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A revised classification of the Carboniferous and Permian Nautilida

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Abstract. Classification schemes for the Carboniferous and Permian coiled nautiloids were controversially discussed between the 1940s and the 1980s, but have rarely been a topic in the palaeontological literature since then. Depending on the respective affiliation of the authors with regard to their research base, either the *Treatise on Invertebrate Paleontology* or the *Osnovy Paleontologii* schemes were used. New findings from the last 40 years now make it possible to draw a more differentiated picture of the phylogeny and thus classification of the Nautilida. A new classification scheme is presented here, which is based on the integration of as many characters as possible, such as the general conch shape and its ontogeny, the shell sculpture and the shape of the septum and the course of the suture line. In addition, the stratigraphic succession of species and genera was taken into account. In the new classification presented here, seven suborders are distinguished within the order Nautilida, five of which known from Carboniferous and Permian strata. These are the Temnocheilina Flower, 1963 (superfamilies Trigonoceratoidea Hyatt, 1884, Koninckioceratoidea Hyatt, 1900), Domatoceratina subordo nov. (superfamilies Grypoceratoidea Hyatt, 1900, Permoceratoidea Miller & Collinson, 1953 and Subclymenioidea Shimansky, 1962), Tainoceratina Shimansky, 1957 (superfamilies Tainoceratoidea Hyatt, 1883 and Pleuronautiloidea Hyatt, 1900), Liroceratina Flower, 1955 (superfamilies Liroceratoidea Hyatt, 1900, Ephippioceratoidea Miller & Youngquist, 1949 and Clydonautiloidea Hyatt, 1900) and Solenochilina Flower, 1950 (superfamilies Aipoceratoidea Hyatt, 1884 and Scyphoceratoidea Ruzhencev & Shimansky, 1954). The new families and subfamilies Dasbergoceratidae fam. nov., Epistroboceratidae fam. nov., Stenopoceratidae fam. nov., Foordiceratidae fam. nov., Metacoceratidae fam. nov., Planetoceratidae fam. nov., Chouteauoceratinae subfam. nov. and Vestinautilinae subfam. nov. are introduced.

Keywords. Nautiloidea, Nautilida, Carboniferous, Permian, classification.

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Introduction

Problems in the classification of coiled nautiloids

Carboniferous and Permian coiled nautiloids have been described for more than 200 years (e.g., Sowerby 1812–1815, 1823–1825) (Fig. 1). However, classification schemes for these cephalopods (order Nautilida Agassiz, 1847) have mainly been developed from the 1950s to the 1980s and have not been intensively discussed over the last 40 years. Therefore, there is no general agreement on the systematics of the group. The main reason for this situation is probably that the Late Palaeozoic coiled nautiloids are a less intensively studied fossil group compared to their distant ammonoid relatives. A new count of the Carboniferous and Permian taxa that have been described so far indicates a much lower diversity of nautiloids; about 960 species in about 150 genera have been described from these two periods. This compares with more than 3000 species of ammonoids (Korn & Ilg 2007 and additional data) for the same periods. Furthermore, the counts show that the diversity of the Carboniferous and Permian coiled nautiloids shows significant temporal fluctuations; about 340 species are known from the Early Carboniferous (Mississippian), about 210 species from the Late Carboniferous (Pennsylvanian), about 170 species from the Early Permian (Cisuralian), about 50 species from the Middle Permian (Guadalupian) and about 190 species from the Late Permian (Lopingian). They belong to 30 families (Fig. 2).

Coiled nautiloids have often been recorded together with ammonoids in Carboniferous and Permian fossil assemblages. However, the co-occurrence of the two cephalopod groups must be seen as a small overlap zone, with nautiloids preferring the comparatively shallower areas of the shelf seas and ammonoids the deeper ones. In fossil collections from deeper shelf sediments, nautiloids have often been regarded as a by-product (or 'bycatch'). Due to their rarity and apparently slow morphological evolution, they were usually not considered as index fossils and thus often went unnoticed. Perhaps for these reasons, taxonomic research has developed much slower on nautiloids than on ammonoids. While the ammonoids have undergone considerable changes in systematic classification over the last 100 years, including a prominent increase in the number of new higher taxa (suborders, superfamilies, families) as well as genera, there have been comparatively few changes in the nautiloids when considering taxa above the rank of genus.

