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Devonian ancestors of *Nautilus*

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With 9 figures

Kurzfassung: Ein Nautilide aus dem oberen Famenne, welcher teilweise die morphologische und phylogenetische Lücke zwischen dem Givet und dem Tournai füllt, wird unter dem Namen *Dasbergoceras* n. gen. beschrieben. Sein locker aufgerolltes, schmales Jugendgehäuse zeigt enge Beziehungen zu der stratigraphisch älteren Familie Lechritrochoceratidae. Die Ornamentierung mit kräftigen Rippen und feinen Spiralstreifen ist offenbar ein ursprüngliches Merkmal dieser Formen. Ein engeres Umfassen der Windungen der Frühstadien wird als ein post-permisches Merkmal angesehen. Die Konstruktion der Septen, welche den rezenten *Nautilus* von allen Nautiliden des Tertiärs unterscheidet, könnte von den kretazischen Vorfahren der *Cimomia-Aturia*-Linie hervorgebracht worden sein. Der Ursprung der Nautiliden liegt vermutlich in der Ordnung Orthoceratida des frühen Ordoviziums.

Abstract: A Famennian nautilid is described that partially fills the morphologic and stratigraphic gap between Givetian and Tournaisian records of the order. A new generic name *Dasbergoceras* gen. nov. is proposed for it. Its loosely coiled, slender juvenile shell indicates close relationships to earlier Lechritrochoceratidae, rather than the Oncoceratida. The shell ornamentation, with oblique ribs and longitudinal striation, appears to be the primitive feature of the order. Tight coiling of the adult shell progressively developed during the Early Carboniferous while tightly coiled embryonic shells seem to be a post-Permian feature. The septal morphology, which is the most important feature distinguishing Recent *Nautilus* from all the Tertiary nautilids, may be inherited from Cretaceous ancestors of the *Cimomia-Aturia* lineage. The nautilids probably originated from the kionoceratid Orthoceratida in late Early Ordovician.

Introduction

Once the most celebrated example of a "living fossil" Recent *Nautilus* appeared to be devoid of any reliable fossil record even at the generic level (TEICHERT & MATSUMOTO 1987). The fossil evidence of the evolutionary lineage that leads to *Nautilus* abounds in gaps that make it extremely difficult to trace. The most widely acknowledged gap is between the living species and their supposed ancestors in the Eocene (HEWITT 1988), but the most enigmatic is the evolutionary history of the lineage before the Tournaisian (FLOWER 1988), when undoubted Nautilida first appeared. Coiled nautiloids are extremely rare in the Late Devonian and the main purpose of the present paper is to describe and interpret new findings of such fossils from the Famennian of Germany.

Problems in tracing the evolution of the Nautilida result both from a poor fossil record and, more significantly, from difficulties with evaluating the detailed morphologies of their fossilized conchs. Also, like other molluscs, the conch does not provide much data on the

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internal, soft bodied anatomy, being solely a product of the shell mantle. Except for the external morphology of the shell (with its tendency to produce homeomorphs) one can only infer from its structure some features of the ontogeny of the animal (if the first whorl is preserved well enough) and adaptive values of the hydrostatic apparatus. The latter is believed to be expressed in concavity and thickness of the septa (HEWITT & WESTERMANN 1988) but also, perhaps even more, in their geometry (SEILACHER 1975, 1988; HEWITT & WESTERMANN 1986).

With such scarce data proper interpretation is of crucial importance. In this paper we attempt to fit into stratigraphically ordered chronomorphoclines the available evidence from fossil nautilid conchs that provides the most information on the anatomy of their bearers. The morphology of embryonic shells, muscle attachment scars, and the shape of septa in successive proposed members of the *Nautilus* lineage will be thus discussed in following chapters.

The study has been based mostly on collections housed at the Institut für Geologie and Paläontologie, Universität Tübingen (abbreviated GPIT), the Senckenberg Museum, Frankfurt/Main (SMF) and at the Museum für Naturkunde, Humboldt-Universität Berlin (MB).

Evolution of septal topology

Any cephalopod septum can be described as a membrane suspended on the conch interior wall with its topology controlled by two factors: (1) a difference in fluid pressure between the soft animal body and the last phragmocone chamber and (2) the strength and position of the attachments area of the soft body to the inner conch surface. These two factors control distribution of convexities and concavities, as well as the course of the suture line (SEILACHER 1975, 1988). The resulting topology does not necessarily need to perform any specific function, but at least in some cases its adaptive significance is apparent. The crucial point in the evolution of septa seems to be the development of convex (as seen from the conch aperture) surfaces. From this moment at least, parts of the septum wall began to work as a vault instead of being extended under action of external pressure. They thus offered much greater resistance to ambient pressure (PFAFF 1911; JAKOBS 1990).

Unlike the ammonites, only a few lineages within the Nautiloidea developed this way of phragmocone strengthening (see DZIK 1984). Invariably this resulted in a directional evolution towards more and more complicated folding of the suture line; suggestive of a profound shift in selection pressure. It may thus be of importance that in Recent *Nautilus* the shape of septa is relatively complicated, with some rudimentary vaulted surfaces. Much phylogenetic value has been given to this feature by some authors (MATSUMOTO 1983; DZIK 1984) who consider it to be inherited by *Nautilus* from *Cimomia*-like ancestors. Unfortunately, both the developmental mechanisms controlling the pattern of septal folding and its functional meaning remain unclear. Although in all the members of the *Aturia* lineage the dorso-lateral parts of the septum are highly arched, the central to ventral part of the septum remains deeply concave and the lateral flutings result in development of vaulted areas only in marginal regions of the septum. In this respect the *Aturia* septum is unlike the superficially similar Jurassic lineage of *Pseudonautilus* as well as most of the ammonoids, but resembles rather some Devonian clymeniids (KORN 1992). Similar mechanisms were thus probably involved in formation of septa in both groups.

No Tertiary nautilid is known that would closely approach *Nautilus* in the shape of the suture line (its course cannot be precisely traced from the published illustrations of the allegedly related *Nautilus praepompilius* SHIMANSKY 1957). Eocene *Enciphoceras regale* (SOWERBY), the type species of the genus, seems to preserve primitive features of the

cenoceratids (SCHULTZ 1976; HEWITT 1988) and is no more similar to *Nautilus* than its Early Cretaceous possible congener *E. insigne* (SHIMANSKY) (see SHIMANSKY 1975). There are some Cretaceous nautilids, usually classified in *Cimomia*, that show more undulated septa, for instance Cenomanian "*C.*" *schroederi* (WIEDMANN), compared with *Nautilus* by MATSUMOTO (1983). They seem to be rooted in the Jurassic *Cenoceras*; *E. expletus* (ZWIERZYCKI) from the Hauterivian of Tendaguru, Tanzania may represent a transitional form (WIEDMANN 1960).

Because the record of possible ancestors of modern *Nautilus* is poor, much reliance on inferred lineages has to be drawn from ontogenetic studies of the conch.

Size of embryonic shell in the nautilids

The most primitive Nautiloidea, like the ammonites, had a very small, subspherical embryonic shell followed in early ontogeny by a tubular, phragmocone-bearing larval shell with two septa (DZIK 1981). In several independent lineages this style of early ontogeny was replaced by simple development, supposedly within the egg, of a cylindrical embryonic shell bearing a cicatrix at its tip. Generally an increase in egg size followed this (DZIK 1984), but in Paleozoic Nautilida the embryonic shell remained relatively small and only gently curved, with prominent longitudinal ornamentation.

In the Silurian genus *Cyrtocycloceras*, relatives of possible orthoceratid ancestors of the nautilids, a cylindrical, cyrtococonic embryonic shell was distinctly morphologically separated from following developmental stages (DZIK 1981: fig. 1C).

The umbilical perforation in some Permian nautilids was quite narrow, but the embryonic shell remained cyrtococonic in shape. Even in the Ladinian genus *Syringonautilus*, with its umbilical perforation only 1mm in diameter, the aperture of the embryonic shell (marked by a constriction) was located just before the end of the first whorl (SOBOLEV 1989). Not before the Carnian had the embryonic shell become coiled tightly enough to comprise the whole first whorl in *Cenoceras boreale* DAGYS & SOBOLEV 1989. This was the completion of a long evolutionary process that started already within the kionoceratid orthoceratids.

