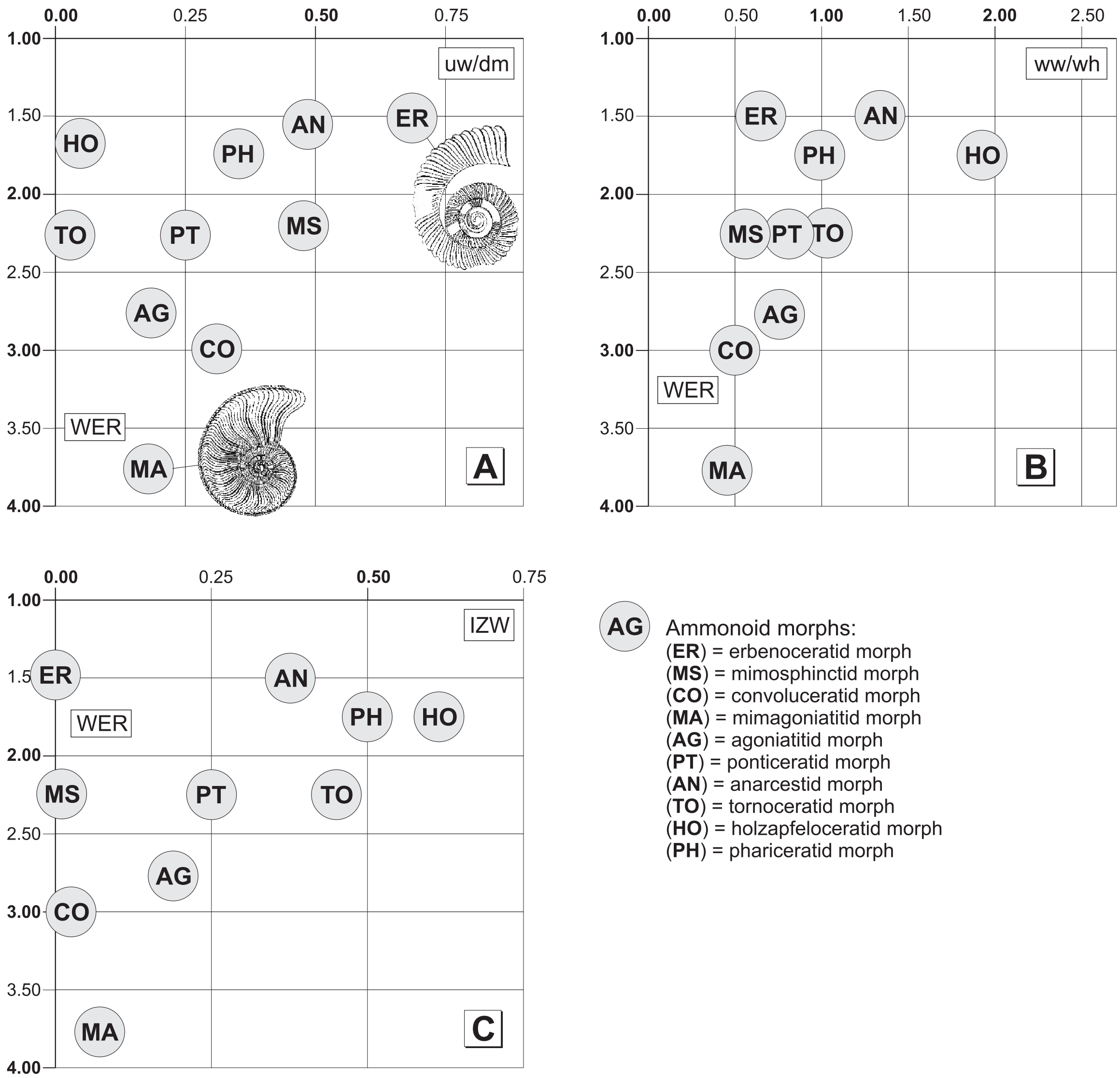


Fig. 4. The 10 Early and Middle Devonian ammonoid morphs (mean values indicated by circles) in bivariate co-ordinate diagrams. Note that the differences between the discriminated morphs are best visible regarding the characters whorl expansion rate (WER), umbilical width, and whorl imprint zone width (IZW). Line drawings from Erben (1965). A. Whorl expansion rate (WER)/umbilical width index (uw/dm). B. Whorl expansion rate (WER)/whorl width index (ww/wh). C. Whorl expansion rate (WER)/imprint zone width (IZW)

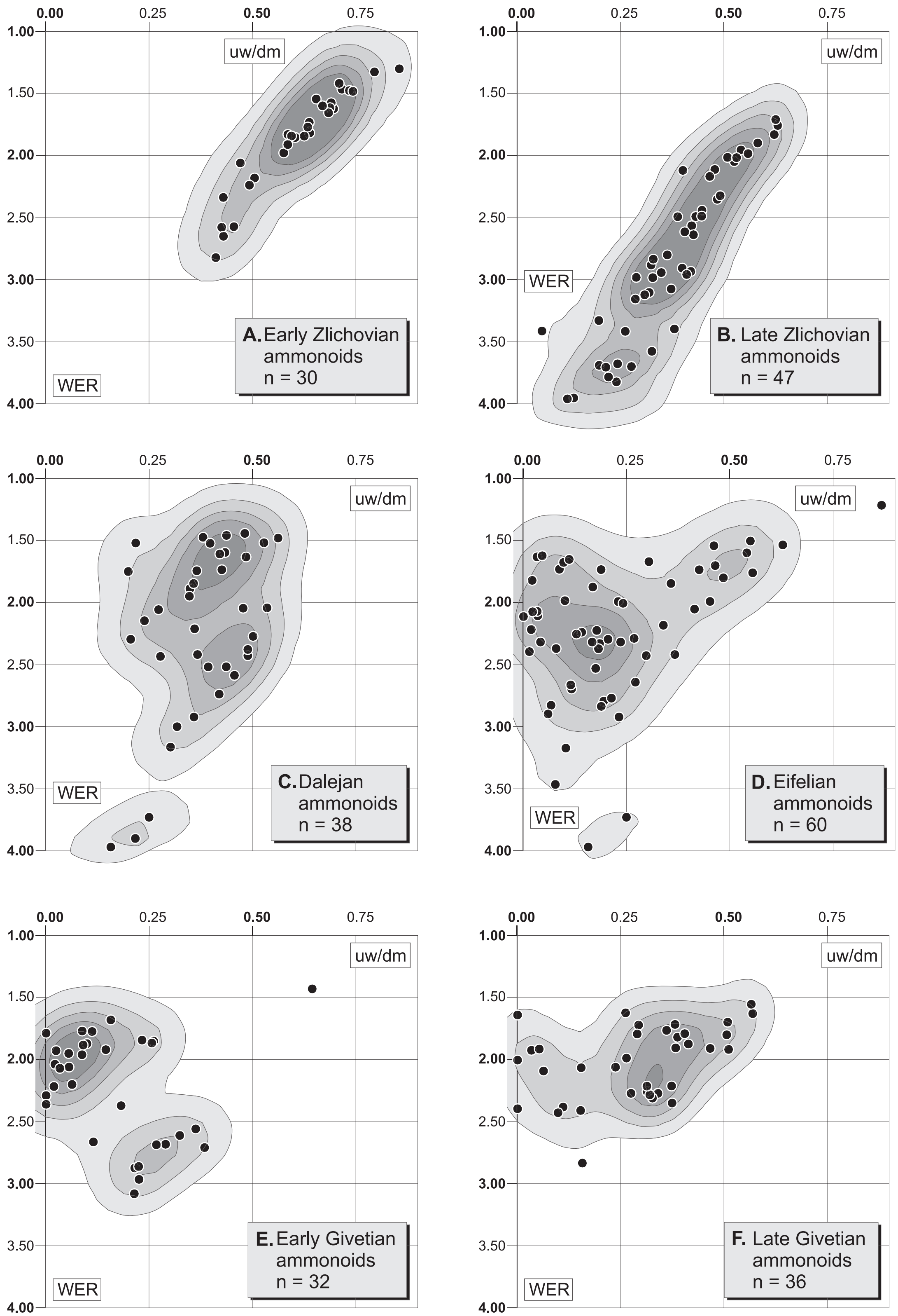


Fig. 5. Bivariate diagrams of whorl expansion rate (WER)/umbilical width index (uw/dm) of Early and Middle Devonian ammonoids during the six separated time units. Each species is represented by one dot

siomorphic ammonoid forms, i.e. the genera *Ruanites*, *Erbenoceras* etc. This resulted in the presence of morphs ER, MS and CO as relicts (e.g. *Gyroceratites*). Although less important, the MA morph is still present in the Dalejan. Two new morphs appear within the Dalejan, the first is the agoniatitid morph (AG), and the second is the anarcestid morph (AN). Both are derived from ancestors within the mimagoniatitid morph, which is supported by the cladistic analysis, and which is further congruent with their stratigraphical distribution. The agoniatitid morph is already present by the early Dalejan, but occurs more frequently in the late Dalejan and continues into the Givetian. It is characterised by a slight lowering of the whorl expansion rate from almost 4.0 in the ancestral mimagoniatitids to approximately 3.0 and less. Simultaneously, the imprint zone width increases from about 0.05 to 0.25. Early Dalejan genera, such as *Latanarcestes* and *Chlupacites* (which do not belong to the family Agoniatitidae, but to the lineage leading to the anarcestids) possess the general AG morph conch geometry, but differ in their thicker conchs with subcircular whorl cross section.

