Evolution of the Goniatitaceae and Viséan–Namurian biogeography

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Evolutionary lineages within the Carboniferous ammonoid superfamily Goniatitaceae can be recognized using cladistic and stratophenetic analyses, showing that both approaches lead to coinciding results. In the late Viséan and Namurian A, ammonoid provinces can be defined by the distribution of lineages within the goniatite superfamily Goniatitaceae. The first province corresponds to the Subvariscan Realm (where the superfamily became extinct near the Viséan–Namurian boundary), and the second embraces the majority of the occurrences, e.g. the South Urals, Central Asia, and North America (where the superfamily with different independent lieages continued up into the late Namurian A). In the Viséan, the superfamily was, in two short epochs, globally distributed with major transgressions, which probably led to migration events. The first is at the end of the late Viséan A (*G. fimbriatus* and *G. spirifer* Zones, when the genus *Goniatites* had a world-wide distribution with various species), and the second at the beginning of the late Viséan C (*L. poststriatum* Zone, when *Lusitanoceras* is globally distributed).

K e y   w o r d s : Ammonoidea, Goniatitaceae, Early Carboniferous, phylogeny, palaeo-biogeography.

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Introduction

Late Viséan and early Namurian goniatite faunas have been reported from numerous localities in the northern hemisphere, from Alaska and Canada, the Western and Central United States, various regions in Europe and North Africa, Novaya Zemlya and the South Urals, Central Asia, as well as from China. They have been described in several monographs and articles, mostly published during the last 30 years. These data allow a comparison of the faunal compositions in the different regions, and provide a tool for

palaeogeographical reconstructions of the plate configuration during the late Early Carboniferous.

Ammonoid provincialism in the late Viséan and early Namurian has already been postulated several decades ago. Kullmann (1962) distinguished between an epicontinental fauna (to which he referred the Subvariscan Realm), and a geosynclinal fauna (= Tethyal fauna), in which he placed the faunas collected from the Cantabrian Mountains of Spain, North Africa, South Urals, etc., and accounted for dissimilarities in the faunal spectra mostly to differences in water depth. Kullmann (1962) suggested that the two provinces, during the Namurian, contained different types of goniatites: the epicontinental fauna being characterized by goniatites with various ornament types, while typical for the geosynclinal fauna were goniatites with modified internal structures, such as advanced sutural development, and evolute coiling of the inner whorls.

The Goniatitaceae is one of the major late Viséan and early Namurian goniatite superfamilies with an almost world-wide geographical distribution. It is recorded from numerous regions in Europe, from North Africa, North America, as well as from several localities between the Ural Mountains and Japan. The Goniatitaceae is also a superfamily containing numerous species, of which most occur in the late Viséan. Conchs of Goniatitaceae species display a rather high number of distinctive characters. Sutural features, conch geometry, and ornamental features allow cladistic analyses of these forms, and the dense sampling enables stratophenetic approach. Thus relationships between the various genera can probably be uncovered.

Discrimination of faunal provinces will be achieved here by pointing out differences in the distribution of independent evolutionary lineages. The data on which the cladistic and stratophenetic analyses are based are taken from the literature (Ruzhencev & Bogoslovskaya 1971; Korn 1988), and the data of the geographical distribution from the Database GONIAT, Tübingen (Korn & Kullmann 1996).

Conch morphology characters of the Goniatitaceae

Apomorphies. — The members of the superfamily Goniatitaceae, like many Carboniferous goniatites, display a suture line containing the elements Em E1 A L U I (terminology of Wedekind 1918), of which during phylogeny the E1 lobe (family Delepinoceratidae) or A lobe (family Agathiceratidae) became subdivided. The majority of the forms possess an E lobe with a general V-shaped outline, and an acute or subacute ventrolateral saddle. Characteristic for all the members of the superfamily is the course of ontogenetic development of the external lobe. In juveniles, it is Y-shaped, but during ontogeny it changed to a V-shaped outline. Without exception among the Viséan and Namurian species, all forms have pointed lobes (in contrast, the latest Carboniferous and Permian agathiceratids had rounded lobes and saddles). The conch is usually pachyconic or globular with an extremely low whorl expansion rate, and a very narrow or closed umbilicus. Many forms bear crenulated growth lines and/or spiral lines, which always result from crenulation.

The phylogenetic origin of the superfamily Goniatitaceae is unclear (Ruzhencev & Bogoslovskaya 1970). In Central and Western Europe, the first species of the superfamily appears near the mid-Viséan boundary and can be classified in the genus

Goniatites (Korn 1996), possessing a conch morphology dissimilar to any early Viséan goniatites. The pointed ventrolateral saddle of the suture line, maintained in the subsequent lineages, is unique among the early late Viséan goniatites. Additionally, the narrow umbilicated, globose conch form and the strongly crenulated growth lines on an otherwise unornamented shell are novelties (apomorphies) in this group. Juvenile stages of species of *Goniatites* seem to recapitulate an adult sutural outline of its ancestor, which probably possessed a Y-shaped external lobe.

Morphological trends in the evolution. — A transformation of several characters can be observed within the evolutionary history of the Goniatitaceae (Ruzhencev & Bogoslovskaya 1970). Primarily, the sutural development displays a significant pattern, and allows separation of several independent evolutionary lineages, characterized by different modes of sutural subdivision (Figs 1, 2). Trends of sutural and conch transformations within the Goniatitaceae are:

(1) The median saddle height increase (relative to the ventrolateral saddle).

0.40 in the earliest late Viséan (e.g., *Goniatites hudsoni*, *G. crenistria*),

0.50 in the late Viséan B (e.g., *Arnsbergites*, *Hibernicoceras*, *Paraglyphioceras*),

0.60 to 0.70 near the Viséan–Namurian boundary (e.g., *Neogoniatites*, *Dombarites*), and

more than 0.80 in the early Namurian (e.g., *Platygoniatites*, *Delepinoceras*, *Proshumardites*).

This tendency is shown by almost all the evolutinary lineages, and a reversal apparently did not occur. The height increase of the median saddle is a common feature among many Carboniferous goniatites (Ruzhencev & Bogoslovskaya 1971, 1978), hence it should not be used as a criterion for the definition of higher taxa. The height increase, however, is important for the separation of genera and species

(2) The E lobe widening (the width measured at its half depth, relative to its total depth = E lobe index). On the basis of this character, four independent lineages can be recognized, these are:

Goniatites → *Hypergoniatites*, with no remarkable widening (E lobe index always between 0.50 and 0.60),

Paraglyphioceras → *Neogoniatites*, with a continuous widening rate during phylogeny (E lobe index 0.65 to 0.95),

Lusitanoceras → *Proshumardites*, with a moderate widening of the E lobe (E lobe index 0.65 to 0.95, but with secondary dissection of the A lobe), and

Lusitanoceras → *Delepinoceras*, with a prominent widening during phylogeny (E lobe index 0.65 to 1.50), leading to a secondarily tridentate E1 lobe.