A relatively large embryonic shell seems to be a primitive (plesiomorphic) feature of post-Paleozoic nautilids. A tightly coiled embryonic shell, morphologically similar to that of Recent *Nautilus*, developed in the nautilids presumably during the Triassic. In the Early Triassic genus *Syringonautilus* (see SCHASTLIVTCEVA 1988) the diameter of the embryonic shell is estimated as being about 15 mm, but in its supposed Early Permian relative *Neothrinoceras* the embryonic shell was much larger, perhaps exceeding 20 mm in diameter (RUZHENTSEV & SHIMANSKY 1954). Similar sizes characterize Jurassic cenoceratids and their direct Cretaceous successor *Euciphoceras insigne* (SHIMANSKY) from the Aptian-Albian of Mangyshlak. It had an embryonic shell of about 25 mm in diameter (SHIMANSKY 1975). The Cretaceous genus *Eutrephoceras* has a much smaller embryonic shell of only about 10 mm diameter (LANDMAN 1988) and this is also typical of the Tertiary genera *Cimomia* (HEWITT 1989) and *Aturia* (MILLER 1947). *Cimomia*, *Deltoidonautilus* (see HEWITT 1989) and *Aturia* share dorsal position of the siphuncle in the embryonic shell. It may mean that all these three genera are closely related and that the siphuncle migrated proterogenetically in the *Aturia* lineage. Species of Recent *Nautilus* have an embryonic shell 25 to 30 mm in diameter (LANDMAN 1988).

There are some Tertiary nautilids that have an embryonic shell size and morphology comparable with Recent *Nautilus*. MILLER (1947: pl. 76, fig. 4) illustrated a medial section of a juvenile nautilid from the Eocene Kinsaid Formation of Texas identified by him as belonging to *Cimomia vaughani* (GARNER). It shows an embryonic shell of about 20 mm in

diameter and differs from that of *Nautilus*, as well as from other Tertiary nautilids, in larger umbilical perforation. MILLER's specimen cannot be attributed to the genus *Cimomia*, as long as Eocene *Cimomia imperialis* (J. SOWERBY), closely related if not conspecific with the type species of the genus, has basically different embryonic shell morphology (HEWITT 1988, 1989). If specific identification of this specimen is correct, "*C.*" *vaughani* may thus appear close to the ancestry of *Nautilus*, in having similar septal morphology. The morphology of the embryonic shell in Tertiary *Euciphoceras*, another candidate for the ancestry of *Nautilus* (TEICHERT & MATSUMOTO 1987; HEWITT 1988, 1989) remains unknown.

Transformations of muscle attachments

Data on the morphology of the muscle attachments in fossil nautilids are very limited. The only Tertiary record that we have been able to trace is the illustration of *Cimomia landanensis* (VINCENT) from the Paleocene of Angola (MILLER 1951: pl. 5, fig. 1) which shows a morphology of the muscle attachment area closely similar to that of Recent *Nautilus* (Fig. 1). In the Late Cretaceous species *Eutrephoceras bellerophon* (LUNDGREN) the attachment area is much more dorso-laterally shifted (MUTVEI 1957: text-fig. 18D) which may be due to extremely globose shell form in the species. A possible Jurassic example of muscle scar morphology has been presented by DZIK (1984: fig. 80b) for the Oxfordian genus *Pseudaganides aganiticus* (SCHLOTHEIM). Unlike later forms, the attachment is more uniformly extended over the flanks of the shell, while at the venter it seems to be missing or at least is very narrow. This is a little reminiscent of the oldest undoubted representative of the Nautilida with known muscle attachment morphology, *Apheleceras hibernicum* (FOORD & CRICK) from the Viséan (MUTVEI 1957: pl. 16, figs. 1–3).

Among possible Early Palaeozoic members of the Nautilida only the lechritrochoceratids show the morphology of the muscle attachment scars (TUREK 1975, 1976), comparable closely with that of *Apheleceras*. If derivation of the Nautilida from uranoceratids, as proposed by DZIK (1984) is correct, a lateral shift in distribution of the main areas of the attachment scar took place between *Uranoceras* (?) *longitudinale* (ANGELIN) (MUTVEI 1957: text-fig. 11B) and the lechritrochoceratids here represented by *Kosovoceras modestum* (BARRANDE) (Fig. 1). The orthoceratids, that have been proposed to represent roots of the whole branch, possessed quite simple muscle attachments.

Ornamentation of the shell

Longitudinal (spiral) striation of the shell surface of at least early stages seems to be a primitive feature of all nautilid successors of *Cenoceras* (MATSUMOTO 1983). The lineage of *Cenoceras* has been traced back to the Carnian (KUMMEL 1956) and is probably rooted in Anisian species of *Syringonautilus*. At least some of its species show longitudinal striation and differ from *Cenoceras* and its derivatives in a more evolute shell and somewhat larger umbilical perforation. This concerns also the oldest species from the Scythian (SCHASTLIVTCEVA 1988). It is not easy to find similar nautilids in the Permian and the only form with a flat evolute shell ornamented with longitudinal striae is a species of *Neothrinoceras* from the Artinskian of the Urals (RUZHENTSEV & SHIMANSKY 1954). Known only from a juvenile specimen it shows even wider umbilical perforation than *Syringonautilus*.

In spite of the relative abundance of the Nautilida in the Late Palaeozoic the fossil evidence of the evolution of the lineage leading to the Mesozoic nautilids is extremely incomplete. Perhaps the Viséan form *Epidomatoceras maccoyi* TURNER belongs here as

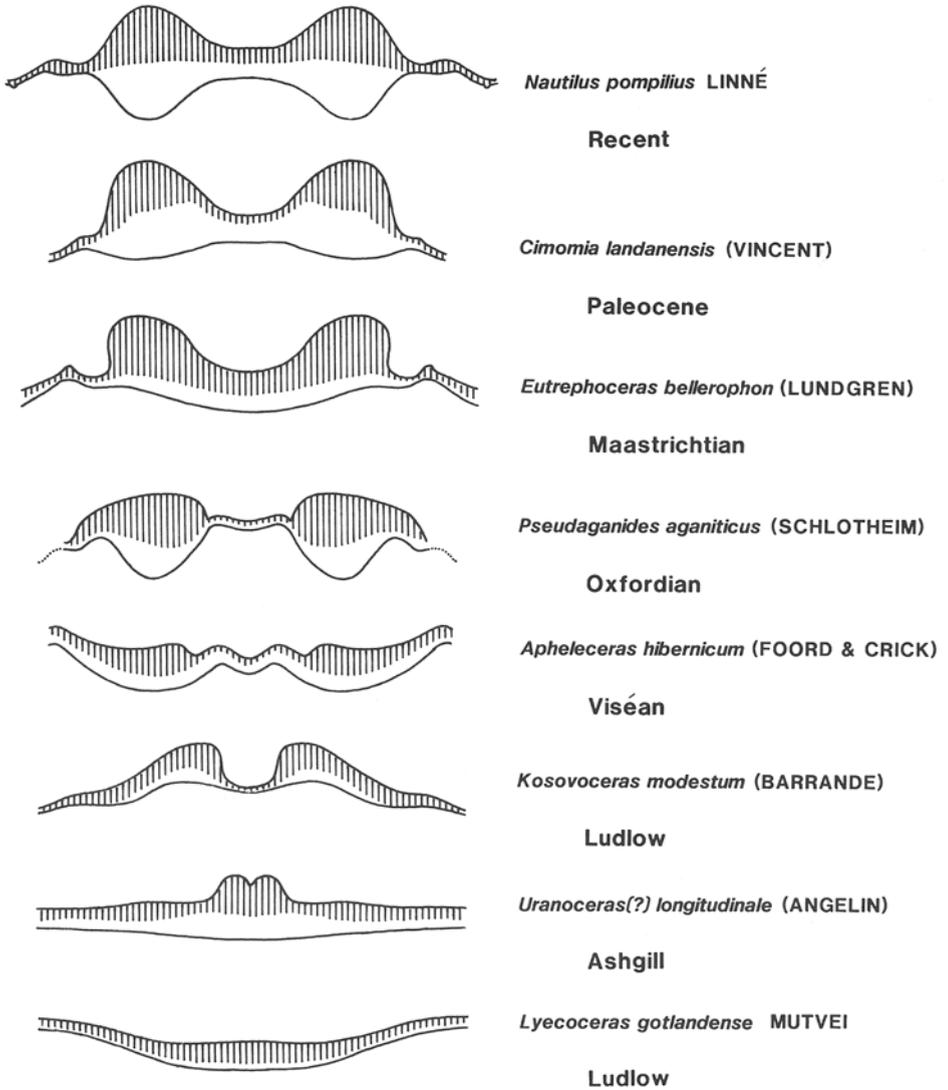


Fig. 1. Muscle attachments in the Nautilida and possible related nautiloids. Based on data from MILLER (1951), MUTVEI (1957), TUREK (1975), and DZIK (1984).

suggested by its evolute shell and its striated early stages with the umbilical perforation slightly larger than in *Neothrinoceras*. An adult specimen of this species was collected in the Viséan shales at Lugasnaghta, Ireland. It is about 80 mm in diameter (Fig. 2), so these nautilids were of relatively small size. Because data is scarce on Tournaisian nautilids the lineage cannot be precisely traced back in time. Even more difficulty arises in tracing the phylogeny across the Devonian-Carboniferous boundary. To do it one needs first to identify, which of Carboniferous nautilids is the most primitive.