The anarcestid morph is dominant in the late Dalejan, where several genera (*Anarcestes*, *Sellanarcestes*, etc.) are species rich. These forms show a very low whorl expansion rate of approximately 1.50, which is as low as in the earliest ammonoids, and a wide umbilicus. However, this character combination supports an interpretation that they are derived from mimagoniatids, as shown by the presence of intermediate forms such as *Latanarcestes*, and by their stratigraphical occurrence well above the mimagoniatitids. This suggests that the morphological trend that in the Zlichovian led to higher whorl expansion rates and was almost completely reversed during the Dalejan. It does not mean that the early Zlichovian and late Dalejan ammonoids (especially the morphs ER and AN) display similar conchs. The anarcestids show, in contrast to the erbenoceratids, circular or semilunate cross sections of the whorls which embrace the preceding one with an IZW of 0.35 or even more.

Eifelian

The diagram for the Eifelian shows a significantly modified picture (Text-fig. 5D): The MA and CO morphs no longer exist, the MA morph has almost completely disappeared, and the anarcestids (morph AN) have also declined. Predominant are the AG morphs and the newly introduced TO and HO morphs, which among one another are connected by morphologically intermediate forms.

In the Eifelian, the agoniatids (AG morph) are very diverse. They show a wide variability in conch geometry, ranging from thickly discoidal conchs with moderately wide umbilici (as in some species of *Agoniatites*) to extremely slender, oxyconic conchs with very narrow umbilicus (*Pinacites*, *Exopinacites*). The whorl expansion rate of all the species ranges between 2.50 and 3.00, but may be exceeded according to irregularities in the coiling during ontogeny of some species. The anarcestid morph is represented by *Cabrieroceras*, a genus that resembles *Anarcestes*, but has extremely wide semilunate whorl cross sections.

New appearances in the Eifelian include very narrowly umbilicate forms, the tornoceratid morph (TO, represented by *Parodiceras*) with a whorl expansion rate of about 2.25, and the holzapfeloceratid morph (HO) with lower aperture and a whorl expansion rate of only 1.75. These two morphs cannot be sharply separated, and are connected by intermediates.

Early Givetian

The early Givetian is a low-disparity period (Text-fig. 5E), as can be seen in the bivariate plot of the whorl expansion rate and umbilical width. Except for the problematic genus *Tamarites*, no widely umbilicate species existed, and only three morphs (AG, TO, and HO) occupy a comparatively small area of the morphospace.

The agoniatid morph is still rather important because of diversification of the genus *Agoniatites*, but the predominant early Givetian ammonoid morphs are the narrowly umbilicate anarcestid descendants, the tornoceratid morph (represented by the typical genus *Tornoceras*) and holzapfeloceratid morph (e.g. *Holzapfeloceras*, *Maenioceras*). These two morphs together show the maximum density in the bivariate plot (Text-fig. 5E).

Late Givetian

A faunal changeover from the early to the late Givetian (Text-fig. 5F) is mainly documented by the entry of the two new and advanced ammonoid groups, the pharciceratids and the gephuroceratids. Only a few of the late Givetian ammonoids belong to the morphs TO and HO which dominated the Eifelian and early Givetian faunas.

The newly appeared forms belong to two relatively easily separable morphs, the ponticeratid (PT) and the pharciceratid morph (PH). As will be shown in the sections describing the cladistic analysis of the Early and Middle Devonian ammonoids, these formerly unified taxa are herein regarded as independent lineages. The ponticeratid morph (which is most prominent only in the Frasnian) derived from the agoniatitid morph in slightly reducing the whorl expansion rate to a mean value of 2.25, and the pharciceratid morph evolved from the holzapfeloceratid morph in increasing the umbilical width to 0.25 to 0.55 of the conch diameter.

A. Conch form

1	coiling form	gyrocone (**0**), advolute (**1**), embracing (**2**)	o	D
2	umbilical window	large (**1**), small (**2**), none (**3**)	o	D
3	form of first whorl segment	uncoiled (**0**), coiled (**1**)	o	
4	secondary uncoiling in early ontogeny	no (**0**), yes (**1**)	o	
5	imprint zone (in % of whorl height)	0 (**0**), 6 (**1**), 12 (**2**), 24 (**3**), 36 (**4**), 48 (**5**), 60 (**6**)	o	
6	whorl cross section in first whorl	compressed (**0**), circular (**1**), depressed (**2**)	o	D
7	whorl cross section in juveniles	compressed (**0**), circular (**1**), depressed (**2**)	o	D
8	whorl cross section in adults	compressed (**0**), circular (**1**), depressed (**2**)	o	
9	umbilical width (in % of conch diameter)	over 70 (**0**), 60 (**1**), 45 (**2**), 30 (**3**), 15 (**4**), less than 5 (**5**)	o	
10	decrease of umbilical width in ontogeny	none (**0**), not remarkable (**1**), remarkable (**2**),	o	
11	whorl expansion rate	1.40 (**0**), 1.80 (**1**), 2.20 (**2**), 2.80 (**3**), 3.20 (**4**), over 3,60 (**5**),	o	
12	increase of WER during ontogeny	none (**0**), not remarkable (**1**), remarkable (**2**),	o	
13	conch thickness (in % of conch diameter)	30 (**0**), 50 (**1**), 70 (**2**)	o	
14	outline of venter	oxyconic (**0**), rounded (**1**), slightly flattened (**2**), flattened (**3**)	o	
15	umbilical edge	rounded (**0**), angular (**1**)	o	

B. suture line

16	general septal form	synclastic (**0**), anticlastic (**1**)	o	
17	external lobe	simple (**0**), pouched (**1**), subdivided (**2**), twice subdivided (**3**)	o	
18	lateral tie point	none (**0**), yes (**1**)	o	
19	shape of lateral lobe	widely rounded (**0**), narrowly rounded (**1**), pointed (**2**)	o	
20	position of lateral lobe	inner flank (**0**), midflank (**1**), outer flank (**2**)	o	
21	umbilical tie point	none (**0**), one (**1**), two (**2**), many (**3**)	o	
22	adventive tie point	none (**0**), one (**1**)	o	
23	dorsal tie point	none (**0**), yes (**1**)	o	
24	dorsal saddle	none (**0**), yes (**1**)	o	

C. ornament

25	growth line direction	rursiradiate, rectiradiate (**0**), prorsiradiate (**1**)	o	
26	lateral sinus	none (**0**), yes (**1**)	o	
27	ventrolateral projection	none (**0**), low (**1**), high (**2**)	o	
28	ventral sinus	shallow (**0**), deep (**1**), very deep (**2**)	o	
29	ribs in juveniles	none (**0**), yes (**1**)	o	
30	ribs in adults	none (**0**), yes (**1**)	o	
31	rib shape	simple (**0**), fastigate dorsolat. (**1**), fastigate ventrolat. (**2**)	uo	
32	undulated surface of flanks	none (**0**), yes (**1**)	o	
33	umbilical nodes	none (**0**), yes (**1**)	o	
34	external band	none (**0**), yes (**1**)	o	D
35	ventrolateral furrows in juveniles	none (**0**), yes (**1**)	o	
36	ventrolateral furrows in adults	none (**0**), yes (**1**), only depression (**2**)	uo	
37	internal shell thickenings	none (**0**), yes (**1**)	o	
38	venter serrate	none (**0**), yes (**1**)	o	
39	ventral impressions	none (**0**), yes (**1**)	o	

Fig. 6. List of characters and character states used for cladistic analyses of Zlichovian, Dalejan, agoniatitid, and anarcestid ammonoids [o = ordered characters, uo = unordered characters, D = polarised characters]

A. Conch

1	imprint zone (in % of whorl height)	0 (**0**), 6 (**1**), 12 (**2**), 24 (**3**), 36 (**4**), 48 (**5**), 60 (**6**)	o	
2	umbilical width (in % of conch diameter)	less than 5 (**0**), 15 (**1**), 30 (**2**), 45 (**3**), 60 (**4**), over 70 (**5**)	o	
3	modification of umb. width in ontogeny	none (**0**), not remarkable (**1**), remarkable (**2**),	o	
4	whorl expansion rate	1.40 (**0**), 1.80 (**1**), 2.20 (**2**), 2.80 (**3**), 3.20 (**4**), over 3,60 (**5**)	o	
5	modification of WER during ontogeny	none (**0**), not remarkable (**1**), remarkable (**2**)	o	
6	whorl cross section (ww/wh) in adults	0.60 (**0**), 0.90 (**1**), 1.20 (**2**)	o	
7	whorl cross section (ww/wh) in juveniles	1.00 (**0**), 1.60 (**1**), 2.20 (**2**)	o	
8	outline of venter	slightly flattened (**0**), broadly rounded (**1**), narrowly rounded (**2**), subacute, acute (**3**)	o	

B. suture line

9	general septal form	synclastic (**0**), anticlastic (**1**)	o	D
10	external lobe	simple (**0**), pouched (**1**), subdivided (**2**), twice subdivided (**3**)	o	D
11	height of median saddle	none (**0**), 0.2 (**1**), 0.4 (**2**), 0.6 (**3**), 0.8 (**4**), 1.0 (**5**), 1.20(**6**)	o	
12	shape of lateral lobe	shallow (**0**), V-shaped (**1**), lanceolate (**2**)	o	
13	shape of lateral lobe point	broadly rounded (**0**), narrowly rounded (**1**), acute (**2**)	o	
14	number of U lobes on flanks (phar.)	none (**0**), one (**1**), two (**2**), three (**3**), about 10 (**4**), about 16 (**5**), about 24 (**6**)	o	D
15	E lobe prong	none (**0**), very weak (**1**), V-shaped (**2**)	o	
16	shape of ventrolateral saddle	asymmetric (**0**), symmetric (**1**)	o	
17	form of umbilical lobe point	broadly rounded (**0**), narrowly rounded (**1**), acute (**2**)	o	
18	number of U lobes on flanks (geph.)	0 (**0**), 1 (**1**), 2 (**2**), 3 (**3**), about 5 (**4**), about 8 (**5**), about 12 (**6**)	o	
19	shape of umbilical lobes	none (**0**), rounded (**1**), acute (**2**)	o	

C. ornament

20	ribs	none (**0**), yes (**1**)	o	
21	ventrolateral furrows	none (**0**), yes (**1**), only depression (**2**), tricarinate venter (**3**)	uo	
22	internal shell thickenings	none (**0**), yes (**1**)	o	

Fig. 7. List of characters and character states used for cladistic analyses of pharciceratid and gephuroceratid ammonoids [o = ordered characters, uo = unordered characters, D = polarised characters]

CLADISTIC ANALYSIS

Methods

For the cladistic analyses of Early and Middle Devonian ammonoids (except for the pharciceratids and gephuroceratids), a character list was assembled (Text-fig. 6), consisting of a total of 39 characters. Of these characters, 15 are based on conch geometry (Text-fig. 1), 9 on septal and sutural morphology, and 15 on ornament and sculpture features. Many of the characters had to be coded with more than two character states. This is particularly important for those states based on conch morphometry and sutural subdivision. Ornament characters mainly occur in only two states.