(3) The evolute coiling of the inner whorls. Derived species with evolute inner whorls evolve from completely involute forms, which stratigraphically occur at the beginning of the evolutionary history, for example: the inner whorls are involute in *Goniatites*, *Goniatitella*, and in *Hypergoniatites*, but evolute in *Hibernicoceras*, *Arnsbergites*, *Paraglyphioceras*, *Lusitanoceras*, and *Dombarites*. Cross sections of stratigraphically later genera remain unknown, but, according to published photographs, it can be assumed that in derived forms such as *Delepinoceras* and *Proshumardites* only very few initial whorls are evolute.
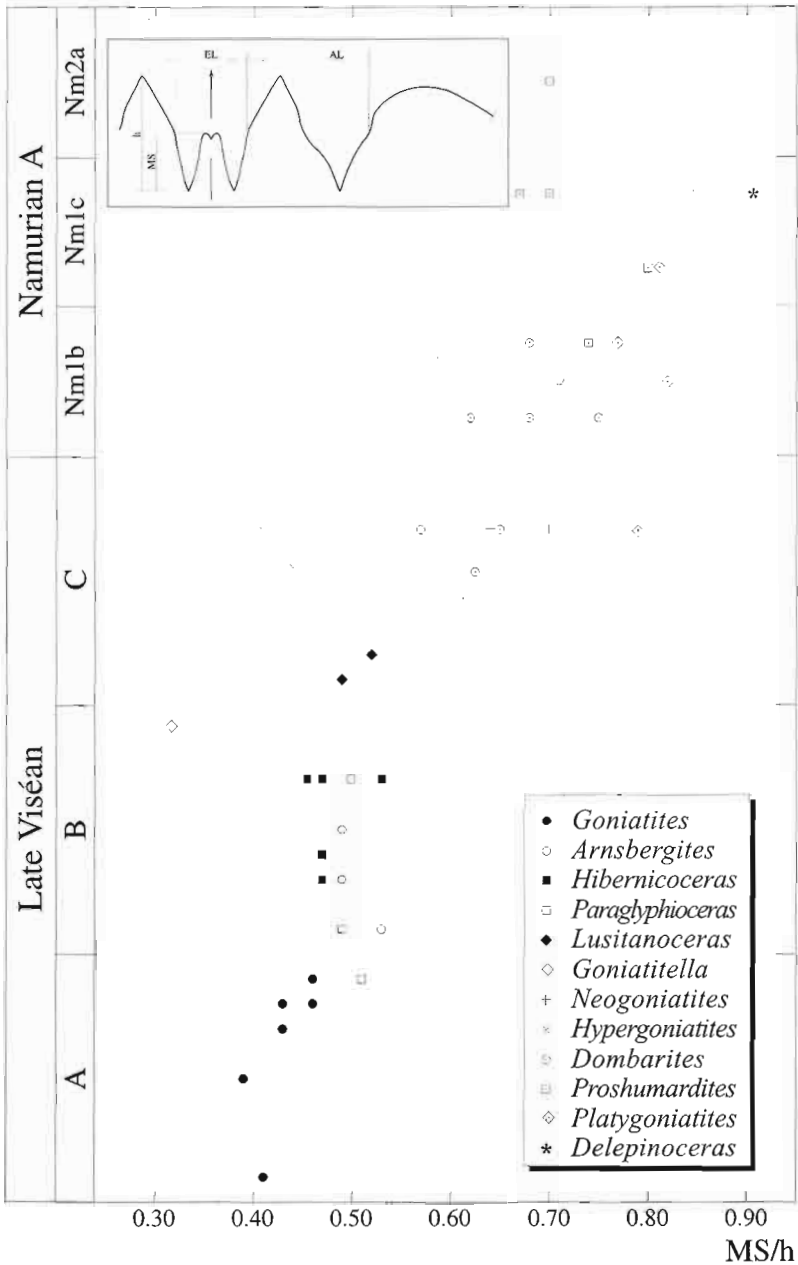
Fig. 1. Diagram showing the height increase of the median saddle in the evolution of the late Viséan and early Namurian species of the superfamily Goniatitaceae. MS/h refers to the ratio between the height of the median saddle (MS) and the total height of the ventrolateral saddle (h). Note that there is a continuous height increase (except for the late Viséan genera *Goniatitella* and *Hypergoniatites*), and that no independent evolutionary lineages can be traced in the remaining species. In the box: Sutural parameters used in the diagrams and for the cladistic analysis. See also explanation to Fig. 2.
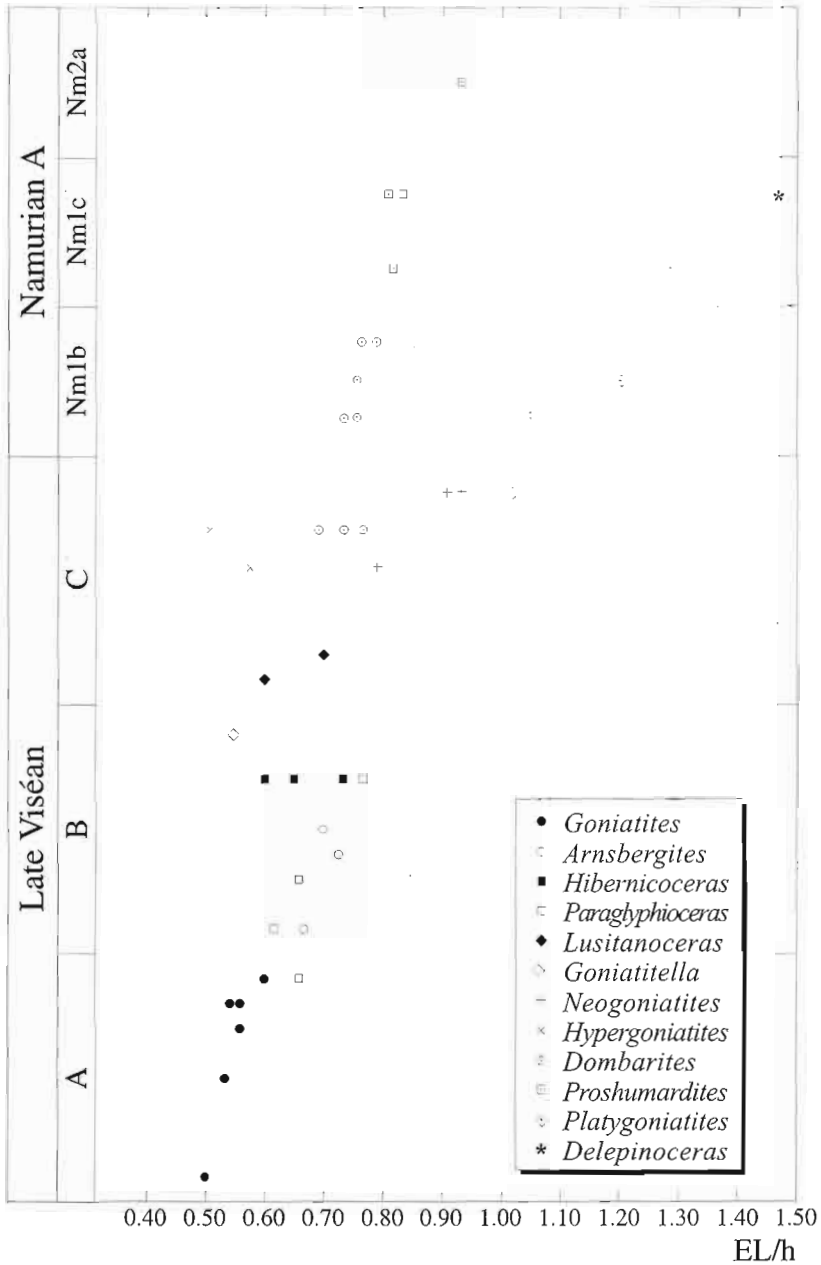
Fig. 2. Diagram showing the widening of the external lobe in the evolution of the late Viséan and early Namurian species of the superfamily Goniatitaceae. EL/h refers to the ratio between the width of the external lobe (EL; measured at half the height of the ventrolateral saddle) and the total height of the ventrolateral saddle (h). Note that a continuous widening takes place (except for the late Viséan genera *Goniatitella* and *Hypergoniatites*). In the early Namurian, two independent evolutionary lineages can be seen, one leading to *Proshumardites* (family Agathiceratidae; with moderate widening of the external lobe), and one leading to *Delepinoceras* (family Delepinoceratidae; with prominent widening of the external lobe). See insert in Fig. 1.

Table 1. Character matrix for the late Viséan and Namurian species of the Goniatitaceae. Characters (18) and (20) are weighted as being of double value. Abbreviation: orn. – ornament.

Character definitions (columns 0–23):

0. Ontogeny of external lobe from Y-shaped to V-shaped: no (0), yes (1)
1. Distance of prongs of external lobe: very short (0), moderate (1)
2. Median saddle higher than 45% of ventrolateral saddle: no (0), yes (1)
3. Median saddle higher than 55% of ventrolateral saddle: no (0), yes (1)
4. Median saddle higher than 65% of ventrolateral saddle: no (0), yes (1)
5. Median saddle higher than 75% of ventrolateral saddle: no (0), yes (1)
6. Median saddle higher than 85% of ventrolateral saddle: no (0), yes (1)
7. External lobe V-shaped (0), Y-shaped (1)
8. Ventrolateral saddle: acute or subacute: no (0), secondarily rounded (1)
9. Ventrolateral saddle tectiform: no (0), yes (1)
10. External lobe wider than 0.60: no (0), yes (1)
11. External lobe wider than 0.90: no (0), yes (1)
12. External lobe wider than 1.20: no (0), yes (1)
13. External lobe wider than 1.50: no (0), yes (1)
14. External lobe with tridentate branches: no (0), yes (1)
15. Adventive lobe: flanks linear (0), sinuous or else (1)
16. Adventive lobe: flanks not angular (0), angular or tridentate (1)
17. Adventive lobe tridentate: no (0), yes (1)
18. Inner whorls involute (0) or evolute (1)
19. Drastic size reduction of the conch: no (0), yes (1)
20. Whorl expansion rate: low (0), moderate (1)
21. Preadult whorls triangularly coiled: no (0), yes (1)
22. Apertural shape in juveniles: rectiradiate (0), prorsiradiate (1)
23. Course of growth lines: with projections and sinuses (0), linear (1)

	suture line																		conch				orn.	
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	**18**	19	**20**	21	22	23
Eoglypioceras truncatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Goniatites crenistria	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arnsbergites falcatus	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0
Hibernicoceras hibernicum	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0
Paraglyphioceras rotundum	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Lusitanoceras poststriatum	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	1	1	1	0
Goniatitella agricola	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1
Neogoniatites milleri	1	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Hypergoniatites exiguus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Dombarites tectus	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	1	0
Proshumardites delepinei	1	0	1	1	1	1	1	0	0	1	1	0	0	0	0	1	1	1	1	0	0	1	1	0
Platygoniatites molaris	1	0	1	1	1	1	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	1	1	0
Delepinoceras bressoni	1	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0	1	0	0	1	1	0