Tornaisian nautilids

Coiled nautiloid shells are unknown from the *Gattendorfia* Stufe of the earliest Carboniferous. The earliest evidence of the presence of the Nautilida in the Carboniferous has been found in the Chouteau Limestone of Missouri (MILLER & FURNISH 1939). Somewhat younger is the classic fauna from the "calcschistes de Tournai". They seem to have come from the lithic unit of the Calcaire de Vault, because both goniatites and nautiloids in old museum collections, collected from this horizon, are preserved with shells. In the overlying Calcaire de Calonne only internal moulds occur (see DELÉPINE 1940). The Tornaisian nautilid faunas of Belgium represent the Upper Tornaisian. The Calcaire de Vault in its type area does not contain stratigraphically diagnostic conodonts, but those suggest an age older than the *Scaliognathus anchoralis* Zone (GROESSENS 1974).

Among these Late Tornaisian nautilids from Belgium *Vestinautilus pinguis* (DE KONINCK) is closest morphologically to the type specimens of *E. maccoyi* in the angular cross-section of the early whorls. Probably slightly younger (see WEYER 1972) is *V. altidorsalis* (WINCHELL) from the Coldwater Shale of Michigan. It had its early whorls finely striated and reversely trapezoidal in cross-section. This species, in turn, resembles the Middle Tornaisian species *Triboloceras digonum* (MEEK & WORTHEN) from the Chouteau Limestone of Missouri (MILLER & FURNISH 1939; MILLER et al. 1949). "*Chouteauoceras*" *americanum* (MILLER & FURNISH), from the same beds, is morphologically the simplest Carboniferous nautilid. If this is an expression of its phylogenetic position, this species would unavoidably be close also to the ancestry of *Epidomatoceras*. The above expressed

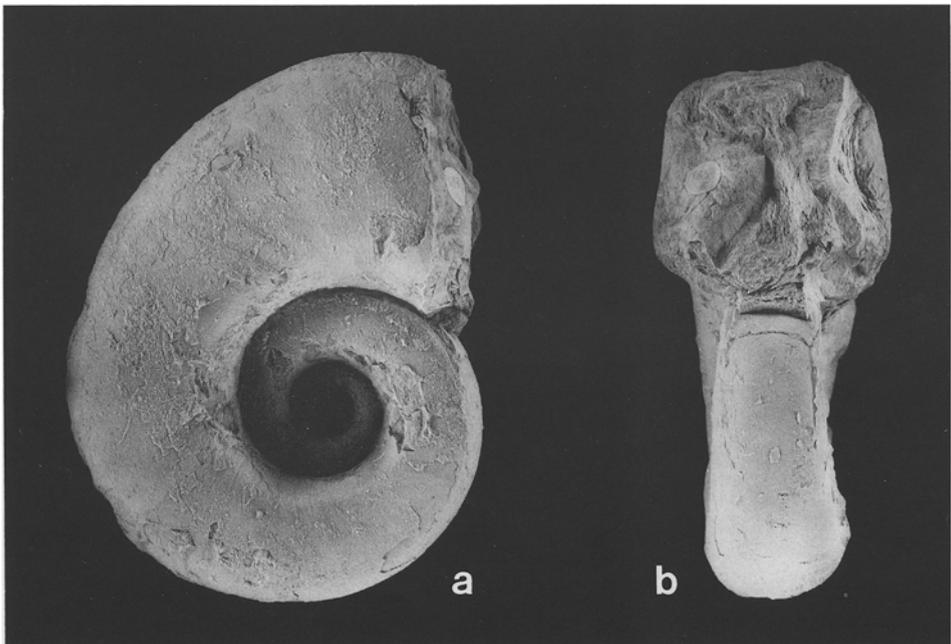


Fig. 2. *Epidomatoceras maccoyi* TURNER 1954; specimen SMF 51292 (coll. KORN 1986) from the Viséan shales of Luganaghta, Co. Leitrim, Ireland, a morphotype with extremely rounded whorls, $\times 1$.

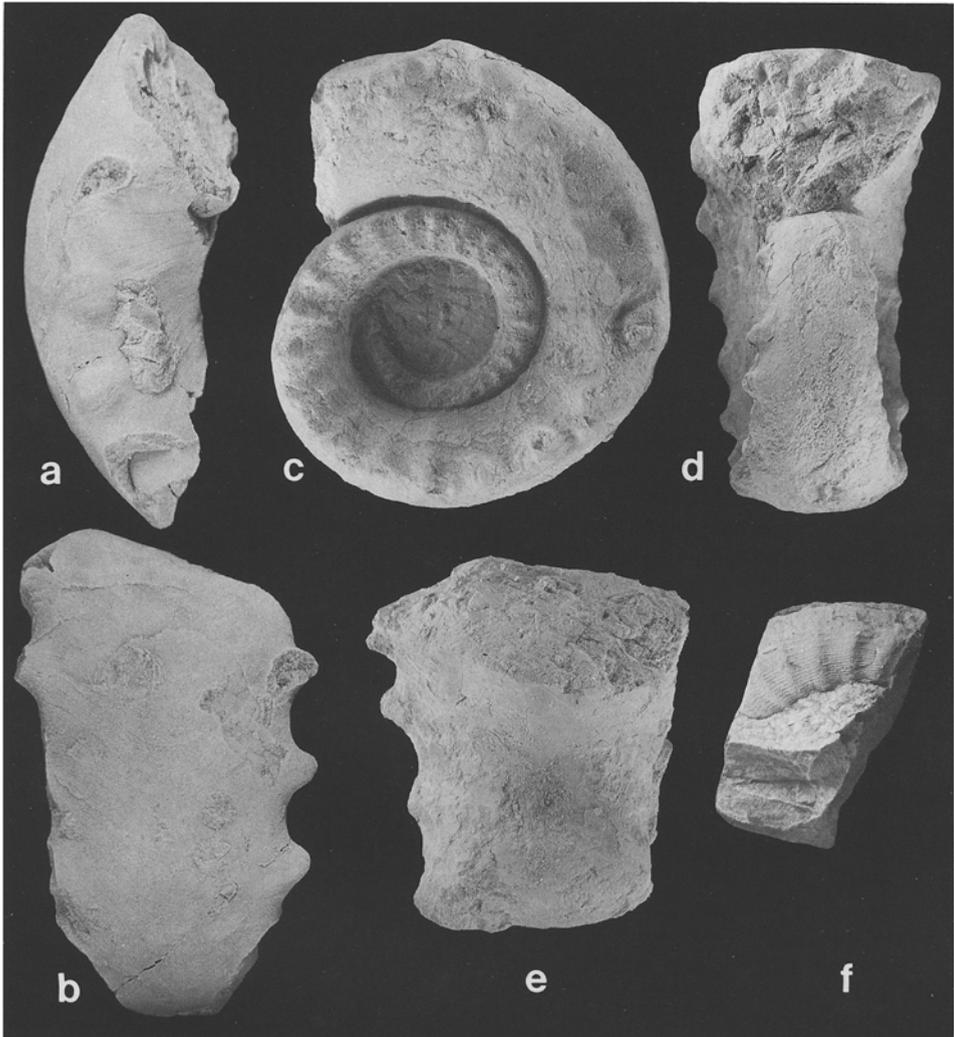


Fig. 3. Nautilids from the late Famennian (*Wocklumeria* Stufe) of the Rhenish Massif. a–c: *Dasbergoceras alternans* (TIETZE 1871). a–b: Fragment of juvenile whorl (SMF 51289, coll. KORN 1977) from the topmost bed of the Wocklum Limestone (Upper *paradoxa* Zone) at Ober-Rödinghausen (road cutting); lateral and ventral views, $\times 2$. c–d: Juvenile conch (SMF 51292, coll. KORN 1989) from the Lower *paradoxa* Zone at Dasberg (road cutting), lateral and apertural views, $\times 1$. e: Part of body chamber (SMF 51290, coll. KORN 1988) from the Lower *paradoxa* Zone of a trench on Dasberg, dorsal view, $\times 1$. f: Possible nautilid shell fragment from beds with *Phacops granulatus* of mine Prinz Wilhelm near Velbert. Specimen MB c: 880 identified by KAYSER (1881: pl. 6, fig. 4a–c) as *Cyrthoceratites cancellatus* ROEMER 1844, $\times 1$.

scenario is not without weak points, however. Assemblages of nautilids from the Marshall Sandstone or the cephalopod limestones of Germany, roughly coeval to the Belgian ones, comprise species ornamented with feeble longitudinal striae, instead of being ornately

ribbed. In this respect they resemble rather older North American faunas. It is thus possible that the available record of the Early Carboniferous evolution of the Nautilida is not only incomplete, but also strongly biased ecologically.