For the pharciceratid and gephuroceratid ammonoids, a separate character list (Text-fig. 7) was developed. This was necessary because these ammonoid groups show more complex sutural characters, which require a more inclusive character list. The complete character matrices are shown in Appendix 2.

The phylogenetic analyses were performed using the program PAUP, version 4.0 (Swofford 1999). In some of the cases, more than one most parsimonious tree was calculated by application of branch-and-bound search, and hence strict consensus trees were computed. Weighting of characters was not put in practice, but scaling was necessary because of the different number of character states; characters with only two states were scaled 3, those with three states were scaled 2, and those characters that unfold four and more states with 1.

The cladistic analyses could not be worked out on the species level because:

Far too many species had to be included in the analyses (which would leave an unacceptable ration of character states to taxa).

Many species are only insufficiently known (leading to unacceptable numbers of absent or ambiguous state assignations in the matrix).

Gain of additional detailed information (of phylogeny on the species level rather than the genus level) had to be paid with an unrelated high effort.

For the analyses, only one species of each genus was chosen, either the type species or the best described species of the genus. The high number of Early and Middle Devonian ammonoid genera did not allow a comprehensive analysis of all genera at the same time, therefore six independent analyses were executed:

Early Emsian (Zlichovian),
Late Emsian (Dalejan),
Agoniatitid ammonoids,
Anarcestid ammonoids,
Pharciceratid ammonoids,
Gephuroceratid ammonoids.

Zlichovian ammonoids

General conditions: Stratigraphical control is limited for many of the early Emsian (Zlichovian) species, and also the duration of the genera is under dispute. Becker & House (1994), for instance, after compilation of all available data regarding the stratigraphical distribution of these species, proposed a zonal scheme that is defined by several ammonoid genera and species within a putative succession. However, recent data gathered from sections in the Tafilalt of the eastern Anti-Atlas in Morocco do not support this zonation (Belka et al. 1999; Klug 2001). Sections in North Africa demonstrate that:

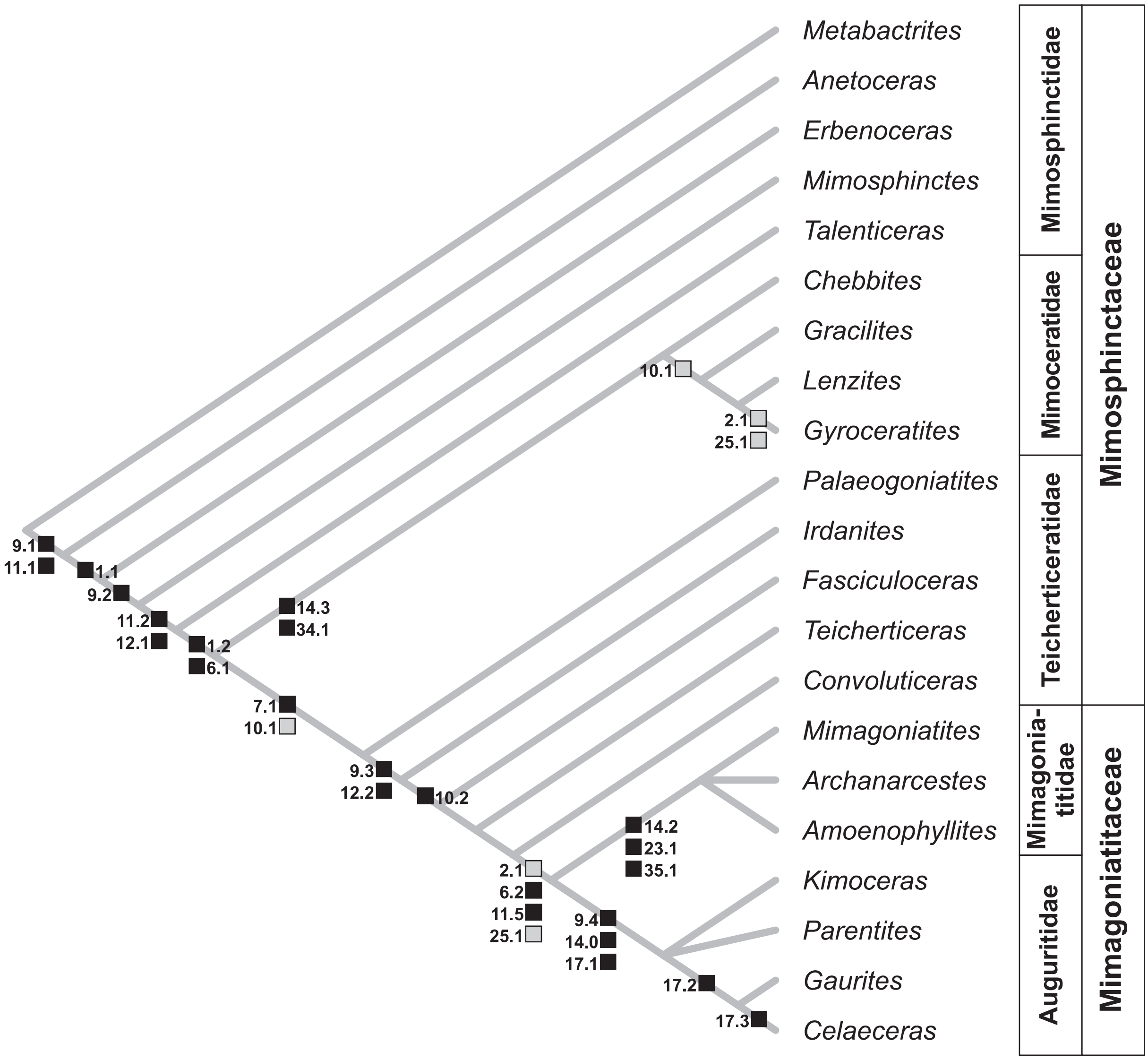


Fig. 8. Cladogram of Zlichovian ammonoids and most important apomorphic characters [■ = apomorphies, ▢ = homoplasies]

Plesiomorphic genera such as *Metabactrites*, *Ruanites*, and *Erbenoceras* are, right from their lowest occurrence, accompanied by more advanced genera like *Chebbites*, *Irdanites*, and *Gyroceratites*. Therefore there seems to be no plausible reason to separate *Ruanites obliqueseptatus* and *Teicherticeras teicherti* Zones.

Gyroceratites laevis appears significantly earlier than *Mimagoniatites fecundus* (in contrast to the range chart shown by Becker & House 1994). Probably, the stratigraphical scheme should be modified by exchanging the two zones named after these index species.

Tree data: 21 genera, of which *Metabactrites* was chosen as outgroup; 25 informative characters; two most parsimonious trees of 163 steps length, consistency index of 0.58 and retention index of 0.87 (rescaled consistency index 0.50); strict consensus tree presented in Text-fig. 8.

Tree topography: Early Emsian (Zlichovian) ammonoids are mainly characterised by loosely coiled or advolute conchs, and an umbilical window that is present in almost all the species. The computed tree displays largely anagenetic development that is determined by several morphological trends during the Early Emsian:

Coiling form (character 1) - There occurs a trend from gyrocone (*Metabactrites*) to advolute (*Erbenoceras*) and finally embracing whorls (*Chebbites*).

Umbilical window (character 2) - Narrowing of the umbilical window is a general trend that subsisted in different lineages of the early ammonoids, displayed in the monophyletic Mimoceratidae and Mimagoniatitaceae.

Whorl cross section (characters 6-8) - In the earliest ammonoids, all growth stages display compressed whorls, and during phylogeny, at least the inner whorls became circular and depressed.

Umbilical width (characters 9, 10) - Continuous closure of the umbilicus took place during the early Emsian; umbilical width was reduced from 0.75 in *Metabactrites*, 0.60 in *Anetoceras*, 0.45 in *Mimosphinctes*, 0.30 in *Gracilites* to less than 0.15 in the Auguritidae.

Whorl expansion rate (characters 11, 12) - The tendency towards higher apertures lead to a continuous increase of the whorl expansion rate, which started with 1.30 in *Metabactrites*, passed through *Erbenoceras* with 1.75 and *Gracilites* with 2.30, and finally reached in *Mimagoniatites* and the genera of the family Auguritidae its maximum of more than 3.50. Additionally, the ontogenetic acceleration of this rate is more striking in the advanced forms.