Classification schemes for the Carboniferous and Permian coiled nautiloids have been published several times (e.g., Flower & Kummel 1950; Kummel 1953, 1964; Shimansky 1957, 1962, 1967, 1979; Dzik 1984; King 1993), but they reveal great differences. There are several reasons for this:

(1) General rarity of the study material. – Nautiloids are usually much rarer than, e.g., ammonoids at most localities. Therefore, the possibilities to describe specimens and to characterise species are

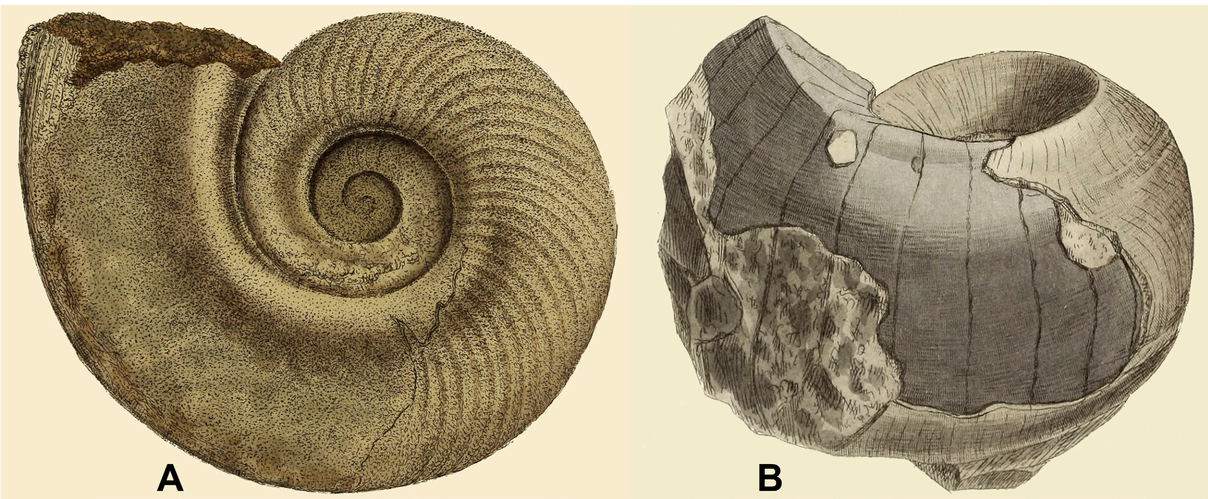

Fig. 1. Reproductions of two of the first ever described and illustrated Carboniferous nautiloids. **A**. *Aphelaeceras discus* (Sowerby, 1813), from Sowerby (1812–1815). **B**. *Vestinautilus cariniferus* (Sowerby, 1824), from Sowerby (1823–1825).