A new Famennian nautilid

Published reports on coiled nautiloids from the Famennian are rather questionable. The only specimen of allegedly centroceratid affinities (*Carilloceras*) is too fragmentary to be reliably classified as a nautilid. KAYSER (1882: p. 57, pl. 1, fig. 7) described a crushed whorl fragment of a coiled mollusc shell with longitudinal striation and transverse ribbing preserved in shale from beds with *Phacops granulatus* of the Rhenish Massif. It resembles some nautilid cephalopods, but no remnants of the phragmocone structures are preserved in the original specimen (Fig. 3f). The most important is TIETZE's (1870) description of a whorl fragment of a coiled cephalopod shell with ventral siphuncle, lateral tubercles, and longitudinal striation from the limestones of Dzikowiec in the Sudetes, most probably from the Lower *paradoxa* Zone of the *Wocklumeria* Stufe. The specimen, named *Cyrtoceras alternans* TIETZE, is missing in the collections of the Wrocław University and was probably destroyed in World War II. From the rather schematic drawing and brief description it is difficult to determine its relationship. The presence of a prominent ornamentation at such an early stage of the ontogeny suggests its lechritrochoceratid nature.

It is therefore of much importance to study similar fossils in approximately coeval strata of the Rhenish Massif. Three specimens are available which most probably represent a single species. The best preserved shell fragment (SMF 51289) from the topmost bed of the Wocklum Limestone (Upper *paradoxa* Zone) of the locality Ober-Rödinghausen (road cutting) shows juvenile ornamentation where the whorls possess a rounded trapezoidal cross-section. There are only growth lines at the shell surface that show a deep sinus at its flat venter (Fig. 3b). Tubercles at the ventrolateral margins have rounded tips and extend a little ventrad as shallow ribs, quite different to those in Middle Devonian rutoceratids (Fig. 3). A somewhat later stage in ontogeny is shown by specimen SMF 51290 from bed 2 (Lower *paradoxa* Zone) in a trench at Dasberg. Its dorsal side shows ornamentation that is devoid of any longitudinal components and a very indistinct depression corresponding to the contact with the preceding first whorl (Fig. 3e). In longitudinal section, at a whorl height of 6 mm, remnants of the siphuncle have been found that appears to be located subcentrally. The ventral margin of the siphuncle is almost half way between the whorl centre and venter. The diameter of the siphuncle is 1 mm. Another, more complete specimen (SMF 51291) from the same horizon of a nearby locality at Dasberg, has an almost completely preserved first whorl, showing a very wide umbilical perforation, 27 mm in diameter and a slender apical part of the shell (Fig. 3c–d). The shell apex is not preserved, but apparently was somewhat less than 2.5 mm in diameter. The shell wall is not preserved in the initial parts of the conch, but it is clear that instead of tubercles transverse ribs are developed there. Somewhat questionable longitudinal marks may possibly correspond to ornamentation at the shell surface.

The shell of the Famennian species is superficially similar to Carboniferous *Temnocheilus*-like nautilids. However, the well known embryonic shell of *Temnocheilus* (see SHIMANSKY 1967: pl. 9, fig. 8), like most of the coeval nautilids, is rather robust in appearance with the umbilical perforation only 8 mm in diameter. It seems therefore that *Temnocheilus* developed from *Vestinautilus*-like nautilids and the tuberculation is a secondary character without any special phylogenetic significance.

The Famennian species definitely deserves separation from other known nautilids at least at the generic level. The available data does not allow us to be confident that the Sudetes specimen of *Cyrtoceras alternans* TIETZE is conspecific with the Rhenish ones. Nevertheless, as the evidence to the contrary seems to be at least very weak (the more ventral position of the siphuncle in TIETZ's drawing may be a result of the preservation) we hesitate to introduce a new species name for the Rhenish population, until the possibility of additional collections of toptype materials from Dzikowiec has been explored.

Taxonomic conclusion

Dasbergoceras gen. nov.

Type species: *Cyrtoceras alternans* TIETZE 1871.

Diagnosis: *Temnocheilus*-like, tuberculate conch with very wide umbilical opening and ventral position of the siphuncle.

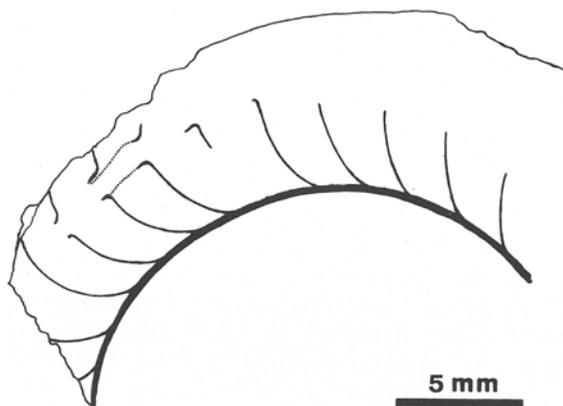


Fig. 4. *Dasbergoceras alternans* (TIETZE 1870), specimen SMF 51290 from Dasberg; longitudinal section of a part of the first whorl showing position of the siphuncle.

Possible Middle Devonian nautilids

Five groups of Middle Devonian coiled nautiloids can be seriously considered as possible ancestors of the post-Devonian Nautilida. They are at least partially interrelated. Ventral position of a relatively narrow siphuncle and fringed shell with a tendency to develop parabolic nodes characterize the genera *Ptenoceras* and *Hercoceras*. Both fringes and longitudinal ribs associated with a wide ventral siphuncle are typical of several genera clustered around *Halloceras*. A narrow ventral siphuncle, a trapezoidal shell cross-section, with dorsolateral spiral ribs and ventro-lateral tubercles, are typical of *Centroceras* and related forms. This Middle Devonian branch of coiled nautiloids with a subcentral siphuncle differs from the preceding ones in the delicate longitudinal striation of a weakly tuberculated shell and a much smaller diameter of its apex.

1. *Ptenoceras* group

Ptenoceras alatum BARRANDE from the Siegenian (Pragian) Koněprusy Limestone of Bohemia is a controversial species in respect to its phylogenetic position. It was believed to

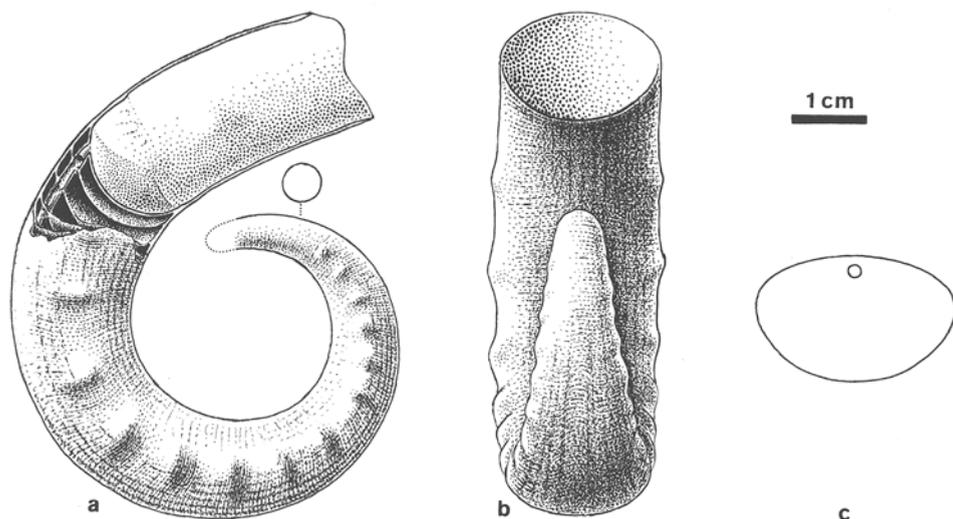


Fig. 5. *Pleuronoceras nodosum* (BRONN 1837), reconstruction of the shell based on the specimen GPIT 1697/2 (and several unnumbered MB) from the Eifelian of Gerolstein, Eifel Mts.