External lobe (character 17) - The simple E lobe of the earliest ammonoids was, during the early Emsian, in the auguritid clade transformed towards a trifid and even further subdivided (in *Celaeceras*) sutural element. Transformation of the E lobe paralleled the modification of a subcircular whorl cross section into an oxyconic form (character 14).

Internal lobe (character 23) - In the family Mimagoniatitaceae, a tie point controlled, pointed internal lobe is evolved; this is the apomorphic character of the early Emsian mimagoniatitids.

Growth line features (characters 25-28) - The rursiradiate direction from the beginning of ammonoid evolution was, within independent lineages, transformed into a prorsiradiate direction, and a high ventrolateral projection was developed in the advanced forms such as mimoceratids and the mimagoniatitids.

External band (character 34) - The presence of an external band (i.e. the ventral ornament that shows an extremely deep sinus of the growth lines, with the consequence that, due to superposition of growth lines ventrolateral rims were generated) is the cardinal feature that specifies the monophyletic family Mimoceratidae.

Ventrolateral furrows (character 35) were introduced in juvenile stages of the mimagoniatitids as an apomorphic character.

Dalejan ammonoids

General conditions: For the purpose of avoidance of major errors in the cladistic analysis of the late Emsian ammonoids, only those genera have been chosen which clearly belong to the family Mimagoniatitidae or its descendants. This means that genera such as *Gyroceratites* and *Fasciculoceras*, which persist from the Zlichovian into the Dalejan, were precluded.

Tree data: 16 genera, of which *Convoluticeras* was chosen as outgroup; 18 informative characters; two most parsimonious trees of 129 steps length, consistency index of 0.56 and retention index of 0.82 (rescaled consistency index 0.46); strict consensus tree presented in Fig. 9.

Tree topography: Cladogenetic development is the main feature of the late Emsian ammonoid phylogeny, and two main monophyletic groups are expressed in the cladogram. One representing the agoniatitid branch, and the other one the anarcestid branch. Several results are significant:

Two major monophyletic groups are displayed, the suborders Agoniatitina and Anarcestina.

The agoniatitid group is characterised by two criteria, the presence of ventrolateral furrows in juveniles (character 35), and the slightly flattened venter (character 14).

According to the tree, the umbilical window (character 2), which is present in the earliest ammonoids, was independently closed three times (in the advanced mimagoniatitids, in *Chlupacites*, and in the anarcestids).

The V-shaped and tie point-induced internal lobe (character 23) that was acquired by the mimagoniatitids, was discarded twice, in the agoniatitids and in the anarcestids

During the late Emsian, in the anarcestid monophylum there occurs a trend towards lower whorl expansion rates (character 11). At the same time, the embracing rate of the whorls (character 5) was enlarged to a value of approximately 40% of the whorl height.

The ontogenetic acceleration of the whorl expansion rate (character 12), which is typical for *Convoluticeras* as well as the mimagoniatids and agoniatids, was driven back in the anarcestid clade.

The anarcestids form two monophyla, one with *Anarcestes*, *Sellanarcestes*, and *Paranarcestes* (subfamily Anarcestinae; characterised by very low whorl expansion rates), and the other with *Praewerneroceras*, *Crispoceras*, and *Werneroceras* (subfamily Werneroceratinae; characterised by an angular umbilical edge, character 15).

An effective lateral tie point which is responsible for a deep lateral lobe (character 18) originated twice, in the agoniatitids and also in the anarcestids.

The lateral lobe (character 20) migrated from the midflank position, as portrayed in the mimagoniatitids, towards a dorsolateral position in the anarcestids.

The agoniatitid ammonoids

General conditions: The agoniatitid ammonoids form a group that is defined by several common features, which all the genera share:

A high whorl expansion rate (usually over 2.50 in preadult and adult whorls), that notably accelerated during ontogeny, as a consequence of alteration of coiling parameters.

Inner whorls that display ventrolateral furrows and a slightly flattened venter.

A comparatively small imprint zone that only rarely exceeds 0.30.

The inner whorls are ribbed in many of the taxa.

For these reasons, both *Atlantoceras* and *Pseudoprobeloceras* have to be placed in the agoniatitid analysis, in which they casually can be related with the agoniatites.

Tree data: 15 genera, of which *Convoluticeras* was

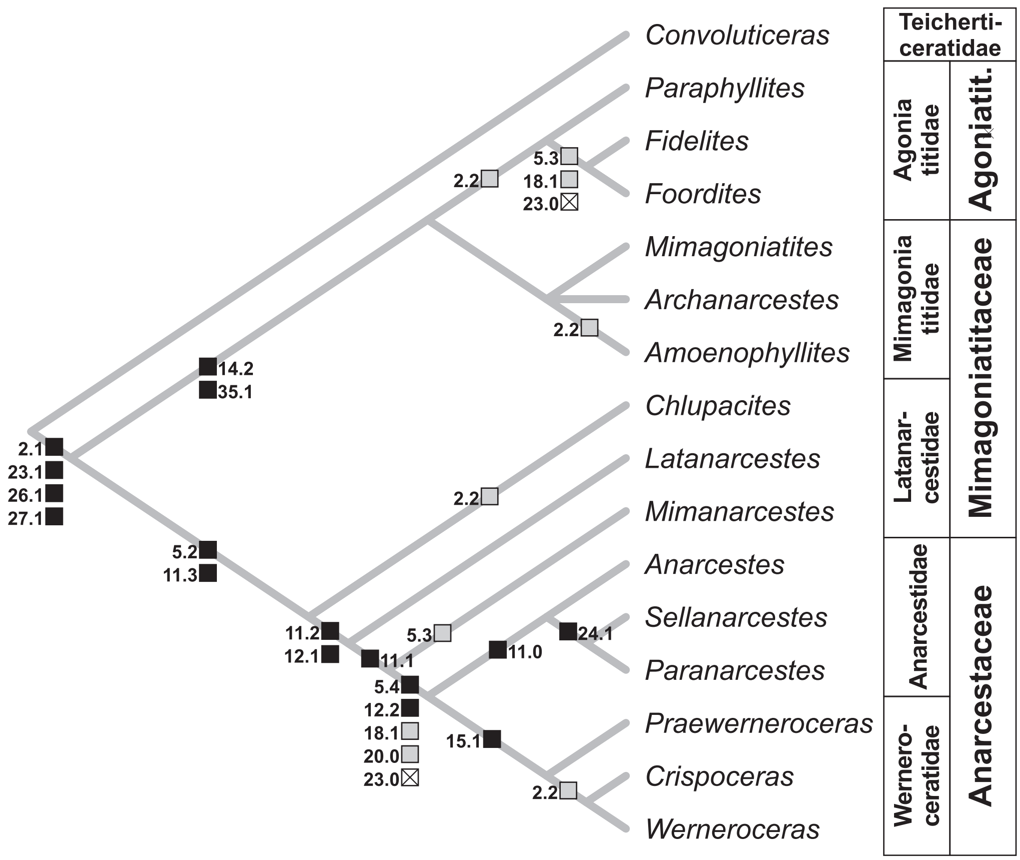


Fig. 9. Cladogram of Dalejan ammonoids and most important apomorphic characters [■ = apomorphies, ▩ = homoplasies, □ = reversals]

chosen as outgroup; 18 informative characters; three most parsimonious trees of 117 steps length, consistency index of 0.66 and retention index of 0.81 (rescaled consistency index 0.53); strict consensus tree presented in Text-fig. 10.

Tree topography: Arrangement of the late Emsian agoniatitid genera is already expressed in the late Emsian tree, and hence at this place only the Eifelian and Givetian genera will be discussed. The agoniatitid tree is a consequence of several morphological trends which took place mainly during the Middle Devonian:

The umbilical window (character 2) was closed twice independently, in *Amoenophyllites* and in *Paraphyllites*.

The imprint zone (character 5) was enlarged from 10% in the mimagoniatitids to 25% in the family Agoniatitidae.

The whorl expansion rate (character 11) was successively reduced, from more than 3.50 in the mimagoniatitids towards 2.50 in the advanced forms.

The agoniatitids consist of two different monophyla, one lineage leading to *Exopinacites* (with an umbilical lobe, character 21), and another lineage leading to *Pseudoprobeloceras*.

The acceleration of the whorl expansion rate (character 12) was slightly reduced in the clade with *Pseudoprobeloceras*.

The form of the venter (character 14), which is flattened in many agoniatitids, was modified into an oxyconic form in the family Pinacitidae.

The external lobe (character 17) was divided by ascension of a median saddle, once in the pinacitids, and once in *Pseudoprobeloceras*, the latter giving rise to the suborder Gephuroceratina.

An effectual lateral tie point (character 18) was established by the family Agoniatitidae.

The dorsal tie point (character 23) of the family Mimagoniatitidae was discarded by early agoniatitids but later regained in the *Pseudoprobeloceras* clade.

The anarcestid ammonoids

General conditions: Anarcestid ammonoids display a character set which principally separates them from the contemporaneous agoniatitids:

They have large embracing rates (IZW larger than 0.3) of their whorls and low apertures.

They do not display characters such as ventrolateral furrows, and posses a rounded venter.