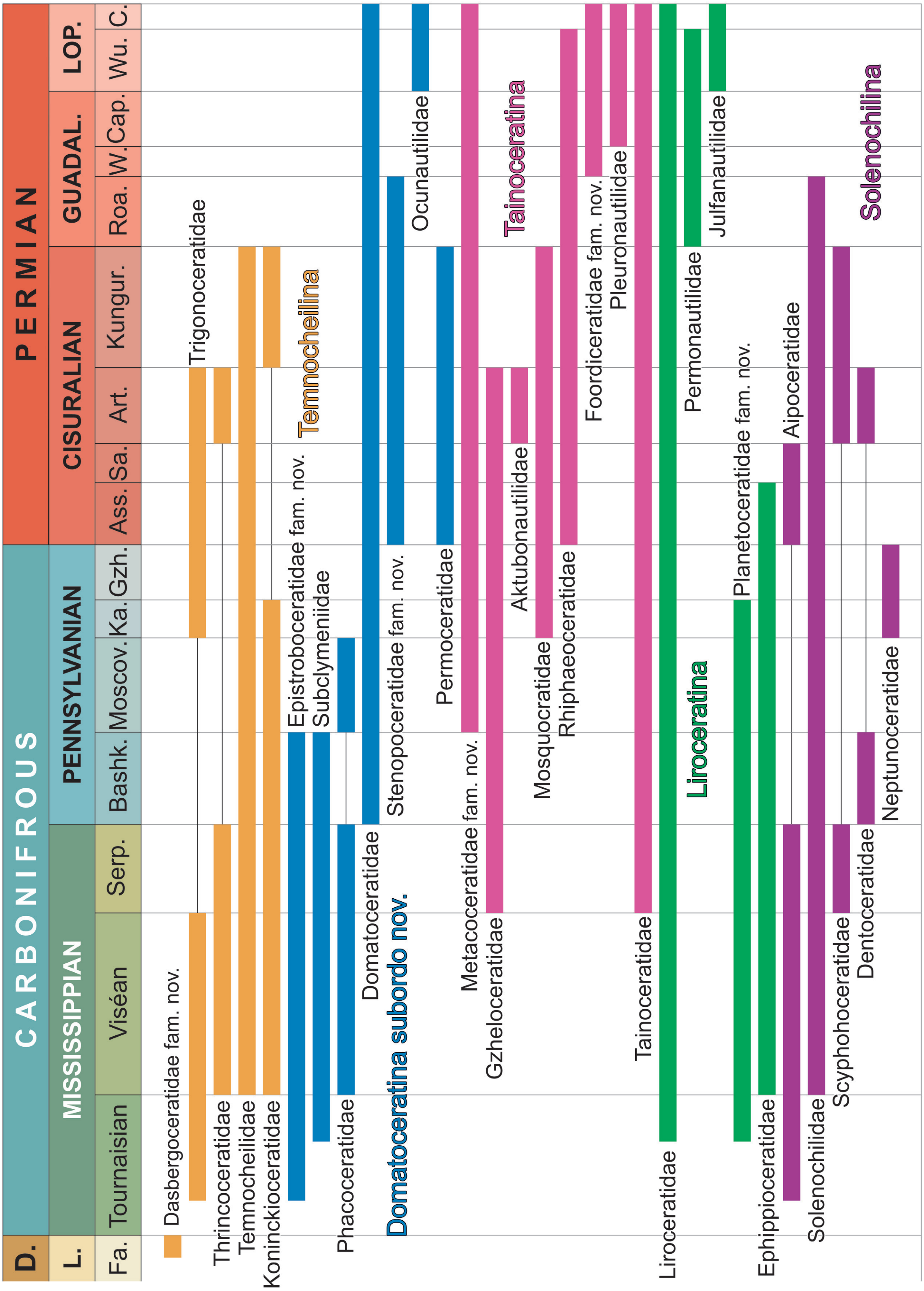

Fig. 2. The stratigraphic range of the families of Carboniferous and Permian coiled nautiloids.

much lower. Many species of Carboniferous and Permian coiled nautiloids are known from a single specimen only. Estimates of intraspecific variation are therefore rarely possible.

(2) Unfavourable preservation of many specimens. – Coiled nautiloids in very good preservation are known from only a few localities. The best example is probably the occurrence of Early Permian cephalopods in the South Urals (Ruzhencev & Shimansky 1954), where the first whorl is often well preserved, allowing the study of early ontogeny. Many other localities, preferably representing shallower water sediments, often yield only specimens lacking a preserved first whorl. And even if the first whorl is preserved, mechanical preparation usually does not allow extraction.

(3) Low number of species-specific characters. – Nautiloids usually offer relatively few conch characters to study. There is a variety of conch geometries and sculptures, but most Late Palaeozoic species have a very simple, concavely curved septal surface. Suture lines are therefore usually not suitable for distinguishing phylogenetic units. The suture line is usually determined by the shape of the whorl profile; flattened or concave areas of the whorl profile result in lobes. In addition, nautiloids tend to have only a few volutions, making ontogenetic trajectories of conch geometry difficult to analyse.

(4) Poorly developed methodology for systematic descriptions. – In contrast to the study of ammonoids, there has been little use of quantitative methods in the study of coiled nautiloids. For example, cross sections of conchs to study ontogenetic development have very rarely been made, and rigorous morphometric methods to analyse adult conchs have not been carried out on a large scale.