(4) The aperture shape in juveniles. Within the late Viséan, two apertural types in immature specimens are present: the rectiradiate type, where the growth lines run in an almost radial direction (*Goniatites, Hypergoniatites, Paraglyphioceras*, and *Goniatitella* with linear growth lines), and the prorsiradiate type, where the growth lines prominently arch forward on the flanks to form a broad ventral projection (*Arnsbergites, Hibernicoceras, Lusitanoceras*).
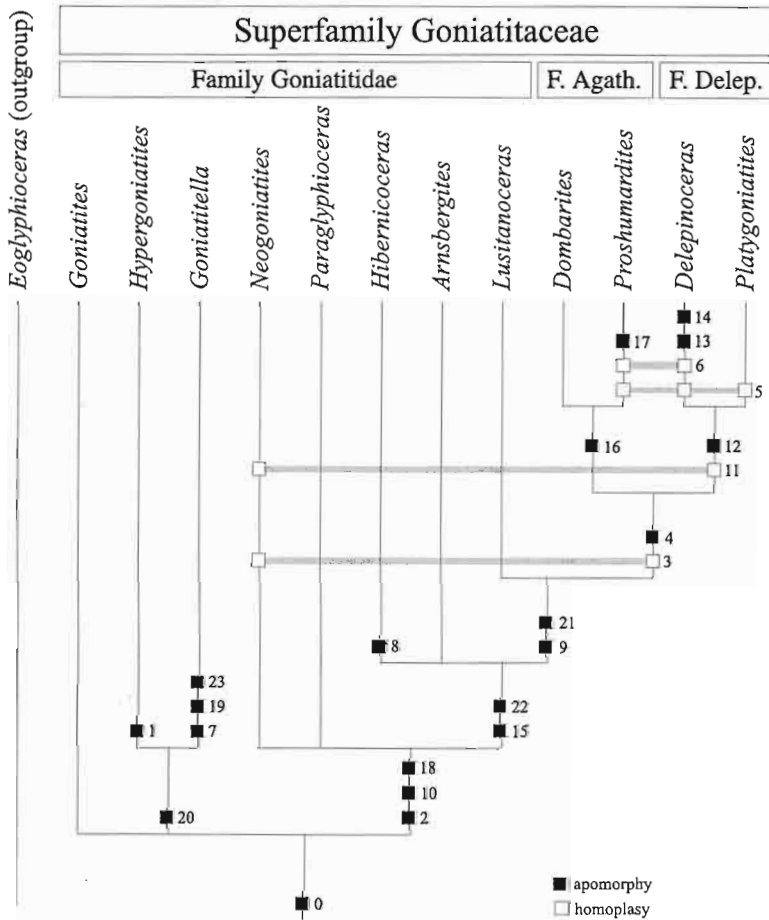
Fig. 3. Cladogram representing one of two most parsinomous trees using PAUP 3.0 (Swofford 1989) of the Goniatitaceae. Numbers of autapomorphies and homoplasies in both figures refer to condition (1) in the character matrix shown in Table 1. Note that the superfamily Goniatitaceae is characterized by one synapomorphy, the ontogenetic development from a juvenile Y-shaped external lobe towards an adult V-shaped external lobe (character **0**). *Goniatites*, which is regarded as the ancestor of all the other genera of the superfamily, does not possess an autapomorphy, but the other two independent lineages are defined by (**20**) the higher whorl espansion rate (*Goniatitella, Hypergoniatites*), and by (**18**) the evolution of the inner whorls, (**2**) the height increase of the median saddle, and (**10**) the widening of the external lobe (occuring in all the other genera). The latter clade is shown as an unresolved trichotomy. The ancestral *Paraglyphioceras* cannot be defined by an autapomorphy. The same is true for *Neogoniatites*, but this genus shares two homoplasies with genera of the families Agathiceratidae and Delepinoceratidae, the continuing height increase of the median saddle (**3**), and the widening of the external lobe (**11**). *Neogoniatites*, however, is distinguished by lacking some of the features from these genera, and is thus be interpreted as an independent lineage. The sutural development is then the main character for further hierarchized subdivision of the clade. The beginning sinuosity of the flanks of the adventive lobe (**15**) in *Arnsbergites* is followed by the tectiform outline (**9**) in *Lusitanoceras*. From the latter genus derive the two families Agathiceratidae, defined by the angularity of the adventive lobe (**16**) and finally its trifurcation (**17**), and the family Delepinoceratidae, defined by the rapid widening of the external lobe (**12, 13**), leading to tridentation of its prongs (**14**) in the terminal stage of this lineage. Abbreviations: F. Agath. – family Agathiceratidae, F. Delep. – family Delepinoceratidae.

Cladistic analysis. — Phylogenetic relationships within the family Goniatitidae and their immediate descendants Delepinoceratidae and Agathiceratidae have been discussed by Bogoslovskaya (1966) and Ruzhencev & Bogoslovskaya (1970, 1971). These authors, however, accepted only four late Viséan genera within the Goniatitidae (*Goniatites, Hypergoniatites, Neogoniatites,* and *Hibernicoceras*), and treated *Goniatites* as a very voluminous genus unifying more than 30 different species. This concept was not followed by Korn (1988), who distinguished nine genera within the Goniatitidae:

Goniatites de Haan, 1825,
Hibernicoceras Moore & Hodson, 1958,
Lusitanoceras Pereira de Sousa, 1923,
Paraglyphioceras Brüning, 1923,
Arnsbergites Korn, 1988,
Goniatitella Korn, 1988,
Neogoniatites Ruzhencev & Bogoslovskaya, 1970,
Hypergoniatites Ruzhencev & Bogoslovskaya, 1970, and
Junggarites Liang & Wang, 1991 (problematic genus).

A cladogram (Fig. 3), based mainly on sutural characters, is presented here showing proposed relationships of the Early Carboniferous genera of the Goniatitidae, Agathiceratidae, and Delepinoceratidae. For the cladistic analysis, well known representative species have been chosen (Table 1).

Included characters are only those, which can be regarded as significant on the genus-level, such as the coiling of the inner whorls, the suture line (especially the ratios of dimensions in sutural elements, although these are sometimes only suitable for discrimination of species), and the apertural outline. Of these, the coiling of the inner whorls and the increase of the later whorl expansion rate are relatively weighted as being of double value, since this has been shown to be a rather stable feature in the evolution of late Viséan ammonoids (Ruzhencev & Bogoslovskaya 1971; Korn 1988). Characters such as the conch ornament type, which are proved to be less stable, and often can only be used for discrimination on the species-level within the genera, are largely omitted from the analysis.

From the cladogram, the paraphyletic nature of the familiy Goniatitidae is obvious. This is especially because the advanced taxa in the phylogenetic tree, which show anadvanced sutural development, have been cut-off to form the monophyletic families Delepinoceratidae and Agathiceratidae, characterized by different sutural developments, but with conch shapes which do not vary much throughout their phylogeny.

The transformation from *Goniatites*, which is regarded as ancestral to the succeeding genera *Hypergoniatites* and *Goniatitella*, is unresolved because of the lack of intermediate forms.

Evolutionary lineages within the Goniatitaceae

The cladogram (Fig. 3) can easily be transformed into an evolutionary tree (Fig. 4), in which the stratigraphical distribution of the genera and possible ancestor-descendant sequences are presented. This indicates the rather gradual evolution of the superfamily

Goniatitaceae with several independent lineages, which will be described below. Some of the proposed phylogenetic lineages are well documented, such as *Lusitanoceras* → *Platygoniatites* → *Delepinoceras* by continuous widening of the external lobe and subdivision of its branches, and *Lusitanoceras* → *Dombarites* → *Proshumardites* by successive widening and trifurcation of the adventive lobe.