be an oncoceratid on the basis of an allegedly radial organization of the siphuncular deposits. This has been questioned by DZIK (1984) and the species is interpreted as being closely related, possibly congeneric, to Eifelian *Doleroceras resimum* ZHURAVLEVA and *Pleuronoceras nodosum* (BRONN). *D. resimum* is known from four specimens from the central Urals, one of which shows the posterior part of the adult body chamber with excellently preserved muscle scars (ZHURAVLEVA 1972). Another adult living chamber from the same locality was named *D. insperatum* by ZHURAVLEVA (1974: p. 100, pl. 11, fig. 6). The muscle attachment in *D. resimum* is split into series of isolated scars but, unlike typical breviconic oncoceratids, they are arched ventrally being somewhat distant from the last septum. TUREK & MAREK (1986) identified the same pattern of the muscle attachments in *P. alatum*. An unnumbered specimen of *P. nodosum* housed at the Museum für Naturkunde, Berlin (collected by DOHM in 1913) shows a partially preserved scar of the same morphology (Fig. 5).

The presence of metameric muscle scars in the *Ptenoceras* group can be interpreted either as an evidence of oncoceratid affinities or as a result of secondary metamerization of a muscle attachment of the *Uranoceras*-type (DZIK 1984).

2. *Hercoceras* group

Hercoceras mirum BARRANDE from the Eifelian Třebotov Limestone of Bohemia is the best known species of the group. At the adult stage it shows a strongly constricted conch that is armed with long, laterally oriented hollow spines. Early growth stages (BARRANDE 1865: pl. 102, figs. 1–3) show that the embryonic shell was tightly coiled and ornamented only with growth lines. At the second whorl, parabolic nodes appear that subsequently change into tubercles and finally into spines. The early ontogeny of *Hercoceras* is thus similar to *Ptenoceras* except for the loose whorl coiling of the latter.

Juvenile shells, virtually undistinguishable from corresponding stages of *Hercoceras* were described from the Emsian of the northern Urals by ZHURAVLEVA (1974: p. 112, pl. 13, figs. 1–4) under the name *Adeloceras kakvense* and classified in the family Rutoceratidae of the order Nautilida. Closely similar juveniles, different in having slightly earlier ontogenetic development of true spines (ZHURAVLEVA 1974: p. 101, pl. 12, fig. 1) were named *Spanioceras putum* and interpreted as members of the family Ptenoceratidae within the order Oncoceratida. Without reliable data about adults it is not possible to say whether these specimens represent species of *Hercoceras* or not, but the available data do not substantiate their separation to different orders of the nautiloids.

Another possible member of the group is the Eifelian form *Nassauoceras subtuberculatum* (SANDBERGER & SANDBERGER). The topotype material has to be restudied before its generic position is established.

The tightly coiled embryonic shell and ventral siphuncle make *Hercoceras* unlikely as a direct ancestor of the Famennian nautilids despite the superficial similarity of the post-embryonic conchs. It may be a successor of *Ptenoceras* and perhaps should be classified together with it.

3. *Halloceras* group

Early ontogenetic stages of *Halloceras* are preserved in the specimen GPIT 1697/1 (Fig. 6). Although the apex is not preserved, it is clear that at the earliest, presumably embryonic, stage the shell was ornamented only with growth lines. Later ontogenetic stages are ornamented with longitudinal ribs and undulated metameric fringes (see also COLLINS 1965: pl. 7, figs. 7, 8; pl. 10, figs. 5–12). They gradually change into parabolic nodes at the lateral sides of the shell and they may form true nodes in some specimens. The twenty or so well preserved specimens from the *Calceola* marls of Gerolstein, in the Eifel Mts., housed in Berlin and Tübingen, vary greatly in shell form, from loosely gyroconic to evolute, whorl expansion rate, and especially in ornamentation. The latter may be quite elaborate with ventral tubercles in addition to lateral ones. We are unable to decide how many species are represented and what is the range of population variability.

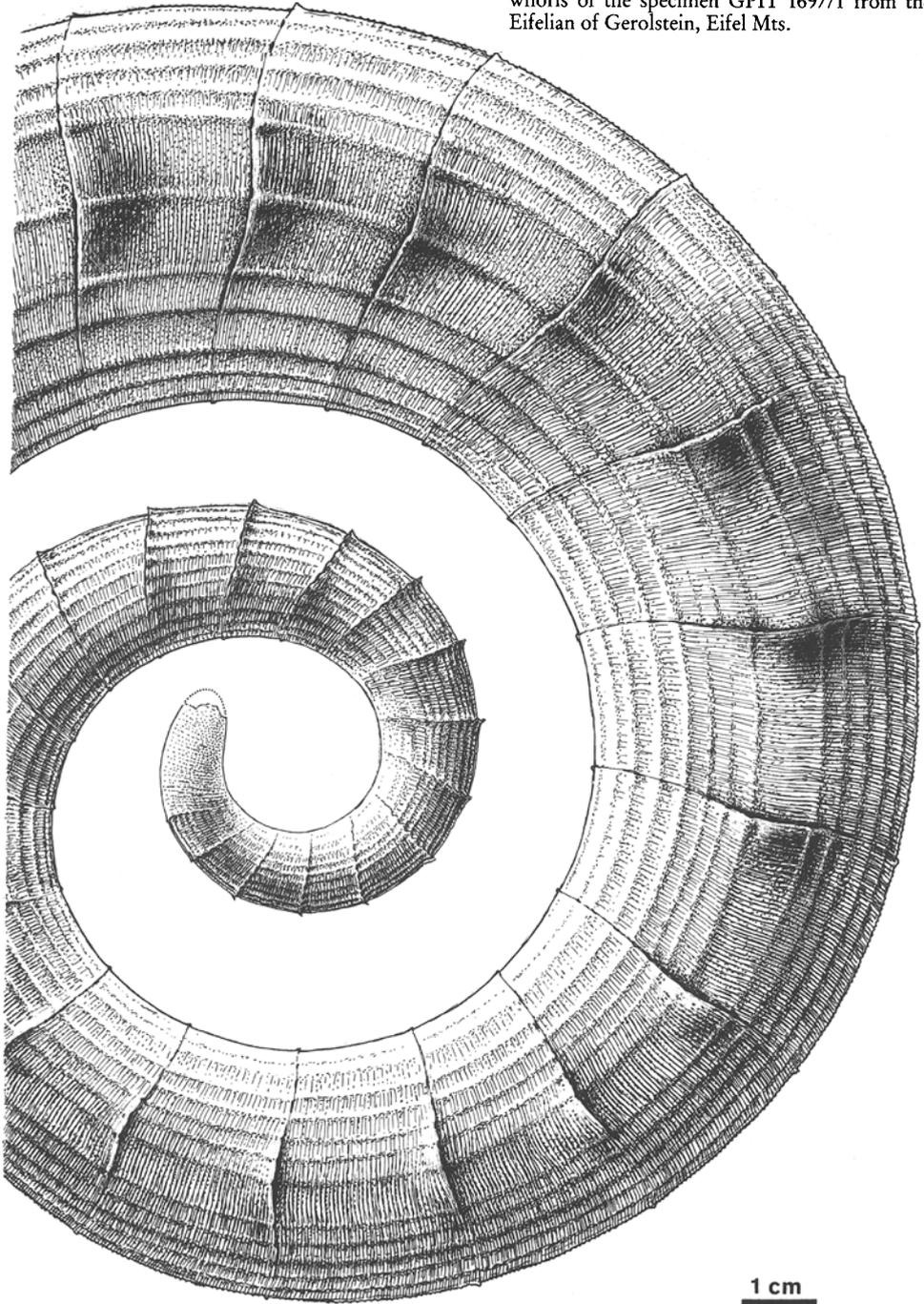
Juvenile conchs of ?*Halloceras eifeliense* KUZMIN from the Emsian of Novaya Zemlya (ZHURAVLEVA 1974: pl. 15, Figs. 3–4) somewhat resemble juveniles of German *Halloceras* species. Another name, *Anepheleceras torulosum* (KUZMIN) was applied to a closely similar juvenile shell form the same locality (ZHURAVLEVA 1974: pl. 15, figs. 1–2). That specimen, in having ventro-lateral transverse ribs split into tubercles, fits quite well corresponding stages of *Halloceras*. Specific distinction of the Novaya Zemlya specimens from the German ones is out of doubt as they differ in being quite tightly coiled. They may belong to a separate lineage that in the Eifelian of the same area is represented by *Bastindoceras aculeatum* (KUZMIN).