(5) Different personal views of authors. – There are differences between the various nautiloid researchers in the evaluation of certain characters, particularly when it comes to reconstructing the phylogeny and justifying the resulting classification schemes. However, it should be noted that the classification, initially based primarily on the shape of the adult conch, has been replaced over time by a subdivision that also includes internal characters, such as the shape and sculpture of the juvenile conch.

Flower (1963: 94), with some frustration but not without humour, summed up the state of taxonomic study of coiled nautiloids at that time with a metaphor: "Probably anyone attempting revisionary investigation of relationship and the shaping of an appropriate taxonomy finds himself, like the man who put the clock together, with a few wheels left over." Sixty years later, the situation has improved considerably in many areas. Knowledge of fossil nautiloids has been greatly enhanced by the monographic description of many new occurrences. As a result, the phylogenetic scheme and the possibility of classification have improved considerably. Nevertheless, there are still large gaps in our knowledge, reflected in the lack of potential intermediates.

A new classification scheme for Carboniferous and Permian coiled nautiloids is presented here. This scheme attempts to take into account all available conch and sculpture parameters. Also integrated in this scheme is the stratigraphic succession of the taxa, although to a much lesser extent than the morphological features.

Previous classification schemes

The classification schemes of the Carboniferous and Permian coiled nautiloids vary greatly from author to author. A first scheme developed by Hyatt (1883–1884, 1891, 1898, 1900) of the group that he called Order Nautiloidea consisted of the suborders Holochoanites Hyatt, 1898, Mixochoanites Hyatt, 1898, Schizochoanites Hyatt, 1898, Orthochoanites Hyatt, 1898 and Cyrtochoanites Hyatt, 1898. The Orthochoanites included the units (which were not explicitly called superfamilies) Orthoceratida Hyatt, 1900 (with three families), Plectoceratida Hyatt, 1900 (five families), Pleuronautilida Hyatt, 1900 (two families), Ryticeratida Hyatt, 1900 (two families), Rhadinoceratida Hyatt, 1900 (four families), Hercoceratida Hyatt, 1900 (four families), Koninckioceratida Hyatt, 1900 (two families) and Digonoceratida Hyatt, 1900 (two families). The Carboniferous and Permian coiled nautiloids are distributed among several of these units. Regarding the classification scheme of Hyatt (1898, 1900), it should be noted that at that time the knowledge of the Early Carboniferous nautiloids was already quite good because of some monographs (de Koninck 1844, 1878; M'Coy 1844), but much less was known about the Late Carboniferous and particularly Permian nautiloids, of which only a few species were known.

In the first half of the 20th century, only minor modifications were proposed in a series of papers by Arthur K. Miller (e.g., Miller *et al.* 1933; Miller & Unklesbay 1942; Miller & Youngquist 1949), but in the second half of the 20th century, several competing phylogenetic reconstructions and hence classification schemes for the Carboniferous and Permian nautiloids were developed:

Flower & Kummel (1950). – In the first comprehensive presentation of the systematics of all nautiloids, Flower & Kummel (1950) distinguished a total of 14 orders, four of which correspond to the order Nautilida as used today: Nautilida Agassiz, 1847 (ten families; Carboniferous to Recent), Solenochilida Flower, 1950 (one family; Carboniferous to Permian), Rutoceratida Flower, 1950 (four families; Devonian to Triassic) and Centroceratida Flower, 1950 (four families; Carboniferous to Triassic). Possible phylogenetic relationships between these were only vaguely presented, but the four orders are said to have originated in the family Barrandeoceratidae Foerste, 1925. Flower & Kummel (1950) did not use the taxonomic categories of superfamily and suborder.

Kummel (1953, 1964). – In his contribution to the *Treatise of Invertebrate Paleontology*, Kummel (1964) took a much more conservative approach, which was based on his earlier monograph on the Triassic nautiloids (Kummel 1953). Kummel (1964) did not distinguish any suborders within the order Nautilida. Instead, he accepted the five superfamilies Aipocerataceae Hyatt, 1883, Tainocerataceae Hyatt, 1883, Trigonocerataceae Hyatt, 1884, Clydonautilaceae Hyatt, 1900 and Nautilaceae de Blainville, 1825. Although this scheme differs in some respects from that published by Shimansky (1957), there are many similarities. These superfamilies correspond in several respects to the suborders distinguished by Shimansky (1957).