Goniatites. — In the late Viséan A, the genus is represented by at least four successive species in Central Europe (Korn 1988). A morphological trend of sutural development can be observed, which includes the following features: (1) widening of the E lobe: from imndex value 0.50 in *Goniatites hudsoni* to 0.60 in *Goniatites spirifer*, (2) increase of median saddle height: from index value less than 0.40 in *Goniatites hudsoni* to 0.50 in *Goniatites spirifer.*

It is is uncertain if the stratigraphically succeeding species form a single phyletic lineage. Ornamental differences, e.g. the strongly biconvex course of the growth lines in *Goniatites crenistria* and the presence of spiral lines already in *Goniatites*(?) *globostriatus* suggest that these species belong to side-branches. It is still unclear, however, if *Goniatites*(?) *globostriatus* in fact belongs to *Goniatites*, or rather to a beyrichoceratid genus. From the Rhenish Massif, no three-dimensionally preserved material which could have been dissected has been traced so far, and specimens from other regions do not display the suture line either. It can be stated with certainty, however, that at least *Goniatites maximus* var. *saourensis* Pareyn, 1961 is, according to its suture line, a beyrichoceratid. This is confirmed by the recent collection of well preserved new material from near Erfoud, Tafilalt, Morocco. Conch and ornament development lead to the interpretation that there was a phyletic lineage *Goniatites hudsoni* → *Goniatites fimbriatus* → *Goniatites spirifer*.

Goniatites → Hypergoniatites. — *Hypergoniatites* is the latest Viséan goniatite genus with an archaic conch morphology, resembling that of species from the late Viséan A, but with a remarkable increase of the whorl expansion rate (see cross sections in Ruzhencev & Bogoslovskaya 1971). It is characterized by a suture line that displays features similar to *Goniatites crenistria*, with a narrow external lobe, pointed ventrolateral saddle, and a V-shaped adventive lobe. The E lobe index is only 0.50 to 0.55, low ratios known elsewhere only in much older representatives of the superfamily Goniatitaceae (Fig. 4). No species of *Goniatites*, however, has an external lobe that is, at its base, as narrow as in *Hypergoniatites*.

There are no intermediate forms known which stratigraphically link *Goniatites* and *Hypergoniatites*. The only genus with an intermediate stratigraphical occurrence is *Goniatitella*, which shares similar conch and sutural relations with *Goniatites* and *Hypergoniatites*, but markedly differs in ornament with coarse spiral lines, and a suture line with Y-shaped external lobe and rounded ventrolateral saddle. For these reasons, it cannot be regarded as a direct ancestor of *Hypergoniatites*. The small size of *Goniatitella* specimens and their suture line that in the adult stage still displays a juvenile outline suggests that it is a paedomorphic (progenetic) form.

Goniatites → Paraglyphioceras → Neogoniatites. — After the abrupt decline of species of the family Goniatitidae with involute inner whorls at the end of the late Viséan A, its representatives with open umbilicate juveniles dominate the goniatite faunas in Central and Western Europe. The first genus of this kind is *Paraglyphioceras*, which already co-occurs with *Goniatites* in the *G. fimbriatus* Zone, represented there by *Paraglyphioceras*(?) *semistriatum* (Nicolaus, 1963), known from crushed material, in which inner whorls and suture lines are not preserved. From the *G. spirifer* Zone, *Paraglyphioceras radiatum* (Hodson & Moore, 1959) is known, of which well preserved material is available from Ireland (Hodson & Moore 1959) as well as the Harz Mountains (Korn 1990b; Gischler & Korn 1992). In these specimens, the inner whorls and the suture line can be examined, allowing comparison with the ancestral *Goniatites* and descendant *Arnsbergites*.

Paraglyphioceras radiatum possesses a morphology which is advanced in comparison with the stratigraphically youngest species of *Goniatites* by the following set of features: (1) the juvenile whorls, up to 4 mm conch diameter, are evolute, (2) the external lobe depth is 1.20 of the width of the adventive lobe (E lobe index = 0.65), (3) the median saddle height exceeds half of the ventrolateral saddle, and (4) the ventrolateral saddle is subacute, rather than acute as in *Goniatites*.
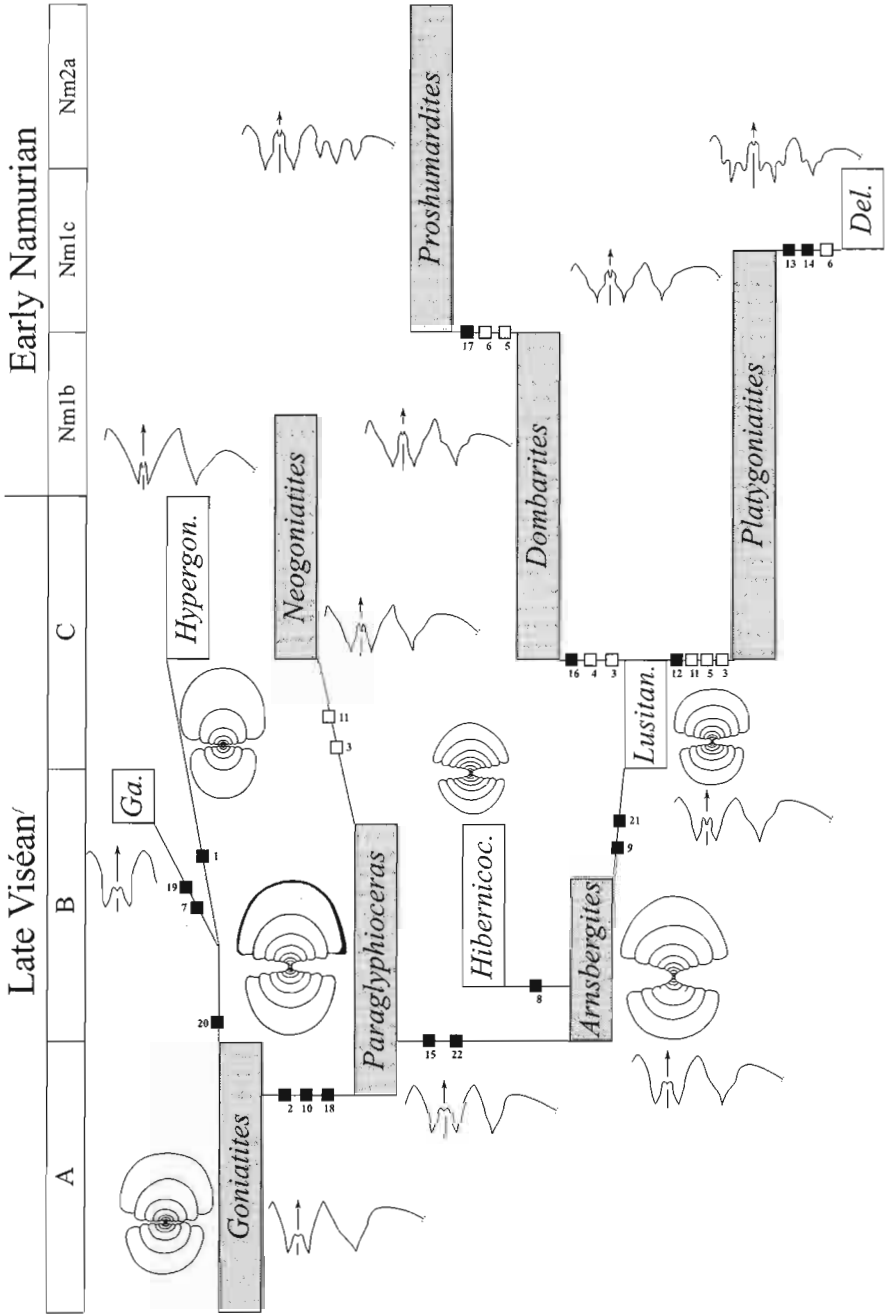
Fig. 4. Phylogram displaying the proposed relationships between the late Viséan and early Namurian genera of the superfamily Goniatitaceae. The same apomorphies and homoplasies as in Fig. 3 are used, but the genera are here arranged according their stratigraphical occurrence. Stratigraphical scheme of the early Namurian after Ruzhencev & Bogoslovskaya (1971), and the late Viséan after Korn (1996). Open boxes show genera without remarkable morphological trends, grey boxes show genera with striking morphological transformation during phylogeny. Cross sections are to the same magnification, suture lines not to scale.
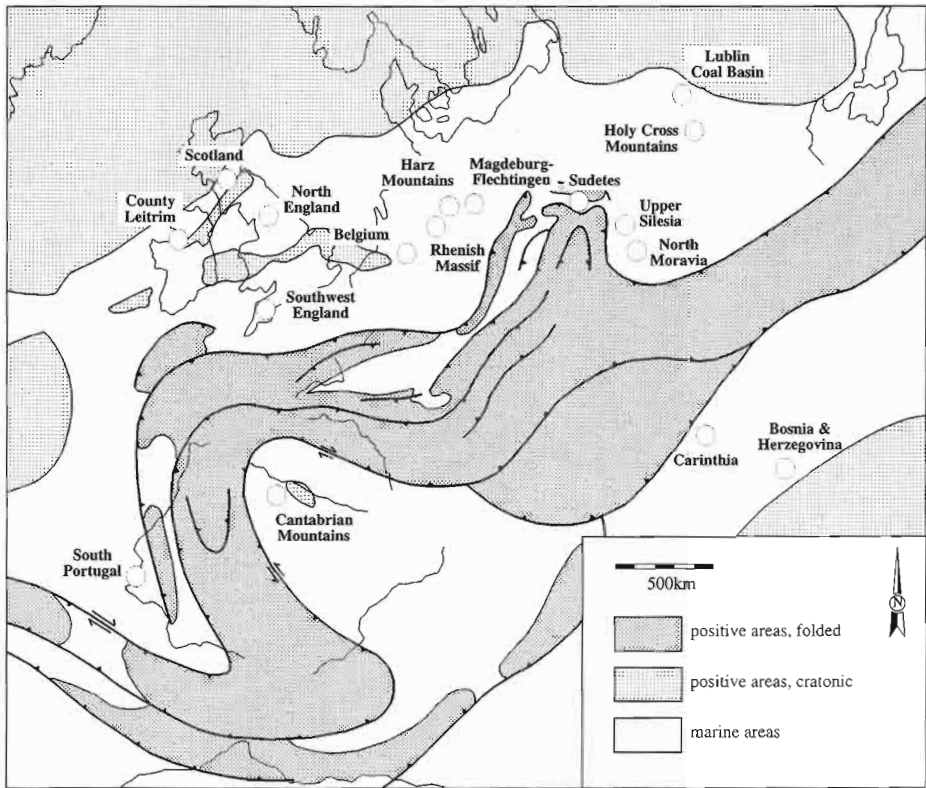
Fig. 5. Palaeogeographical map of Europe during the late Viséan (modified after Ziegler 1989).