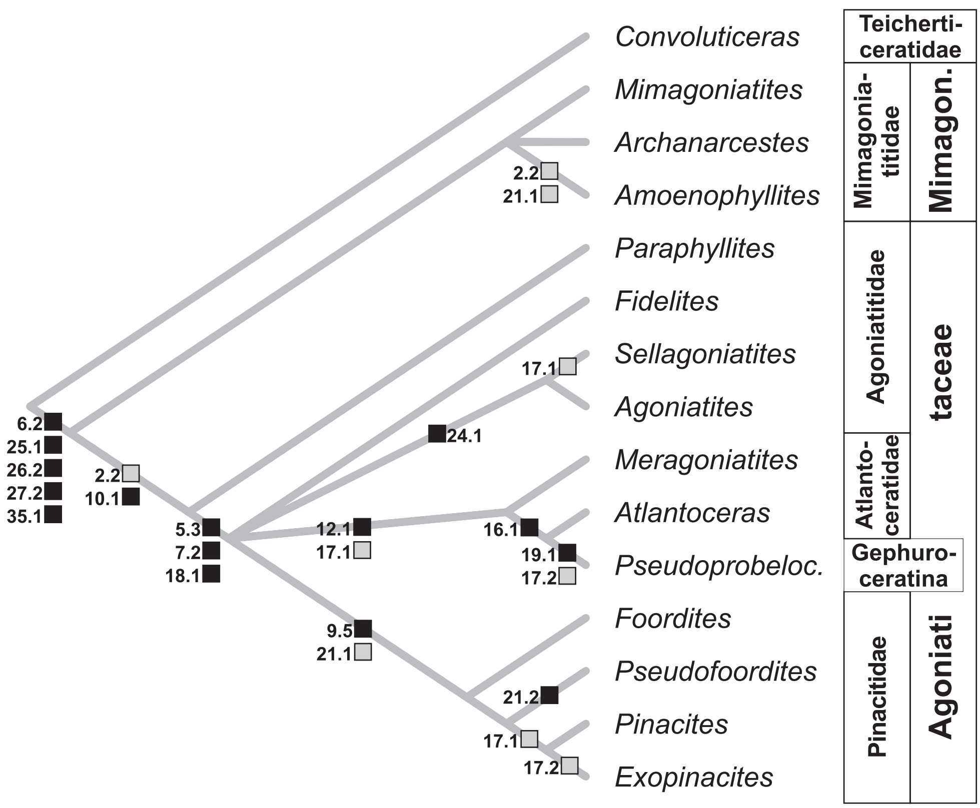


Fig. 10. Cladogram of agoniatitid ammonoids and most important apomorphic characters [■ = apomorphies, □ = homoplasies]

In neither growth stage, ribs are present.

Tree data: 21 genera, of which *Convoluticeras* was chosen as outgroup; 24 informative characters; one most parsimonious tree of 172 steps length, consistency index of 0.55 and retention index of 0.78 (rescaled consistency index 0.43); presented in Text-fig. 11.

Tree topography: Arrangement of the late Emsian anarcestid genera is already expressed in the late Emsian tree, and hence only the Eifelian and Givetian genera will be discussed in detail. They are seen to be derived from the family Werneroceratidae, and form two monophyla, firstly the Sobolewiidae, and secondly another clade composed of the suborders Tornoceratina and Pharciceratina. In detail, the following characteristics of the tree are recognisable:

The umbilical window (character 2) was probably closed twice independently, once in *Chlupacites*, and once in the family Werneroceratidae.

There occurs a remarkable trend in the enlargement of the imprint zone (character 5), from less than 0.05 in the outgroup and the early mimagoniatitids to approximately 0.60 in the advanced forms with very low aperture, such as *Sobolewia* and *Holzapfeloceras*.

The umbilicus is gradually closed during phylogeny (character 9).

The whorl expansion rate (character 11) was rapidly reduced in the early anarcestids, to a value of 1.50, especially in the monophyletic subfamily Anarcestinae.

The umbilical wall is steep and bordered by an angular edge (character 15) in some genera, beginning

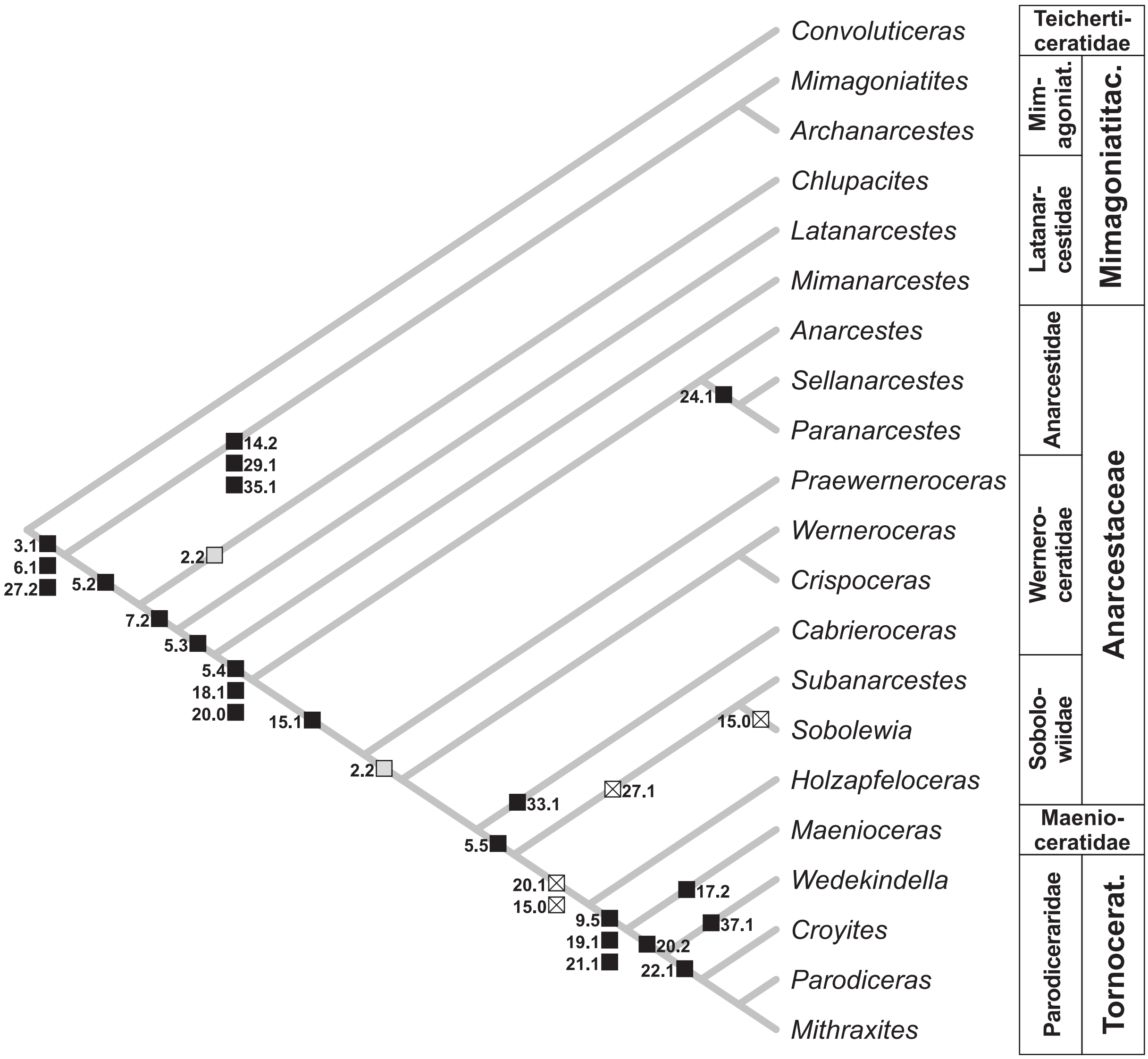


Fig. 11. Cladogram of anarcestid ammonoids and most important apomorphic characters [■ = apomorphies, ■ = homoplasies, ☒ = reversals]

with *Praewerneroceras* and fully unfolded within the Werneroceratidae, but was obviously reversed towards rounded umbilical margin later in phylogeny.

The shape of the lateral lobe (character 19) was broadly rounded in all the early forms, i.e. the mimagoniatitids and early anarcestids, but it was altered into a narrowly rounded form in advanced forms such as *Parodiceras*, and became pointed in *Maenioceras*.

The position of the lateral lobe (character 20), on the midflank in the ancestral mimagoniatitids, migrated towards the umbilicus in the anarcestids. Later in *Holzapfeloceras* and its successors it went back to the midflank or even towards a ventrolateral position.

The internal tie point (character 23), typical for the ancestral mimagoniatitids, was abandoned by the anarcestids and then "re-invented" at least in *Maenioceras*.

The family Sobolewiidae is characterised by only a low ventrolateral projection of the growth lines (character 27), in contrast to the high salient in the other genera.

The monophylum with *Mithraxites*, *Parodiceras*, and *Croyites* (Parodiceratidae) are characterised by an adventive lobe (character 22).

The pharciceratid ammonoids

General conditions: The pharciceratids belong to those Devonian ammonoids which are inadequately known, and hence the compilation of data was problematic. Especially the various species which are usually put in *Pharciceras* are only partly described and require modern revision. Some genera, such as *Wellsites* and *Schindewolfoceras* were excluded from the analysis, because current knowledge of these does not permit the assembling of a sufficient data matrix. Nevertheless, the results of a cladistic analysis is presented here, but it must be noted that the phylogenetic relationships expressed here will be prone to revision after a detailed taxonomic revision. *Tamarites*, a late Givetian ammonoid from Kazakhstan (BOGOSLOVSKY 1965, 1969) is an exotic genus and difficult to place; its combination of different characteristics (ribs, very small imprint zone, very wide umbilicus) is unique, thus it is omitted from the analysis.

Tree data: 12 genera, of which *Holzapfeloceras* was chosen as outgroup; 16 informative characters; one most parsimonious tree of 97 steps in length; consistency index of 0.66 and retention index of 0.72 (rescaled consistency index 0.47); presented in Text-fig. 12.