It seems possible that the *Halloceras* generic group, which deserves family rank, shares common ancestry with the *Ptenoceras* lineage in Silurian oncoceratids which possess undulated fringes at the surface of elongated, curved conchs. It seems thus reasonable to consider both families to be members of the order Oncoceratida.

4. *Centroceras* group

Early ontogenetic stages are known in the Givetian species *Centroceras tetragonum* (D'ARCHIAC & DE VERNEUIL) (DZIK 1984: pl. 42, fig. 3). The embryonic shell is rather loosely coiled and ornamented only with growth lines. No fringes or parabolic nodes occur at subsequent stages and ventro-lateral tubercles develop only as undulations at the ventro-

Fig. 6. *Halloceras* sp., reconstruction of inner whorls of the specimen GPIT 1697/1 from the Eifelian of Gerolstein, Eifel Mts.



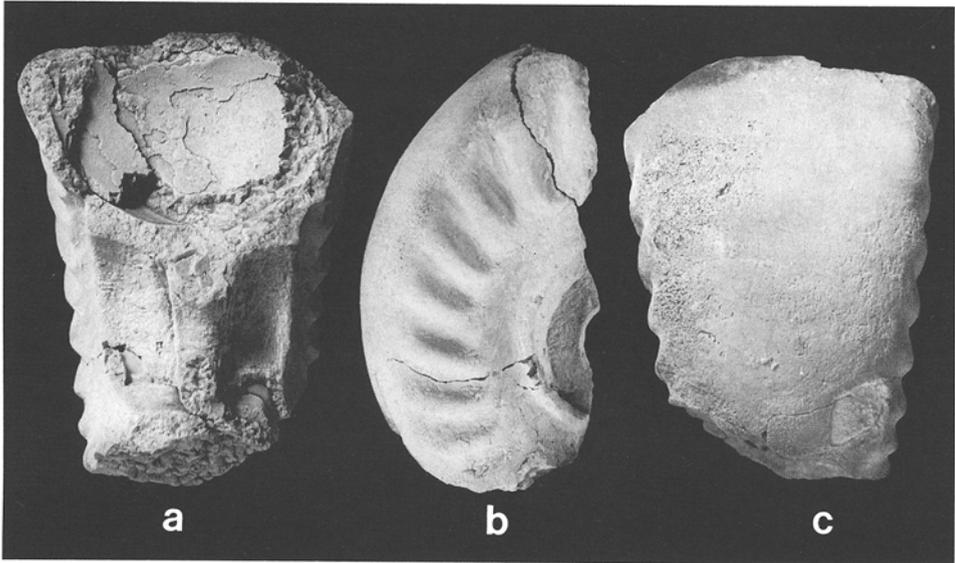


Fig. 7. Fragmentary specimen MB c. 871 representing an unnamed species of *Centroceras* from the Eifelian of the Eifel Mts. (collected by KAYSER in 1874), septal (a), lateral (b), and ventral views (c), $\times 1$.

lateral angulations of the whorl. More prominent but not tuberculated angulations, located dorso-laterally, give the whorl its tetragonal cross-section. This is a pattern of early ontogeny much different from those previously discussed by us despite the similar adult shell ornamentation and ventral position of the siphuncle.

These peculiarities in early ontogeny are even more apparent in another, yet unnamed, species of the genus from the Middle Devonian (presumably Eifelian) of the Eifel Mts. The conch has dorso-lateral angulations typical of the group, and is ornamented only with lateral oblique ribs, showing no resemblance to the other coiled Devonian nautiloids so far discussed. Its embryonic shell, although not completely preserved, was loosely coiled with apical parts presumably rather small in diameter (Fig. 7).

Centroceras seems to be unrelated to the *Ptenoceras-Hindeoceras* branch. Among older coiled nautiloids with ventral siphuncle, *Trochoceras davidsoni* BARRANDE from the Siegenian (Pragian) Koněprusy Limestone of Bohemia, seems to be a good candidate for its ancestry as already proposed by DŽIK (1984).

5. *Kosovoceras* group

Morphology of the Silurian Lechritrochoceratidae is well known owing to thorough descriptions by TUREK (1975, 1976). He proposed the genus *Kosovoceras* for the Late Silurian forms that show gradual development of ventro-lateral tubercles. Somewhat unfortunately *Trochoceras sandbergeri* BARRANDE was chosen as the type species. It does not have any tuberculation, being not much different from older species of *Lechritrochoceras*. Devonian representatives of the lineage invariably possess tuberculation and their generic distinction from typical Silurian *Lechritrochoceras* seems apparent.

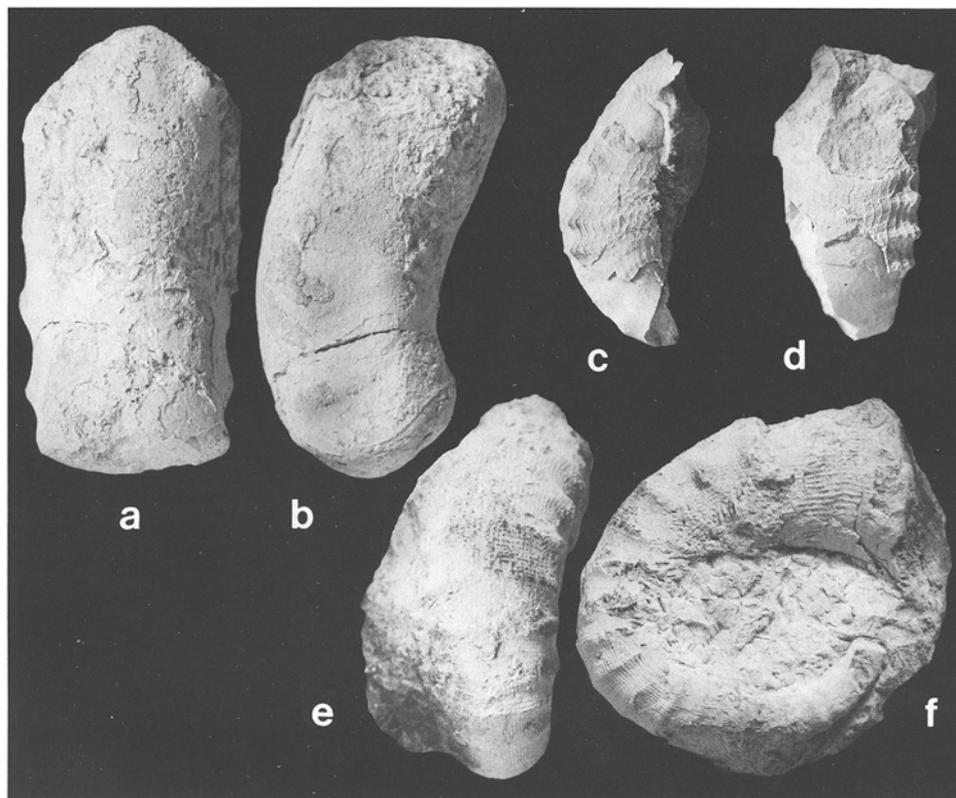


Fig. 8. Middle Devonian (probably late Givetian) lechritrochoceratids., a, b: *Kosovoceras* sp.; internal mould of adult body chamber with constricted aperture MB c 871 from the Middle Devonian of the Eifel Mts., lateral and dorsal views, note subcentrally located siphuncle, $\times 1$. c, d: *Kosovoceras* (?) *multistriatum* (ROEMER 1844); juvenile living chamber MB c. 881 from the Middle Devonian of Enkeberg, Rhenish Massif, lateral and ventral views, $\times 1$. e, f.: *Dasbergoceras* (?) *cancellatum* (ROEMER 1844), juvenile specimen MB c. 878 from the "Eisenstein" (Late Givetian) of the Grottenberg (Bredelar) near Brilon (ROEMER 1844: pl. 6, fig. 4a–c), ventral and lateral views, $\times 1$.

The genus seems to be represented in the Middle Devonian (probably late Givetian) of Enkeberg, Westfalia, by the specimen MB C. 881 (Fig. 8c–d). It may be conspecific with *Cyrtoceratites multistriatus* ROEMER from limestones of Hand near Paffrath, illustrated by ROEMER (1844) with a subcentral siphuncle. The only information about the adult stages of these Middle Devonian nautiloids is provided by a nucleus of an adult body chamber with subcentral siphuncle and dorsally constricted aperture from the Middle Devonian of the Eifel Mts. (Fig. 8a–b).