Additionally, the adult conch of *Paraglyphioceras radiatum* bears a falcate ornament, consisting mainly of densely spaced biconvex riblets.

Paraglyphioceras extends up into the *P. rotundum* Zone. Only in this zone is the genus the most frequent, with the dominant species *P. rotundum* Brüning, 1923. In this species, the suture line displays more derived characters in comparison with *P. radiatum*, for example the external lobe is 1.5 wider than the adventive lobe (E lobe index = 0.75).

A species that closely resembles *P. rotundum* is *P. striatum* (Sowerby, 1813) although the flanks of the lobes are much more sinuous. The sutural ratios of the two species, however, are very similar and suggest a similar stratigraphical origin of the species.

The main trend in the development of the suture line of *Goniatites* continued within the genus *Paraglyphioceras*. A character in common with *Goniatites* is the shape of the aperture that remains stable during the *Paraglyphioceras* lineage.

Neogoniatites has a similar conch form to *Paraglyphioceras*, but differs in the outline of the suture line, which can be regarded as derived, the external lobe is wider, its width is two times greater than that of the adventive lobe (E lobe index = 0.90), and the median saddle is higher (0.60 of the ventrolateral saddle).

It is especially the lack of some characters (lack of angularity of the flanks of the adventive lobe, lack of a tectiform ventrolateral saddle, lack of prorsiradiate juvenile aperture) that characterizes the genus *Neogoniatites* and separates it clearly from other genera such as *Dombarites* and *Platygoniatites* (Figs 4, 5). The two advanced sutural features listed above are thus interpreted as homoplasies. Apparently, the evolutionary lineage leading to *Neogoniatites* became extinct near the Viséan–Namurian boundary.

Paraglyphioceras → *Arnsbergites*. — In the shape of the juvenile aperture, all the other Viséan genera within the family Goniatitidae differ remarkably from *Goniatites* and *Paraglyphioceras*, for instance, species of *Arnsbergites*, *Hibernicoceras*, and *Lusitanoceras* possess in preadult stages a prorsiradiate aperture that is characterized by a prominent ventrolateral projection, and a very shallow or absent ventral sinus.

The stratigraphically oldest of these forms is *Arnsbergites falcatus* (Roemer, 1850), a species that occurs immediately above *Paraglyphioceras radiatum* and *Goniatites spirifer*, but differs from the latter in the evolution of the inner whorls, as well as the much wider external lobe, higher median saddle, and subacute ventrolateral saddle. These modifications are so prominent that they cannot be explained by a gradual development from one of the youngest *Goniatites* species.

Arnsbergites falcatus shares conspicuous ornamental features with *Paraglyphioceras radiatum*, but with the following differences in internal morphology: (1) in *A. falcatus*, more inner whorls are evolute, (2) the juvenile apertural shape is very dissimilar, prorsiradiate in *A. falcatus*, but rectiradiate in *P. radiatum*, (3) the flanks of the adventive lobe are more sinuous in *Arnsbergites*, and (4) the external lobe is wider in *A. falcatus* (E lobe index = 0.72 in comparison with 0.65 in *P. radiatum*).

These modifications agree with general trends in the evolution of the superfamily Goniatitaceae, and hence a close relationship between the two species is postulated here.

Stratigraphically younger species of *Arnsbergites* are characterized by a weakening of the ornament and by the loss of the falcate pattern. Furthermore, the apertural outline changes: In *A. falcatus*, the growth lines run rectiradiate over flanks and venter, but in the younger *A. gracilis* and *A. arnsbergensis*, they run in a rursiradiate direction. In this character, *Hibernicoceras* is very similar to *Arnsbergites*, but differs in the more rounded ventrolateral saddle and the loss of spiral lines on flanks and venter. For these reasons, *Hibernicoceras* is regarded as a descendant of *Arnsbergites*.

Arnsbergites → *Lusitanoceras*. — The phylogenetic position of *Lusitanoceras* within the super-family Goniatitaceae is clear, although a direct ancestor is still unknown. The genus most probably derived from the spirally ornamented *Arnsbergites* by developing an advanced sutural outline with sinuous flanks of the adventive lobe and a tectiform ventrolateral saddle. Conch morphology of the inner whorls is similar with open umbilicus and a prorsiradiate aperture, but a novelty is the triangularity, caused by deep constrictions, of the immature whorls. This character is maintained in almost all the descendants of *Lusitanoceras*.

Lusitanoceras → *Proshumardites* (**Agathiceratidae**). — *Lusitanoceras* is ancestral to *Dombarites*. Species of *Lusitanoceras* are morphologically and stratigraphically close to *Dombarites*, much more so than to the genus *Goniatites*. Although *Lusitanoceras* and *Dombarites* have hardly been recorded from the same localities in succeeding strata, it can be assumed that *Dombarites* more or less directly succeeded *Lusitanoceras*.

In their article on the relationships between the genus *Goniatites* and phylogenetically subsequent genera, Ruzhencev & Bogoslovskaya (1970) proposed a lineage initiating with *Goniatites* (in their interpretation; partly *Lusitanoceras* as interpreted here), and leading to the Permian *Agathiceras* by passing through *Dombarites* and *Proshumardites*. In their morphology, several trends are observable:

(1) Increase of median saddle height:
from 0.50 to 0.55 in *Lusitanoceras*,
from 0.55 to 0.75 in *Dombarites*, and
from 0.65 to 0.85 in *Proshumardites*.

(2) Development of tridentition of the adventive lobe
sinuous flanks in *Lusitanoceras*,
angular flanks in *Dombarites*, and
trident in *Proshumardites*.

(3) Loss of angularity of the ventrolateral saddle.

The concept of Ruzhencev & Bogoslovskaya (1970) in separating between *Pericleites* (in their definition) and *Proshumardites* is not followed here. Apart from the difficulties in interpretation of the original *Pericleites atticus* (Renz, 1910) (Schindewolf 1939), the early Namurian forms possess

a morphology which can be regarded as intermediate between *Dombarites* and *Proshumardites* of the *P. karpinskii* group.

In their conch geometry and ornament, the genera *Lusitanoceras* and *Dombarites* are extremely similar, and in some cases inseparable. Most of the species of this lineage display an ornament with coarse spiral lirae, and rather often a falcate ornament is developed in adults. Triangular coiling of juvenile conchs is common in many species. There are also remarkable shifts in the maximum size of the conchs:

65 to 105 mm in *Lusitanoceras*, usually less than 80 mm,

up to 150 mm in *Dombarites*,

up to 65 mm in *Proshumardites*, but usually smaller, and

up to 45 mm in *Agathiceras*.

Lusitanoceras → Delepinoceras (Delepinoceratidae). — Ruzhencev & Bogoslovskaya (1970) also proposed this lineage, which developed parallel to the one described above. The main transforming feature is the external lobe, whose prongs became tridentate during phylogeny. This is already seen in *Platygoniatites*, where they are already mammiform. The width of the external lobe (E lobe index) increases remarkably, for example:

1.10 in the stratigraphically oldest form *P. omniliratus*,

1.30 in the stratigraphically younger forms *P. molaris* and *P. superior*, and

1.50 in *Delepinoceras bressoni*.

The height of the median saddle increased from 0.80 in *Platygoniatites* to more than 0.90 in *Delepinoceras*.