Tree topography: The pharciceratid tree results from the unfolding of several sutural characters:

Many of the conch shape characters (characters 1-8) are incompatible and thus helpless for an unambiguous analysis.

The general septal form (character 9) is synclastic (i.e. generally concave towards the aperture) in the outgroup and possibly also in *Wedekindella*, but anticlastic (frilled by septal pillars) in the advanced genera.

The external lobe (character 10), simple in the outgroup

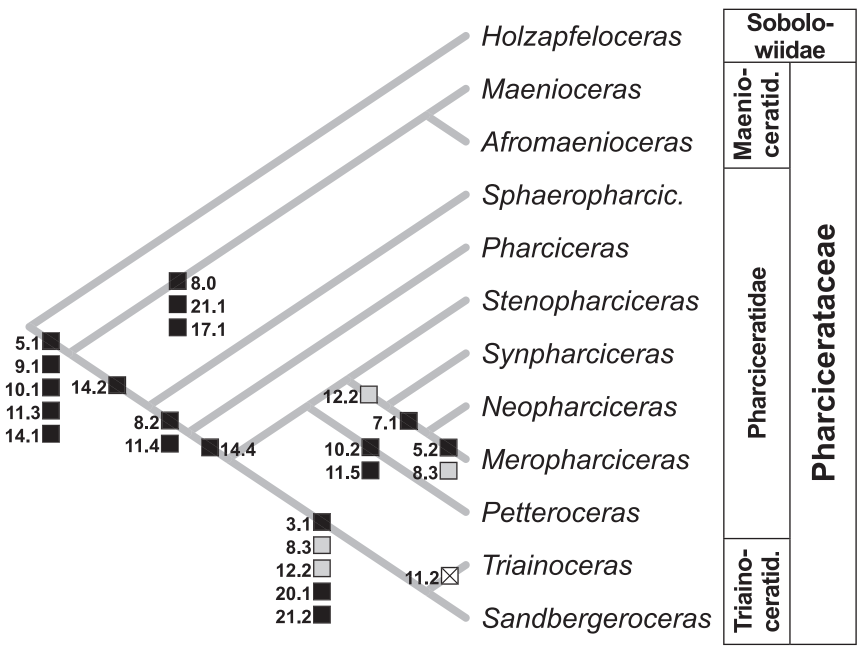


Fig. 12. Cladogram of pharciceratid ammonoids and most important apomorphic characters [■ = apomorphies, ▫ = homoplasies, ⊠ = reversals]

and in *Wedekindella*, is subdivided in *Maenioceras* and in all the subsequent genera (families Pharciceratidae, Triainoceratidae).

The number of umbilical lobes (character 14) was continuously heightened. In *Maenioceras* and in *Sphaeropharciceras*, only one umbilical lobe is visible on the flanks; in *Pharciceras* there are two, and the advanced pharciceratids such as *Neopharciceras* display 12 outer umbilical lobes. As a parallel development, the U lobe number also increased in the triainoceratids.

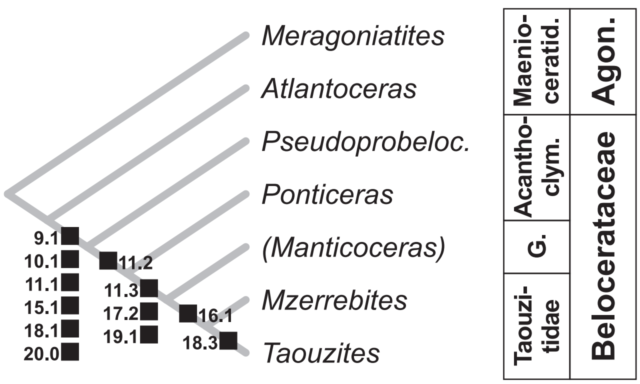
The family Triainoceratidae is the only group that displays ribs (character 15).

The gephuroceratid ammonoids

General conditions: Only few Middle Devonian genera which belong to the Suborder Gephuroceratina are known, and hence the cladogram does not reflect the diversity of the suborder. The Frasnian *Manticoceras* was added to the analysis to demonstrate that the Late Frasnian eobeloceratids are relatively complex forms.

Tree data: 7 genera, of which *Meragoniatites* was chosen as outgroup; 14 informative characters; one most parsimonious tree of 71 steps length; consistency index of 0.75 and retention index of 0.74 (rescaled consistency index 0.56); presented in Text-fig. 13.

Tree topography: The simple tree reflects a continuous development of sutural elements (character 18) which turn from rounded into V-shaped.



ig. 13. Cladogram of gephuroceratid ammonoids and most important apomorphic characters [■ = apomorphies, G = Gephuroceratidae]

TAXONOMIC NOTES

Taxonomy was, in spite of application of cladistic analysis, achieved in the traditional way, operating with monophyletic and paraphyletic systematic units.

The cladograms, which were computed demand a revised classification scheme, which in some parts significantly deviates from previous systems such as MILLER & FURNISH (1957) in the Treatise of Invertebrate Paleontology, or by RUZHENCEV (1960) in his “Printsipy”. Systematic arrangement of the Emsian ammonoids largely reflects the general classification scheme that was introduced by ERBEN (1965), but the patterns presented by the Eifelian and Givetian genera require a new reassessment. The following new system is proposed here (Appendix 3), in square brackets information of whether the taxonomic units are paraphyletic [P] or monophyletic [M].

Family Latanarcestidae fam. nov.

TYPICAL GENUS: *Latanarcestes* SCHINDEWOLF 1933.

FAMILY DEFINITION: Mimagoniatitids with thickly discoidal to globose conch forms, umbilicus moderately wide. Whorl expansion rate 2.25 - 2.75, imprint zone 0.20 - 0.30 of whorl height. Internal lobe very small.

REMARKS: For morphological (and most probably phylogenetic) reasons, the new family is an intermediate between mimagoniatids and anarcestids, mainly expressed by the whorl expansion rate and the width of the imprint zone.

Family Atlantoceratidae fam. nov.

TYPICAL GENUS: *Atlantoceras* BENSAÏD 1974.

FAMILY DEFINITION: Agoniatitids with discoidal conch forms, umbilicus wide. Whorl expansion rate 1.80 -

2.50, imprint zone 0.10 - 0.20 of whorl height. External lobe rather wide, as deep as the lateral lobe, broadly V-shaped.

REMARKS: The new family is morphologically intermediate between agoniatitid ammonoids with simple external lobe, and gephuroceratids with trifid external lobe. In the Atlantoceratidae, the external lobe is markedly deeper than in the Agoniatitidae, probably giving rise to the trifid external lobes which are present in *Pseudoprobeloceras* for the first time.

Meragoniatites gen. nov.

TYPICAL SPECIES: *Agoniatites costulatus meridionalis* BENSAÏD 1974.

GENUS DEFINITION: Genus of the family Atlantoceratidae with discoidal conch form, umbilicus moderately wide. Whorl expansion rate 2.50, imprint zone 0.10 - 0.15 of whorl height Ventrolateral furrows, venter flattened. External lobe deep and V-shaped, lateral lobe wide and deeper than external lobe.

REMARKS: *Meragoniatites* shares characters with both agoniatids and gephuroceratids. Typical for agoniatids is the relatively large protoconch (which is smaller than in *Agoniatites*, but larger than in most gephuroceratids), and the simple external lobe. The depth of the external lobe, almost as deep as the lateral lobe, the loss of strong ribs in juvenile whorls, and the slight reduction of the whorl expansion rate indicate an intermediate position between agoniatids and gephuroceratids.

Family Tamaritidae fam. nov.

TYPICAL GENUS: *Tamarites* BOGOSLOVSKY 1965.

FAMILY DEFINITION: Agoniatitids or gephuroceratids with thinly discoidal conch form, umbilicus very wide. Whorl expansion rate less than 1.50, imprint zone one 0.10 of whorl height Strong ribs, ventrolateral furrows. Sutural formula (E1 Em E1) L U I; external lobe trifid with small lateral incisions.

REMARKS: *Tamarites* is a genus which cannot be placed in any of the known superfamilies with certainty. The combination of characteristics, strong ribbing, almost advolute whorls, and subdivided external lobe is unique for Middle Devonian ammonoids. Among the three features, the extremely low imprint zone may indicate reference to the agoniatid or gephuroceratid ammonoids, rather than to the triainoceratids, as proposed by BOGOSLOVSKY (1969).

Family Taouzitidae fam. nov.

TYPICAL GENUS: *Taouzites* gen. nov.

FAMILY DEFINITION: Gephuroceratids with discoidal conch forms, umbilicus wide in juveniles and narrow in adults. Whorl expansion rate 2.25 - 2.75, imprint zone 0.15 - 0.25 of whorl height. Ventrolateral furrows. External lobe trifid with very high median saddle. Three to five lateral lobes on the flank.

REMARKS: Usually, the genera *Mzerrebites* and *Taouzites* were regarded as pharciceratids. However, the conch shape with very low imprint zone is characteristic for the gephuroceratids, rather than for the pharciceratids.

Taouzites gen. nov.

TYPICAL SPECIES: *Pharcoceras taouzense* TERMIER & TERMIER 1950.

GENUS DEFINITION: Genus of the family Taouzitidae with lenticular conch and narrow umbilicus. Whorl expansion rate 2.75, imprint zone 0.25 of whorl height. Suture line with a wide, subdivided external lobe with a high median saddle, and five V-shaped lateral lobes on the flank, of which the outer three are acute.