Cyrtoceratites cancellatus ROEMER from the late Givetian "Eisenstein" (Late Givetian) of Brilon has a loosely coiled first whorl and is ornamented with longitudinal striations and growth lines that form a very regular cancellate pattern (ROEMER 1844). Its oblique ventro-lateral ribs transform gradually into ventro-lateral tubercles (Fig. 8e–f). Somewhat later stages seem to be represented in fossils, possibly of the same species, from the Middle

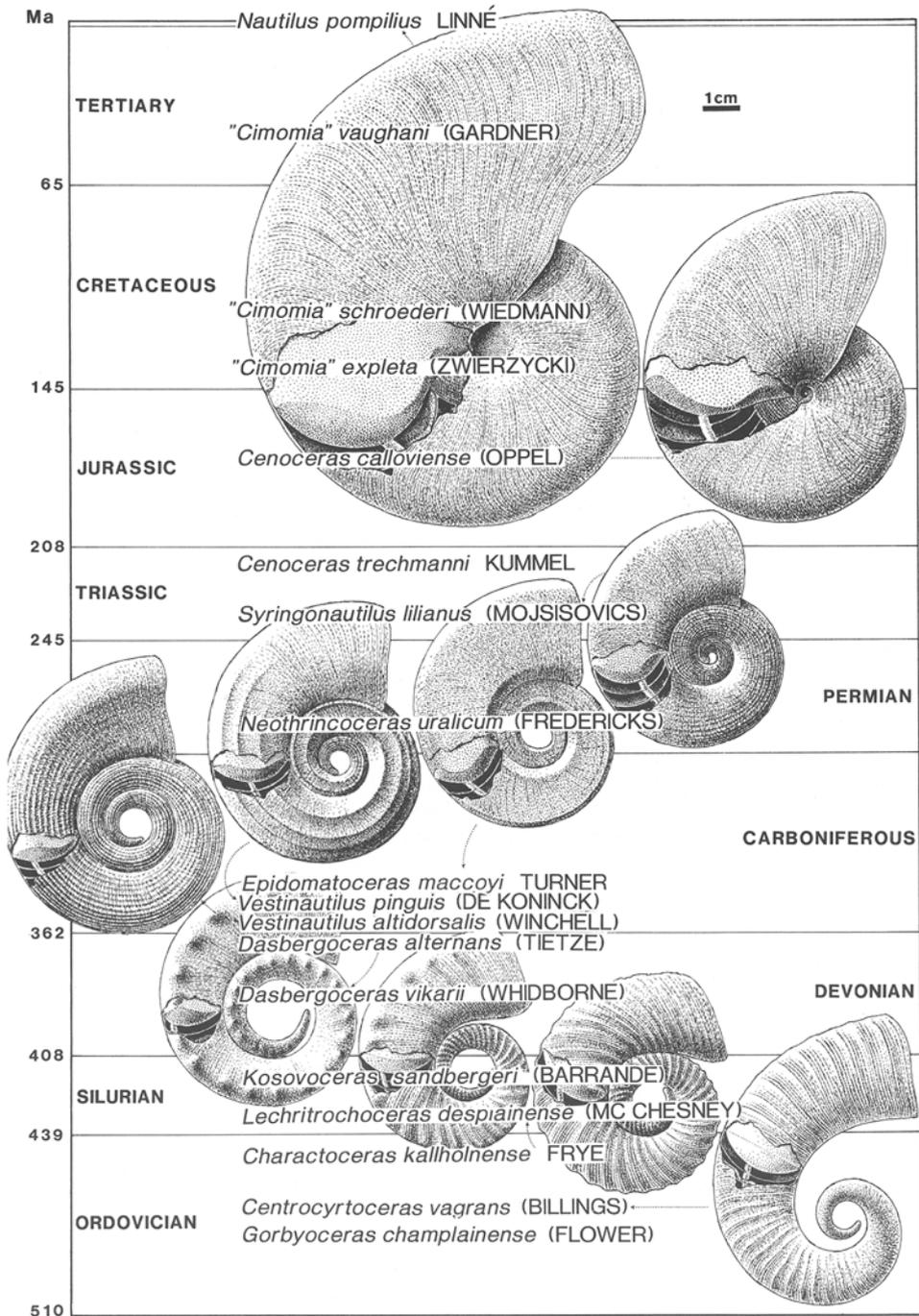


Fig. 9. Stratigraphic succession of the nautiloids that should be considered as possible members of the lineage leading to *Nautilus*. Note morphologic and stratigraphic gaps in the record of the lineage. Time scale after HARLAND et al. (1990).

Devonian (Givetian) of Wolborough described by WHIDBORNE (1890) as *Trochoceras vicarii* (WHIDBORNE), *Trochoceras pulcherrimum* WHIDBORNE, and *Trochoceras obliquatum* (PHILLIPS). Without examining the original British material it is not possible to solve nomenclatorial problems connected with these fossils. In having a wide umbilical perforation and prominent ventro-lateral tuberculation (see also HOLZAPFEL 1895), these lechritrochoceratids closely resemble Famennian *Dasbergoceras alternans* and are most probably ancestral to it.

Ancestry of the Nautilida

The Famennian nautilid described above is therefore closely related to the Middle Devonian lechritrochoceratids. The oldest Lechritrochoceratidae come from the Wenlock. Their shells are ornamented with oblique annulations that resemble Silurian and Ordovician tarphyceratids (including *Barrandeoceras*; see DZIK 1984). They differ from the Tarphyceratida in the presence of prominent longitudinal (spiral) ornamentation and, most importantly, in the loosely coiled slender juvenile stages (in post-Arenigian tarphyceratids embryonic shell was tightly coiled, with a rounded apex). The lechritrochoceratids also differ in siphuncle structure and cannot therefore be directly related to the tarphyceratids. Much more likely is their derivation from loosely coiled uranoceratids. *Charactoceras kallholnense* FRYE from the Ashgill of Sweden has a weakly annulated and longitudinally striated conch which is tightly coiled but with an umbilical perforation 7.5 mm in diameter (FRYE 1982). It may be the ancestor of *Lechritrochoceras*. In its shell ornamentation, *C. kallholnense* resembles the loosely coiled probable uranoceratid *Centrocyrtoceras vagrans* (BILLINGS) from the Early Caradoc (see WILSON 1961). Available data are too limited to reconstruct a detailed phylogeny but, if the longitudinal ornament and subcentral siphuncle are primitive characters of the group, it may find its ancestry in the longitudinally striated, slightly cyrtoconic kionoceratid Orthoceratida. Poorly known *Gorbyoceras champlainense* (FLOWER) from the Llandeilo (Chazyan) of Vermont (FLOWER 1955) predates *Centrocyrtoceras*, and is a member of the same Midcontinent faunal realm.

Conclusions

The fossil record of the evolution of the lineage of *Nautilus* is very incomplete (Fig. 9). There are many morphological and stratigraphical gaps, the most important being between Recent and Cretaceous species. Still inadequately recognized is the pre-Triassic evolutionary origin of *Syringonautilus*. Although the Middle Devonian to Early Carboniferous nautilids are better known, data on both Famennian and Tournaisian nautilids is still very limited. Evidently, the environments preferred by these fossil nautilids are underrepresented in the geological record. Their exact phylogenies remain unknown, and it is unclear whether loosely coiled Early Carboniferous members of the Nautilida are primitive or derived. Even more enigmatic is the origin of the lechritrochoceratids. Their ancestry in the Ordovician uranoceratids, even if likely, is far from certain.