In the other characters, the two genera are basically similar, both show spirally ornamented conchs which can be triangularly coiled in juveniles. *Platygoniatites*, however, is a giant among the late Early Carboniferous goniatites with a diameter attaining almost 200 mm, whereas *Delepinoceras* usually only reaches about 70 mm in diameter. Juveniles of the two genera are very similar to those of *Lusitanoceras* and *Dombarites*, hence a close relationship can be proposed. The slight arching of the flanks of the adventive lobe in *Platygoniatites* may be an indication for an origin of *Platygoniatites* from *Lusitanoceras*, rather than from *Dombarites*.

Palaeogeographical distribution of the Goniatitaceae

Late Viséan and early Namurian ammonoids are known from numerous regions in Europe, North Africa, Asia, and North America. Knowledge of the ammonoid faunas from the various regions is highly variable, comparisons are sometimes based on very incomplete information. Furthermore, the lack of any modern syntheses on the ammonoid assemblages prevents exact correlation. Only from few regions (Tables 2, 3), more or less complete faunal successions are known, allowing application of the stratigraphical scheme introduced by Korn (1996) for the Rhenish Massif.

Geographical distribution of the index species on which the stratigraphical scheme is based is very irregular. Some of the species, such as *Lusitanoceras poststriatum*, occur in almost all the regions; whereas others, such as *Lyrogoniatites eisenbergensis*, are greatly restricted.

Goniatites. — *Goniatites* is frequently found in late Viséan A sediments of Central and Western Europe. Species from other regions can, by their sutural ratios, be compared with the European forms. *G. americanus* Gordon, 1971 from the lower Chainman Shale of the Confusion Range of Utah, for instance, displays a suture that in its ratios resembles that of *G. hudsoni*, and may have a similar stratigraphical age. Higher in the succession, *G. multiliratus* Gordon, 1962 occurs, with sutural ratios such as in *G. spirifer*, indicating a late late Viséan A age.

Table 2. Documentation of the different ammonoid zones of the late Viséan in the various regions within the Subvariscan Realm. Shading indicates the presence of ammonoid-bearing strata (light shading indicates questionable occurrences), black dots indicate the presence of species of the Goniatitaceae, and open dots refer to questionable occurrences. Stratigraphical scheme after Korn (1996). Note that the distribution of faunas in particular regions is rather uniform, differences may express the state of knowledge.

Occurrences of *Goniatites* in other regions are probably in time-equivalent strata. Kullmann (1961) described two spirally ornamented species from the Alba Formation of the Cantabrian Mountains, *G. stenumbilicatus* and *G. globiformis*, and Bogoslovskaya (1966) described two falcate ornamented species from the South Urals as *G. crenifalcatus* and *G. sphaeroides*. It is striking that in both occurences compressed and globular morphotypes are represented, as in *G. hudsoni*, in which they are interpreted as an intraspecific variability. The four species described by Kullmann (1961) and Bogoslovskaya (1966) display sutures with dimensional ratios resembling those of *G. fimbriatus* and *G. spirifer*, and hence, are probably of the same age.

The *Goniatites* → *Hypergoniatites* lineage. — *Hypergoniatites* is a frequent fossil in the latest Viséan sediments of the South Urals (Ruzhencev & Bogoslovskaya 1970, 1971), Novaya Zemlya (Kusina & Yatskov 1988), Central Asia (Pitinova 1975; Nikolaeva 1994, 1995), China (Liang & Wang 1991), and the Cantabrian Mountains (Kullmann 1961; Wagner-Gentis 1980). Several iso-chronous species have been discriminated from these regions, but there is no indication of an occurrence of the genus in the Subvariscan Realm.

After the decline of the genus *Goniatites* in the Subvariscan Realm at the end of the late Viséan A, members of the family Goniatitidae with involute inner whorls occur only in a much higher stratigraphical level. In the *N. suerlandense* Zone of the Rhenish Massif, *Goniatitella agricola* Korn,
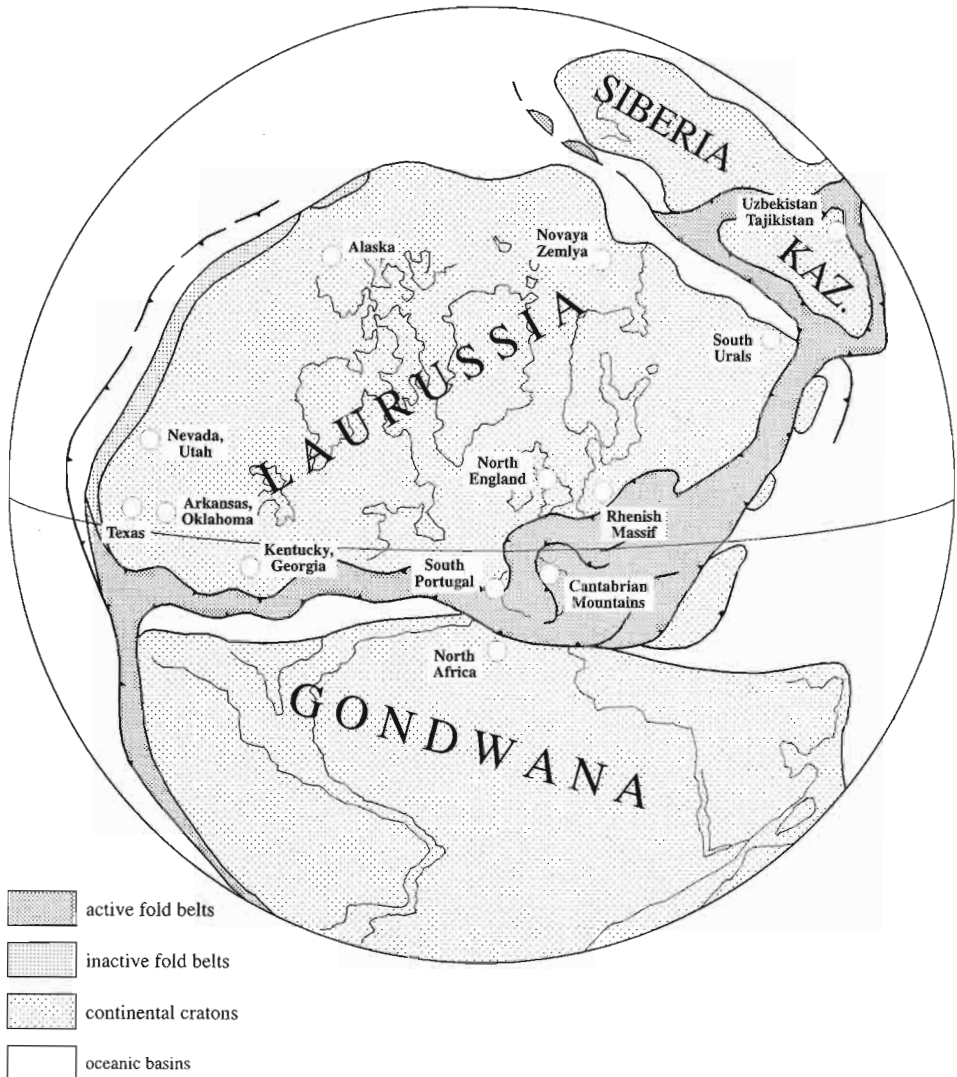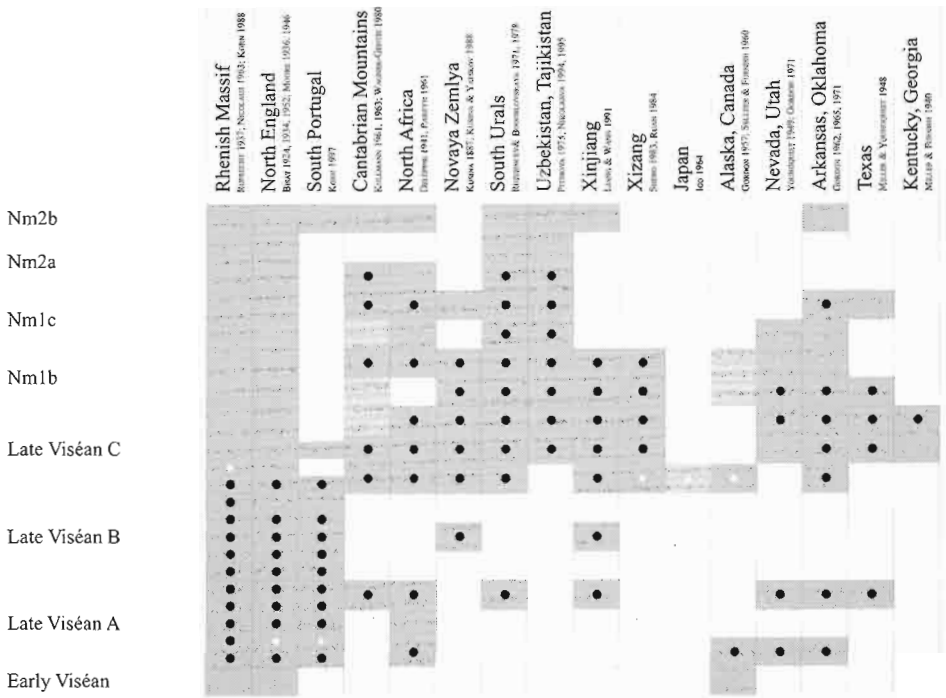
Fig. 6. Palaeogeographical map for the Namurian (after Ziegler 1989).