REMARKS: BECKER & HOUSE (1993) erected the new family Eobeloceratidae, in which they placed *Pharcoceras taouzense* as well as they (1994) also placed their new genus *Mzerrebites*. However *Eobeloceras* is extremely poorly known and hence also the family Eobeloceratidae is a dubious taxon. All the information about the type species, *Ammonites multiseptatus* VON BUCH 1832 from the Eifel Mountains of Germany, let assume that it is in fact a beloceratid rather than a goniatite related to *Taouzites taouzensis*. According to VON BUCH's (1832) and BENSAÏD's (1974) illustrations, *Ammonites multiseptatus* has four lobes on the flank, of which the second one (i.e. the first lateral lobe) is the deepest. By contrast, in *Taouzites* is the prong of the external lobe the widest and deepest lobe.

Croyites gen. nov.

TYPICAL SPECIES: *Holzapfeloceras croyi* HOUSE 1978.

GENUS DEFINITION: Genus of the family Parodiceratidae with thickly discoidal conch and closed umbilicus. Whorl expansion rate 2.10, imprint zone one half of whorl height. Suture line with small external lobe, wide and asymmetric midflank lobe, deep and V-shaped lateral lobe at the umbilicus, and wide internal lobe.

REMARKS: HOUSE (1978) noticed the similarities of the type species with tornoceratid ammonoids, but regarded the form of the latero-umbilical saddle as distinctive for the reference to *Holzapfeloceras*. Unfortunately, neither sutural ontogeny nor shell ornament are seen in *Croyites croyi*. The sutural outline, however is an argument for placing the form in the family Parodiceratidae.

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Bohemia	BARRANDE (1865, 1866, 1867, 1877); ERBEN (1950, 1960, 1962a, 1962b); CHLUPAC (1976); CHLUPAC & TUREK (1977, 1983)
Rhenish Massif, Harz	D'ARCHIAC & DE VERNEUIL (1842); ROEMER (1850); SANDBERGER & SANDBERGER (1850-1856); KAYSER (1872, 1878, 1884); MAURER (1876, 1896); HOLZAPFEL (1895); FRECH (1902); WEDEKIND (1918); CORRENS (1923); EICHENBERG (1930); MATERN (1931); SCHINDEWOLF (1933, 1935); SCHMIDT (1950); ERBEN (1953, 1960, 1962b, 1965); WALLISER (1965); KUTSCHER (1969); HOUSE & ZIEGLER (1977)
Armorican Massif	ERBEN (1962b, 1965); BABIN (1966, 1989)
Great Britain	WHIDBORNE (1890); HOUSE (1956, 1963)
Montagne Noire	FEIST (1970)
Cantabrian Mountains	KULLMANN (1960); MONTESINOS LOPEZ & TRUYOLS-MASSONI (1986); MONTESINOS LOPEZ & HENN (1986); MONTESINOS LOPEZ (1987, 1988)
North Africa	TERMIER & TERMIER (1950); PETTER (1959); HOLLARD (1963); BENSAÏD (1974); GÖDDERTZ (1987); BECKER & HOUSE (1994); BELKA et al. (1999); KLUG (2001)
Turkey	ERBEN (1962a, 1965); KULLMANN (1973)
Altay Mountains	BOGOSLOVSKY (1955, 1958, 1969)
Kazakhstan	BOGOSLOVSKY (1965)
Central Asia	BOGOSLOVSKY (1980, 1984); YATSKOV (1990)
Southwest China	RUAN & HE (1974); SHEN (1975); RUAN (1981, 1984)
Australia	TEICHERT (1948); ERBEN (1965)
Western U.S.	MILLER (1938); HOUSE (1965)
Eastern U.S.	HALL (1860); CLARKE (1899); MILLER (1938); SWEET & MILLER (1956); HOUSE (1962, 1978)
Canada	HOUSE & PEDDER (1963); PROSH (1987); WISSNER & NORRIS (1991)
North Urals, Novaya Zemlya	BOGOSLOVSKY (1959, 1961, 1963, 1969, 1972); YATSKOV (1990, 1992)

Appendix 1. Most of the important publications which provided part of the data base for this analyses of Early and Middle Devonian ammonoids

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Metabactrites	0	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Anetoceras	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Erbenoceras	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Mimosphinctes	1	0	0	?	0	0	0	0	2	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0
Talenticeras	1	0	0	1	0	0	0	0	2	0	2	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Chebbites	2	0	0	0	1	0	0	0	2	0	2	1	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1
Lenzites	2	?	0	0	0	1	0	0	2	1	3	1	0	3	0	0	0	0	0	1	0	0	0	0	0	1	1	2	0	0	?	0	0	1	0	0	0	0	1
Gyroceratites	1	1	0	0	0	1	0	0	2	1	3	1	0	3	0	0	0	0	0	1	0	0	0	0	1	2	2	2	0	0	?	0	0	1	0	0	0	0	0
Gracilites	2	0	0	0	1	1	0	0	3	1	3	1	0	3	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	?	0	0	1	0	0	0	1	1
Teicherticeras	2	0	0	0	1	1	1	0	3	2	3	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	?	0	0	0	0	0	0	0	0
Fasciculoceras	2	0	0	0	1	1	1	0	3	2	3	2	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	2	0	0	1	0	0	0	0	0	0	0	0
Palaeogoniatites	2	0	0	1	1	1	1	1	2	1	3	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Irdanites	2	0	?	0	1	1	1	1	3	1	4	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	2	1	1	0	0	0	0	0	0	0	0	0
Convoluticeras	2	0	0	0	1	1	1	0	3	2	4	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	2	0	0	?	0	0	0	0	0	0	0	0
Mimagoniatites	2	1	1	0	1	2	1	0	3	2	5	2	0	2	0	0	0	0	0	1	0	0	1	0	1	2	2	2	1	0	0	0	0	0	1	0	0	0	0
Archanarcestes	2	1	1	0	1	2	1	1	3	2	3	2	1	2	0	0	0	0	0	1	0	0	1	0	1	2	2	2	1	0	0	0	0	0	1	0	0	0	0
Amoenophyllites	2	2	1	0	1	2	1	0	3	2	5	2	0	2	0	0	0	0	0	1	1	0	1	0	1	2	2	2	1	0	0	0	0	0	1	0	0	0	0
Chlupacites	2	2	1	0	2	2	2	0	3	1	3	2	0	1	0	0	0	0	0	1	0	0	1	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Latanarcestes	2	1	1	0	2	2	2	1	3	1	2	1	1	1	0	0	0	0	0	1	0	0	1	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Mimanarcestes	2	1	1	0	3	2	2	1	2	0	1	1	2	1	0	0	0	0	0	1	0	0	1	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Kimoceras	2	1	1	0	1	2	1	0	4	2	5	2	0	0	0	0	1	0	0	1	0	0	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Parentites	2	1	1	0	1	2	1	0	4	2	5	2	0	0	0	0	1	0	0	1	0	0	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Gaurites	2	1	1	0	1	2	1	0	4	2	5	2	0	0	0	0	2	0	0	1	0	0	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Celaeceras	2	1	1	0	1	2	1	0	4	2	5	2	0	0	0	0	3	0	0	1	0	0	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Paraphyllites	2	2	1	0	1	2	1	0	4	1	5	2	0	2	0	0	0	0	0	1	0	0	1	0	1	2	2	2	0	0	?	0	0	0	1	0	0	0	0
Fidelites	2	2	1	0	3	2	2	0	4	1	4	2	0	2	0	0	0	1	0	1	0	0	0	0	1	2	2	2	1	0	?	0	0	0	1	0	0	0	0
Sellagoniatites	2	2	1	0	3	2	2	0	4	1	3	2	0	2	1	0	1	1	0	1	0	0	0	1	1	2	2	2	?	0	?	0	0	0	1	0	0	0	0
Agoniatites	2	2	1	0	3	2	2	0	4	1	2	2	0	2	0	0	0	1	0	1	0	0	0	1	1	2	2	2	1	0	0	0	0	0	1	0	0	0	0
Foordites	2	2	1	0	3	2	2	0	5	1	3	2	0	2	0	0	0	1	0	1	1	0	0	0	1	2	2	2	0	0	?	0	0	0	1	0	0	0	0
Pseudofoordites	2	2	1	0	4	2	2	0	5	1	3	2	0	1	0	0	0	1	0	1	2	0	0	0	1	2	2	2	0	0	?	0	0	0	1	0	0	0	0
Pinacites	2	2	1	0	3	2	2	0	5	1	3	2	0	0	0	0	1	1	0	1	1	0	0	0	1	2	2	2	0	0	?	0	0	0	1	0	0	0	0
Exopinacites	2	2	1	0	3	2	2	0	5	1	3	2	0	0	0	0	2	1	0	1	1	0	0	0	1	2	2	2	0	0	?	0	0	0	1	0	0	0	0
Meragoniatites	2	2	1	0	3	2	2	2	3	1	2	1	0	2	0	0	1	1	0	1	0	0	0	0	1	2	2	2	1	0	0	0	0	0	1	0	0	0	0
Atlantoceras	2	2	1	0	3	2	2	1	2	0	2	1	0	2	0	1	1	1	0	0	0	0	1	0	1	2	2	2	1	0	?	0	0	0	1	0	0	0	0
Pseudoprobeloceras	2	2	1	0	3	2	2	1	3	1	2	1	0	1	0	1	2	1	1	0	0	0	1	0	1	2	2	2	1	0	0	0	0	0	1	0	0	0	0
Anarcestes	2	1	1	0	4	2	2	1	2	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Sellanarcestes	2	1	1	0	4	2	2	1	3	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Paranarcestes	2	1	1	0	4	2	2	1	2	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Praewerneroceras	2	1	1	0	4	2	2	1	3	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Werneroceras	2	2	1	0	4	2	2	0	3	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Crispoceras	2	2	1	0	4	2	2	0	3	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	2	2	2	0	0	?	1	0	0	0	0	0	0	0
Cabrieroceras	2	2	1	0	4	2	2	2	2	1	1	0	2	1	1	0	0	1	0	0	0	0	0	0	1	2	2	2	0	0	?	0	1	0	0	0	0	0	0
Subanarcestes	2	2	1	0	5	2	2	2	4	1	1	0	2	1	1	0	0	1	0	0	0	0	0	0	0	2	1	2	0	0	?	0	0	0	0	0	0	0	0
Sobolewia	2	2	1	0	6	2	2	2	5	1	0	0	2	1	0	0	0	1	0	0	0	0	0	0	0	1	1	2	0	0	?	0	0	0	0	0	0	0	0
Holzapfeloceras	2	2	1	0	6	2	2	2	4	2	1	0	2	1	0	0	0	1	0	1	0	0	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Maenioceras	2	2	1	0	5	2	2	0	5	2	1	1	1	1	0	0	2	1	2	1	1	0	0	0	1	2	2	2	0	0	?	0	0	0	0	1	0	0	0
Mithraxites	2	2	1	0	5	2	2	0	5	0	0	?	1	1	0	0	0	1	1	2	1	1	?	0	?	?	?	2	0	0	?	0	0	0	0	0	0	0	0
Parodiceras	2	2	1	0	4	2	2	0	5	0	2	0	1	1	0	0	0	1	1	2	1	1	0	0	1	2	2	2	0	0	?	0	0	0	0	0	0	0	0
Croyites	2	2	1	0	5	2	2	0	5	0	2	0	1	1	0	0	0	1	1	2	1	1	?	0	?	?	?	2	0	0	?	0	0	0	0	1	0	0	0
Wedekindella	2	2	1	0	5	2	2	0	5	2	2	1	1	1	0	0	0	1	1	2	1	0	0	0	1	2	2	2	0	0	?	0	0	0	0	1	1	0	0