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References

- BARRANDE, J. 1865. Système Silurien du Centre de la Bohême. Première Partie: Recherches paléontologiques Vol. 2. Classe des Mollusques. Ordre des Cephalopodes sér. 6: pl. 1–107, Prague.
- COLLINS, D. H. 1965. Devonian nautiloids from northern Canada. – Bulletin of the Geological Survey of Canada 182: 31–50, Ottawa.
- DELÉPINE, G. 1940. Les goniatites du Dinantien de la Belgique. – Mémoires du Musée Royal d'Histoire Naturelle de Belgique 91: 1–88, Bruxelles.
- DZIK, J. 1981. Origin of the Cephalopoda. – Acta Palaeontologica Polonica 26: 161–191, Warszawa.
- 1984. Phylogeny of the Nautiloidea. – Palaeontologia Polonica 45: 1–219, Warszawa.
- FLOWER, R. H. 1955: New Chazyan orthocones. – Journal of Paleontology 29: 806–830, Tulsa.
- 1988. Progress and changing concepts in cephalopod and particularly nautiloid phylogeny and distribution. – [In:] WIEDMANN, J. & KULLMANN, J. (eds.) Cephalopods – Present and Past: 17–24, Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- FRYE, M. W. 1982. Upper Ordovician (Haryuan) nautiloid cephalopods from the Boda Limestone of Sweden. – Journal of Paleontology 56: 1274–1292, Tulsa.
- GROESSENS, E. 1974. Distribution de conodontes dans le Dinantien de la Belgique. – Publication de la Société géologique de Belgique 17: 1–193, Bruxelles.
- HARLAND, W. B.; ARMSTRONG, R. L.; COX, A. V.; CRAIG, L. E.; SMITH, A. G. & SMITH, D. G. 1990. A Geologic Time Scale 1989. – 263 pp., Cambridge University Press, Cambridge.
- HEWITT, R. A. 1988. Outline of research on the ecology and evolution of the Eocene nautilid cephalopods from the London Clay, England. – Tertiary Research 10: 65–81, London.
- 1989. Recent growth of nautiloid and ammonite taxonomy. – Paläontologische Zeitschrift 63: 281–296, Stuttgart.
- HEWITT, R. A. & WESTERMANN, G. E. G. 1986. Function of complexly fluted septa in ammonoid shells. I. Mechanical principles and functional models. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 172: 47–69, Stuttgart.
- 1988. Stress and strain in *Nautilus* shells: some limitations on the buoyancy control and vertical migration of ectocochliates. – [In:] WIEDMANN, J. & KULLMANN, J. (eds.) Cephalopods – Present and Past: 705–712, Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- HOLZAPFEL, F. 1895. Das obere Mitteldevon (Schichten mit *Stringocephalus Burtini* und *Maeneceras terebratum*) im Rheinischen Gebirge. – Abhandlungen der königlich Preußischen geologischen Landesanstalt 16: 1–460, Berlin.
- JAKOBS, D. K. 1990. Sutural pattern and shell stress in *Baculites* with implications for other cephalopod shell morphologies. – Paleobiology 16: 336–346.
- KAYSER, E. 1881. Beiträge zur Kenntnis von Oberdevon und Culm am Nordrande des rheinischen Schiefergebirges. – Jahrbuch der königlich Preußischen geologischen Landesanstalt 1881: 51–91, Berlin.
- KORN, D. 1992. Relationship between shell form, septal construction and suture line in clymeniid cephalopods (Ammonoidea; Upper Devonian). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 185: 115–130, Stuttgart.
- KUMMEL, B. 1956. Post-Triassic nautiloid genera. – Bulletin of the Museum of Comparative Zoology, Harvard 114: 324–465, Cambridge, Mass.
- LANDMAN, N. H. 1988. Early Ontogeny of Mesozoic ammonites and nautilids. – [In:] WIEDMANN, J. & KULLMANN, J. (eds.) Cephalopods – Present and Past: 215–228, Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- MATSUMOTO, T. 1983. Cretaceous nautiloids from Hokkaido – I. – Transactions and Proceedings of the Palaeontological Society of Japan, New Series 129: 9–25, Tokyo.
- MILLER, A. K. 1947. Tertiary nautiloids of the Americas. – Memoires of the Geological Society of America 23: 1–234, New York.
- 1951. Tertiary nautiloids of west-coastal Africa. – Annales du Musée du Congo Belge 8: 1–89, Tervuren.
- MILLER, A. K.; DOWNS, H. R. & YOUNGQUIST, W. 1949. Some Mississippian cephalopods from central and western United States. – Journal of Paleontology 23: 600–612, Tulsa.

- MILLER, A. K. & FURNISH, W. M. 1939. Lower Mississippian nautiloid cephalopods of Missouri. – University of Missouri Studies 13: 149–178.
- MILLER, A. K. & GARNER, H. F. 1953. Lower Mississippian cephalopods of Michigan. Part II. Coiled nautiloids. – Contributions of the Museum of Paleontology of the University of Michigan 11: 111–151, Ann Arbor.
- MUTVEI, H. 1957. On the relations of the principal muscles to the shell in *Nautilus* and some fossil nautiloids. – Arkiv för Mineralogi och Geologi 2: 219–254, Stockholm.
- PFAFF, E. 1911. Über Form und Bau der Ammonitensepten und ihre Beziehungen zur Suturlinie. – Jahrbuch des Niedersächsischen geologischen Vereins 4: 208–223, Hannover.
- ROEMER, C. F. 1844. Das Rheinische Übergangsgebirge. Eine palaeontologisch-geognostische Darstellung. – 99 pp. Hannover.
- RUZHENTSEV, V. E. & SHIMANSKY, V. N. 1954. Nizniepiermiskije sviernutyje i sognutyje nautiloidei juznovo Urala. – Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR 50: 1–152, Moskva.
- SCHASTLIVTSEVA, N. P. 1988. Triasovyje ortoceratydy i nautilidy SSSR. – Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR 229: 1–104, Moskva.
- SCHULTZ, O. 1976. Zur Systematik der Nautilidae. – Anzeiger der mathematisch-naturwissenschaftlichen Klasse der Österreichischen Akademie der Wissenschaften 1976: 1–9, Wien.
- SEILACHER, A. 1975. Mechanische Simulation und funktionelle Evolution der Ammoniten-Septums. – Paläontologische Zeitschrift 49: 268–286, Stuttgart.
- 1988. Why are nautiloid and ammonite sutures so different? – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 177: 41–69, Stuttgart.
- SHIMANSKY, V. V. 1967. Kamiennougolnye Nautilida. – Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR 115: 1–244, Moskva.
- 1975. Mielovyje nautiloidei. – Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR 150: 1–208, Moskva.
- SOBOLEV, E. S. 1989. Triasovyje nautilidy Sieviero-Vostocnoj Azji. – Trudy Instituta Geologii i Geofizika SO Akademiyi Nauk SSSR 727: 1–192.
- TEICHERT, C. & MATSUMOTO, T. 1987. The Ancestry of the genus *Nautilus*. – [In:] SAUNDERS, W. B. & LANDMAN, N. H. (eds.) *Nautilus*: 25–32, Plenum Publishing Corporation, New York.
- TIETZE, E. 1870. Ueber die devonischen Schichten von Ebersdorf unweit Neurode in der Grafschaft Glatz, eine geognostisch-paläontologische Monographie. – Palaeontographica 19: 103–158, Cassel.
- TUREK, V. 1975. Genus *Kosovoceras* gen. n. in the Silurian of Central Bohemia (Nautiloidea). – Sbornik geologických ved, vada Paleontologie 17: 7–44, Prague.
- 1976. *Magdoceras* gen. n. and *Inclytoceras* gen. n. from the Silurian of central Bohemia (Nautiloidea, Barrandeoceratida). – Casopis pro Mineralogie, Geologie 21: 137–145, Prague.
- TUREK, V. & MAREK, J. 1986. Notes on the phylogeny of the Nautiloidea. – Paläontologische Zeitschrift 60: 245–253, Stuttgart.
- WEYER, D. 1972. Zum Alter der Ammonoideen-Faunen des Marshall Sandsteins (Unterkarbon; Michigan, USA). – Berichte der deutschen Gesellschaft der geologischen Wissenschaften A, Geologie-Paläontologie 17: 325–350, Berlin.
- WHIDBORNE, G. F. 1890. The Devonian of the south of England. Part II. The fauna of the limestones of Lummaton, Wolborough, Chircombe Bridge, and Chudleigh. – Monographs of the Palaeontographical Society 43: 47–154, London.
- WIEDMANN, J. 1960. Zur Systematik jungmesozoischer Nautiliden unter besonderer Berücksichtigung der iberischen Nautilinae d'ORBIGNY. – Palaeontographica 115A: 144–206, Stuttgart.
- WILSON, A. E. 1961. Cephalopoda of the Ottawa Formation of the Ottawa-St. Lawrence Lowland. – Bulletin of the Geological Survey of Canada 67: 1–106, Ottawa.
- ZHURAVLEVA, F. A. 1972. Otpiecatki muskulov-retraktorov u devonskich ptenoceratid. – Paleontologicheskij Zhurnal 1972: 134–136, Moskva.
- 1974. Devonskije Nautiloidei. Otriady Oncoceratida, Tarphyceratida, Nautilida. – Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR 142: 1–159, Moskva.

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