1988 is very common, a tiny goniatite with coarse spiral lines and a suture line with juvenile outline. This species has not yet been reported from other regions.

The *Paraglyphioceras* → *Neogoniatites* lineage. — The oldest genus of this lineage, *Paraglyphioceras*, is represented by several successive species in the Subvariscan Realm, known from southwest Portugal to the Lublin Coal Basin. Unambiguous reports of this genus from other regions do not exist.

In contrast to this, the subsequent genus *Neogoniatites* is completely absent in Central Europe. It is a common faunal element in the latest Viséan and earliest Namurian rocks. In North America the form is named *Goniatites kentuckiensis* Miller, 1889, in the Cantabrian Mountains *Goniatites (Girtyoceras) palentinus* Kullmann, 1961. In the Urals (Ruzhencev & Bogoslovskaya 1971) several species occur, and in South China *Xainzalites xainzaensis* Sheng, 1983, *Goniatites platyformis*

Table 3. Documentation of the different ammonoid zones of the late Viséan and early Namurian in various palaeogeographical regions. Shading indicates the ocurence of ammonoid-bearing strata (light shading indicates questionable occurrences), black dots indicate the presence of species of the Goniatitaceae, and open dots refer to questionable occurrences. Stratigraphical scheme after Ruzhencev & Bogoslovskaya (1971) and Korn (1996). Note that the distribution of faunas containing species of the Goniatitaceae shows a striking difference. In the Subvariscan Realm, the superfamily becomes extinct before the end of the Viséan, but in almost all the other regions it continues up into the Namurian. Note also that twice in the late Viséan, at the end of the late Viséan A as well as the base of the late Viséan C, the Goniatitaceae had a global distribution.

	Rhenish Massif	North England	South Portugal	Cantabrian Mountains	North Africa	Novaya Zemlya	South Urals	Uzbekistan, Tajikistan	Xinjiang	Xizang	Japan	Alaska, Canada	Nevada, Utah	Arkansas, Oklahoma	Texas	Kentucky, Georgia
Nm2b																
Nm2a				•				•								
Nm1c				•	•			•							•	
Nm1b				•	•	•	•	•	•					•	•	
Late Viséan C				•	•	•	•	•						•	•	•
Late Viséan B	•	•	•		•				•						•	
Late Viséan A	•	•	•			•							•	•	•	
Early Viséan	•	•	•			•						•	•	•		

Sheng, 1983 and *Neogoniatites xainzaensis* Ruan, 1984 may belong to this genus. They occur in rather small numbers of individuals. In none of the regions, however, does the genus play any important role.

Lusitanoceras. — *Lusitanoceras* is a genus with an almost global distribution. By separating different isochroneous species, palaeogeographical relationships may be discovered. Different species of *Lusitanoceras* occur with in the various regions as follows.

(1) Central Europe. A handful of species from localities in the Subvariscan Realm, which can be assigned to *Lusitanoceras*, have been introduced by several authors, and most of them are clearly junior synonyms of only one species, *Lusitanoceras poststriatum* (Brüning, 1923). *L. poststriatum* is known from a large suite of individuals from the type area in the Rhenish Massif, and is represented in all growth stages by three-dimensionally preserved specimens (Korn 1988). Hence intraspecific variability is well known in this species, and formerly erected species and subspecies names such as *Neoglyphioceras cuboides* Brüning, 1923, *Glyphioceras granosum spiraloides* Schmidt, 1925, and *Glyphioceras granosum* forma *jasterdorfiensis* Patteisky, 1930 must be treated as junior synonyms. The meaning of this is that in Central Europe *L. poststriatum* is the only species of that genus. It is unclear, however, as to whether *L. poststriatum* can be separated from *L. granosum* (Portlock, 1843), a species based on one single deformed specimen from County Tyrone in Ireland. The single

distinguishing character is the number of spirals, which is lower in *L. granosum*. Unless new material of *L. granosum* is found, this problem will remain unsolved.

(2) Eastern Central Europe. In the papers of Patteisky (1930), Knopp (1931, 1935: North Moravia), Korejwo & Teller (1967: Lower Silesia), and Żakowa (1971: Holy Cross Mountains), mostly deformed material has been described, not always allowing exact determination of these individuals. The best material derives from drills near Gałęzice (Żakowa 1971: pl. 10: 1–3), which represents several morphotypes of juvenile *Lusitanoceras poststriatum* (Brüning, 1923), comparable with those known from the Rhenish Massif. It is unclear, however, whether all these specimens belong to *L. poststriatum*, because some of them possess only about 80 spirals (Żakowa 1971: pl. 10: 2), hence they show affinities to *L. granosum* (Portlock, 1843).

(3) South Central Europe. A report of poorly preserved goniatites, which may belong to *Lusitanoceras*, from the Palaeozoic of Nötsch can be found in Aigner & Heritsch (1929), but the presented figure allows no closer assignment.

(4) British Isles. Although *Lusitanoceras* occurs quite frequently in localities in North England and Ireland, representation in the literature is rather scarce. Figured specimens have normally been assigned to *L. granosum* (Portlock, 1843). The high number of spiral lines on the specimen figured by Moore (1936: pl. 3: 1, 10), however, suggests that *L. poststriatum* is also represented there. Records of *Lusitanoceras* from northwestern Ireland (Brandon & Hodson 1984) have not been figured yet, so their specific assignment must remain uncertain. The type of *L. granosum* (Portlock, 1843), refigured by Moore (1936: pl. 3: 6) and Gordon (1965: pl. 18: 7), only shows 80 spiral lines from umbilicus to umbilicus (in contrast to *L. poststriatum* which always possesses more than 100), and an almost punctiform umbilicus at 36 mm diameter (unlike *L. poststriatum* with an umbilicus that amounts 0.15 of the conch diameter).

(5) Southwest Portugal. In this region, two sympatric species of *Lusitanoceras* occur, *L. postriatum* and *L. algarviense* Pereira de Sousa, 1923, the type species of the genus. Both are clearly separated by ornament and conch characters, and are not connected by intermediates (Korn 1997). *L. algarviense* is unique because of its falcate adult ornament and by its narrow umbilicus. A similar form is not known, the only one comparable is *L. granofalcatum* (Kullmann, 1961) from the Cantabrian Mountains, with a much wider umbilicus.

(6) Cantabrian Mountains. Species which can be attributed to *Lusitanoceras* were desribed and figured by Kullmann (1961) and Wagner-Gentis (1963, 1980). The first of these species is *L. granofalcatum* (Kullmann, 1961), characterized by a strong falcate ornament in the adult stage over 70 mm diameter, and by about 80 coarse spiral lines. The rather widely umbilicate holotype of the species displays fragments of the suture line, with an adventive lobe lacking angular sinuosity of its flanks and a median saddle with approximately half of the height of the ventrolateral saddle, hence an attribution to the genus *Lusitanoceras* is much more likely than to *Dombarites*.

A number of forms with strong longitudinal ornament have been described by Wagner-Gentis (1963, 1980), who referred them to *Goniatites granosus* Portlock, 1843, *Dombarites acicularis* (Pareyn, 1961), *Dombarites acicularis* (Pareyn, 1961) early form, *Dombarites granofalcatus* (Kullmann, 1961), *Dombarites canitna* Wagner-Gentis, 1980, *Revilloceras barruelense* (Wagner-Gentis, 1963), and *Revilloceras globosum* Wagner-Gentis, 1980.

They have been collected in the section near Revilla, mostly in stratigraphical order. *Dombarites acicularis* (Pareyn, 1961) early form and *Dombarites canitna* Wagner-Gentis, 1980 are here included in *Lusitanoceras granofalcatum* (Kullmann, 1961).

(7) North Africa. Pareyn (1961) described rather small specimens which he classified as *Goniatites–Mesoglyphioceras–granosus* Portlock, *Goniatites–Mesoglyphioceras–granosus* var. *dilatalta*, and *Goniatites–Mesoglyphioceras–granosus* var. *aciculare*.