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Holzapfeloceras	5	0	2	1	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maenioceras	5	0	2	1	1	0	2	0	1	1	3	1	2	1	0	0	0	0	0	0	1	1
Afromaenioceras	4	1	2	1	1	0	2	0	1	1	3	1	1	1	0	0	0	0	0	0	1	1
Sphaeropharciceras	5	2	2	1	1	1	2	1	1	1	3	1	1	2	0	0	0	0	0	0	0	0
Pharciceras	5	2	2	1	1	1	2	2	1	1	4	1	1	2	0	0	0	0	0	0	0	0
Stenophariceras	4	1	2	2	1	0	2	2	1	1	4	1	1	4	0	0	0	0	0	0	0	0
Synpharciceras	5	0	2	1	1	0	2	2	1	1	4	2	1	4	0	0	0	0	0	0	0	0
Neopharciceras	6	0	2	1	1	0	1	2	1	1	4	2	2	6	0	0	0	0	0	0	0	0
Meropharciceras	5	0	2	2	2	0	1	3	1	1	4	2	2	5	0	0	0	0	0	0	0	0
Petteroceras	4	2	2	1	1	1	2	2	1	2	5	1	1	4	0	0	0	0	0	0	0	0
Triainoceras	4	3	1	1	1	1	2	3	1	1	2	2	2	2	0	0	0	0	0	1	2	0
Sandbergeroceras	4	2	1	1	1	1	2	3	1	1	4	2	2	4	0	0	0	0	0	1	2	0
Meragoniatites	2	2	1	2	2	0	2	1	0	0	0	0	0	0	0	0	0	0	?	1	1	0
Atlantoceras	2	3	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	?	1	1	0
Pseudoprobeloceras	2	2	1	2	1	0	2	1	1	1	1	0	0	0	1	0	0	0	?	1	1	0
Ponticeras	2	2	0	1	0	0	1	1	1	1	2	0	0	0	2	0	1	1	0	0	1	0
Manticoceras	2	1	1	3	2	0	2	1	1	1	3	0	0	0	2	0	2	1	1	0	0	0
Mzerrebites	3	2	1	2	1	0	1	2	1	1	3	0	0	0	2	1	2	2	1	0	1	0
Taouzites	3	1	1	3	2	0	0	3	1	1	3	0	0	0	2	1	2	3	1	0	1	0

Appendix 2. Complete character matrices of Early and Middle Devonian ammonoid genera, on which these cladistic analyses are based

Classification of Early and Middle Devonian ammonoids

Order Agoniatitida RUZHENCEV 1957 [P]
Suborder Agoniatitina RUZHENCEV 1957 [P]
Superfamily Mimosphinctaceae ERBEN 1953 [P]
Family Mimosphinctidae ERBEN 1953 [P]
Metabactrites BOGOSLOVSKY 1972
Anetoceras SCHINDEWOLF 1934
Ruanites YATSKOV 1990
Erbenoceras BOGOSLOVSKY 1962
Mimosphinctes EICHENBERG 1931
Talenticeras ERBEN 1965
Family Mimoceratidae STEINMANN 1890 [M]
Chebbites KLUG 2001
Lenzites BECKER & HOUSE 1994
Gyroceratites VON MEYER 1831
Gracilites BOGOSLOVSKY 1972
Family Teicherticeratidae BOGOSLOVSKY 1969 [P]
Teicherticeras ERBEN 1960
Fasciculoceras BOGOSLOVSKY 1969
Palaeogoniatites HYATT 1900
Irdanites KLUG 2001
Convoluticeras ERBEN 1960
Superfamily Mimagoniatitaceae MILLER 1938 [P]
Family Mimagoniatitidae MILLER 1938 [P]
Archanarcestes BECKER & HOUSE 1994
Mimagoniatites EICHENBERG 1930
Amoenophyllites CHLUPAC & TUREK 1983
Family Latanarcestidae fam. nov. [P]
Chlupacites BECKER & HOUSE 1994
Latanarcestes SCHINDEWOLF 1933
Mimanarcestes BOGOSLOVSKY 1969
Family Auguritidae BOGOSLOVSKY 1961 [M]
Kimoceras BOGOSLOVSKY 1980
Parentites BOGOSLOVSKY 1961
Gaurites BOGOSLOVSKY 1980
Celaeceras HYATT 1884
Superfamily Agoniatitaceae HOLZAPFEL 1899 [P]
Family Agoniatitidae HOLZAPFEL 1899 [P]
Paraphyllites HYATT 1900
Fidelites CHLUPAC & TUREK 1983
Sellagoniatites HOUSE 1963
Agoniatites MEEK 1877
Family Pinacitidae SCHINDEWOLF 1933 [M]
Foordites WEDEKIND 1918
Pseudofoordites BOGOSLOVSKY 1959
Pinacites MOJSISOVICS 1882
Exopinacites CHLUPAC & TUREK 1983
Family Atlantoceratidae fam. nov. [P]
Meragoniatites gen. nov.
Atlantoceras BENSAÏD 1974
(?) Family Tamaritidae fam. nov. [M]
Tamarites BOGOSLOVSKY 1965
Suborder Gephuroceratina RUZHENCEV 1957 [M]
Superfamily Gephurocerataceae FRECH 1897 [M]
Family Acanthoclymeniidae SCHINDEWOLF 1955 [P]
Pseudoprobeloceras BENSAÏD 1974
Ponticeras MATERN 1929
Family Taouzitidae fam. nov. [M]
Mzerrebites BECKER & HOUSE 1994
Taouzites gen. nov.
Suborder Anarcestina MILLER & FURNISH 1954 [P]
Superfamily Anarcestaceae STEINMANN 1890 [P]
Family Anarcestidae STEINMANN 1890 [M]
Sellanarcestes SCHINDEWOLF 1933
Anarcestes MOJSISOVICS 1882
Paranarcestes CHLUPAC & TUREK 1983
Family Werneroceratidae ERBEN 1964 [P]
Praewerneroceras CHLUPAC & TUREK 1983
Werneroceras WEDEKIND 1918
Crispoceras CHLUPAC & TUREK 1983
Cabrieroceras BOGOSLOVSKY 1961
Family Sobolewiidae HOUSE 1989 [P]
Subanarcestes SCHINDEWOLF 1933
Sobolewia WEDEKIND 1918
Holzapfeloceras MILLER 1932
Suborder Pharciceratina KORN 1998 [M]
Superfamily Triainocerataceae HYATT 1884 [P]
Family Maenioceratidae BOGOSLOVSKY 1958 [P]
Maenioceras SCHINDEWOLF 1933
Afromaenioceras GÖDDERTZ 1987
Family Pharciceratidae HYATT 1900 [P]
Sphaeropharciceras BOGOSLOVSKY 1955
Pharciceras HYATT 1884
Stenopharciceras MONTESINOS & HENN 1987
Synpharciceras SCHINDEWOLF 1940
Neopharciceras BOGOSLOVSKY 1955
Meropharciceras BECKER & HOUSE 1993
Petteroceras BOGOSLOVSKY 1962
Family Triainoceratidae HYATT 1984 [M]
Triainoceras HYATT 1984
Sandbergeroceras HYATT 1984
Schindewolfoceras MILLER 1938
Wellsites HOUSE & KIRCHGASSER 1993
Order Goniatitida HYATT 1884 [P]
Suborder Tornoceratina WEDEKIND 1918 [P]
Superfamily Tornocerataceae VON ARTHABER 1911 [P]
Family Parodoceratidae PETTER 1959 [P]
Mithraxites BECKER & HOUSE 1994
Parodiceras HYATT 1984
Croyites gen. nov.
Wedekindella SCHINDEWOLF 1928

Appendix 3. Proposal for a revised classification scheme of Early and Middle Devonian ammonoids