Of these, the two variants introduced by him are based on specimens smaller that 14 mm diameter, hence very difficult to compare with the material from other regions. The sutural drawings suggest that var. *aciculare* has to be placed in *Dombarites*, var. *dilatalta* in *Platygoniatites*, and only the first in *Lusitanoceras*. Unfortunately, the conch and ornament characteristics of these specimens do not allow a real comparison with species known from other regions. Besides this, Pareyn (1961) figured

rather well preserved adult specimens of his *Goniatites striatus kentuckiensis* Miller, which have since been regarded by Ruzhencev & Bogoslovskaya (1970, 1971) as *Dombarites falcatoides* Ruzhencev & Bogoslovskaya, 1970.

(8) South Urals. *Lusitanoceras orientalis* (Librovitch, 1940) was described from the Sakmara River (Bogoslovskaya 1966). These well preserved specimens can be compared with specimens from Central Europe, showing that the external lobe in the material from the Urals is narrower.

(9) Kazakhstan. Librovitch (1940) reported the two new species *Lusitanoceras orientalis* and *Lusitanoceras irtyshensis* from the vicinity of the Lake Taran-Kul in the Priirtysh region. Both species are, in their morphologies, very close to *L. poststriatum*, but differ in their narrower umbilicus and more strong curved growth lines.

(10) Novaya Zemlya. *Goniatites polaris* Kusina, 1987 is, according to its suture line, a *Lusitanoceras* species that differs in the absence of triangular inner whorls from most of the other species of the genus.

(11) China. Specimens of *Lusitanoceras* have been described from several regions of China, but most of the material is too poorly preserved for exact determination. They derive from Xinjiang (Liang & Wang 1991) and Xizang (Sheng 1983).

(12) American Midcontinent. *Lusitanoceras granosum* (Portlock, 1843) has been reported from the Batesville Sandstone and Ruddel Shale of several localities in Arkansas (Gordon 1965). Revision of this material is required to confirm the identifications given by Gordon (1965).

The *Dombarites* → *Poshumardites* lineage. — In contrast to the global distribution of *Lusitanoceras*, the subsequent genera of this lineage are restricted in their occurrence, and not a single record from the Subvariscan Realm exists. *Dombarites* is rather widely distributed, and is known from many different regions, e.g. North America (Gordon 1965; Drahovzal & Quinn 1972), the Cantabrian Mountains (Wagner-Gentis 1963), North Africa (Pareyn 1961), Novaya Zemlya (Librovitch *et al.* 1993); the South Urals (Ruzhencev & Bogoslovskaya 1970, 1971), Central Asia (Nikolaeva 1994, 1995), and China (Ruan 1981; Sheng 1983; Gao 1983; Yang 1986; Liang & Wang 1991). In some of the regions *Dombarites* occurs in tremendous numbers of individuals, forming the major component of the faunas.

The distribution of *Proshumardites* is very similar to that of *Dombarites* (see references for *Dombarites*), but the species does not occur in the Namurian of North America. Advanced species are known from the Bloydian and Atokan of Texas, Arkansas, and Oklahoma (Plummer & Scott 1937; Gordon 1965).

The *Platygoniatites* → *Delepinoceras* lineage. — *Platygoniatites* and *Delepinoceras* are, in contrast to *Dombarites* and *Proshumardites*, far more restricted in their distribution (see references for that genus). *Platygoniatites* is known from the Cantabrian Mountains, North Africa (most probably), the South Urals, Central Asia, China (Xinjiang, Guangxi, and Ningxia) and Nevada, but absent in the American Midcontinent. *Delepinoceras* is known from the regions listed for *Platygoniatites*, but also occurs in Arkansas and Oklahoma. There is no evidence of these genera from the Subvariscan.

Sea-level changes and goniatite biogeography

The distribution pattern of the species of the Goniatitaceae is remarkable for of several reasons:

(1) The continuous succession of species of the late Viséan A and late Viséan B in the Subvariscan Realm is in contrast to the discontinuous distribution of the superfamily in other regions.

(2) Twice in the late Viséan, the superfamily is globally distributed (at the end of the late Viséan A and at the base of the late Viséan C). At the end of the late Viséan A,

the genus *Goniatites* is, in the various regions, represented by well distinguishable species, and at the base of the late Viséan C, *Lusitanoceras* has a world-wide distribution with morphologically extremely similar species.

(3) The superfamily becomes, towards the end of the Viséan, suddenly extinct in the Subvariscan, but continues up to the late Namurian in other regions, especially in the South Urals and Central Asia.

The constant presence of the superfamily in the Subvariscan Kulm series may reflect a stability of the environment over a long duration. The sudden decline of the Goniatitaceae in the latest Viséan sediments of the Subvariscan is a mystery. No environmental change which can be regarded as responsible for this extinction can be seen in the sediments. Similarly, no plausible explanation for the absence of the superfamily in other regions can be proposed.

It seems significant that there were two main transgressive epochs in the late Viséan. The first one resulted in the widely distributed *Crenistria* Limestone (Herbig 1994), and the second one led to deposition of the *Actinopteria* Shales. Both immediately precede the intervals from which goniatitids are known in world-wide distribution. These transgressions probably led to mixing of formerly allopatric populations, resulting in co-occurrences of morphologically very similar species with an equal state of sutural development, distinguishable only because of slightly different ornaments.

Conclusions

Results of cladistic and stratophenetic analyses of a group of Palaeozoic ammonoids are closely similar.

The superfamily Goniatitaceae is represented by a few independent evolutionary lineages. According to the distribution of conch shape, ornament, and sutural characters, it can be stated that:

(1) The superfamily is a monophyletic taxon, characterized by one synapomorphy, the ontogenetic change of the external lobe in the suture line from a Y-shaped to a V-shaped outline.

(2) Of the three traditional families within the superfamily, the Goniatitidae is a paraphylum, but the Agathiceratidae and Delepinoceratidae are monophyla.

(3) From the results of a biometrical analysis of sutural elements, trends in the sutural evolution of the superfamily can be observed, allowing a comparison with the modification of other characters such as conch parameters. Such a comparison allows a discrimination of derived homologies from homoplasies.

(4) According to the relatively low number of informative characters, several unresolved trichotomies are expressed in the cladogram.

During the late Viséan and early Namurian, two faunal provinces are easily distinguishable on the basis of the distribution of the Goniatitaceae.

(1) The first province spans from the Lublin Coal Basin in the southeast over the Rhenish Massif towards Ireland in the northwest, and also includes South Portugal. Typical elements of the late Viséan faunas are a succession of genera and species of the Goniatitidae. In this province, *Lusitanoceras* is the youngest genus of the Goniatitaceae at the base of the late Viséan C.

(2) The second province includes the South Urals as well as the Cantabrian Mountains of Europe, but also the occurrences in North America, Noth Africa, Central Asia and China can be regarded as belonging to this province. From these regions, *Paraglyphioceras*, *Arnsbergites*, and *Hibernicoceras* have not been reported. Of the Goniatitaceae, *Hypergoniatites*, *Neogoniatites*, and *Dombarites* occur in beds which are younger than the *Lusitanoceras* level, and clearly dominate the fauna.

In the late Viséan and Namurian, there are only very few species of the Goniatitaceae, which occur in both provinces.

The degree of difference between two faunal provinces is variable during the late Viséan. In two short epochs, almost cosmopolitan faunas occur after major transgressive periods:

(1) Towards the end of the late Viséan A with a global distribution of the genus *Goniatites* with clearly distinguishable species, and

(2) at the base of the late Viséan C with globally distributed, morphologically very similar species of *Lusitanoceras*.

The two phases of faunal homogenization of the two provinces is explained by global transgressions, which led to mixing of formerly allopatric faunas.

Acknowledgements

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Ewolucja goniatytów Goniatitaceae oraz biogeografia wizenu i namuru

DIETER KORN

Streszczenie

Przy zastosowaniu metod analizy kladystycznej i stratofenetycznej rozpoznano linie ewolucyjne w obrębie karbońskiej nadrodziny goniatytów Goniatitaceae. Obie metody dały podobne rezultaty. W późnym wizenie i w namurze A prowincje goniatytowe mogą być zdefiniowane na podstawie rozmieszczenia poszczególnych linii Goniatitaceae. Pierwsza prowincja odpowiada obszarowi subwaryscyjskiemu, gdzie goniatyty tej nadrodziny wymarły w pobliżu granicy wizen–namur. Druga prowincja obejmuje resztę obszarów występowania nadrodziny, a więc np. południowy Ural, środkową Azję i Amerykę Północną, gdzie Goniatitaceae przetrwały do Namuru A. Goniatitaceae miały światowe rozprzestrzenienie podczas dwóch krótkich epok wielkich transgresji w wizenie, które ułatwiały migracje. Pierwsza z tych epok odpowiada późnemu wizenowi A, kiedy rodzaj *Goniatites* (Zony *G. fimbriatus* i *G. spirifer*) miał światowe rozprzestrzenienie. Druga epoka przypadła na początek późnego wizenu C, kiedy to światowe rozprzestrzenienie miał rodzaj *Lustinoceras* (Zona *L. poststriatum*).