It is not clear on what morphological ground the classification scheme proposed by Kummel (1964) was based, as the text discussing the phylogeny mainly contains information about the differences between the groups in terms of adult conchs. It was therefore a narrative of the hypothetical relationships between the groups rather than an analytical approach. This resulted in very similar and sometimes uninformative definitions of superfamilies and families, with no clear statements on the plesiomorphic and apomorphic characters of individual higher taxa.

Ruzhencev & Shimansky (1954), Shimansky (1957, 1962, 1967, 1979). – Based on excellently preserved Early Permian material from the South Urals, Ruzhencev & Shimansky (1954) provided an extensive discussion of the phylogeny of all Permian nautiloids. They used a wide range of characters for their classification scheme, which was intended to reflect the phylogenetic relationships of the taxa within the group. Most importantly, it included the morphology of juvenile conchs, which had not played a major role in previous studies. This scheme, which differed significantly from that previously outlined by Miller & Youngquist (1949), was subsequently developed (Shimansky 1957) and detailed in the *Osnovy Paleontologii* (Shimansky 1962). In this scheme, the order Nautilida Agassiz, 1847 consisted of the five suborders Rutoceratina Flower, 1950 (two superfamilies; Devonian to Permian), Tainoceratina Shimansky, 1957 (four superfamilies; Devonian to Triassic), Centroceratina Flower, 1950 (two superfamilies; Devonian to Triassic), Liroceratina Flower, 1955 (two superfamilies; Devonian to Cretaceous) and Nautilina Agassiz, 1847 (two superfamilies; Triassic to Recent). This scheme recognised that the first four suborders originated in the Devonian.

The phylogenetic diagram shown by Shimansky (1957) is remarkable for its geometry, showing 13 long lineages, typically representing families, for the Carboniferous and Permian periods. There is only one superfamily (Rhiphaeocerataceae Ruzhencev & Shimansky, 1954) with two families that first appeared in the Permian. The order Rutoceratina was considered to be the ancestral root of all post-Devonian coiled nautiloids. According to Shimansky, two lineages survived from the Devonian into the Carboniferous, namely the family Neptunoceratidae Shimansky, 1957 and the superfamily Solenochilaceae Hyatt, 1893.

This scheme was then further modified by Shimansky (1967, 1979) to accept only three suborders within the order Nautilida: Rutoceratina (eight or nine superfamilies with a total of 21 families; Devonian to Triassic), Liroceratina (two superfamilies with five families, Carboniferous to Triassic) and Nautilina (two superfamilies with five families, Triassic to Recent). The phylogenetic scheme (Shimansky 1967: 49) shows the family Rutoceratidae Hyatt, 1884 as the ancestor of the Nautilida. Shevyrev (2006) used the same classification, but with the suborder names Rutocerina, Lirocerina and Nautilina.

In his study and discussion of the phylogeny of the entire Nautiloidea, Dzik (1984) presented an alternative phylogenetic reconstruction for the post-Devonian coiled nautiloids. This attempt utilised a wide range of conch characters, including the juvenile morphology, but also the stratigraphic occurrence of the taxa discussed. The classification scheme of the order Nautilida shown by Dzik differs markedly from the previously published schemes. It contains the largely Palaeozoic suborders Centroceratina (Ordovician to Devonian), an "uncertain suborder" with the superfamily Aipoceratoidea Hyatt, 1884 (Devonian to Permian) and the very voluminous Tainoceratina Shimansky, 1957 (with the families Trigonoceratidae Hyatt, 1884, Phacoceratidae Shimansky, 1962, Tainoceratidae Hyatt, 1883, Grypoceratidae Hyatt, 1900, Clydonautilidae Hyatt, 1900, Syringonautilidae Mojsisovics, 1902 and Liroceratidae Miller & Youngquist, 1949; Carboniferous to Triassic). The third suborder Nautilina Agassiz, 1847 includes the post-Triassic nautiloids, as proposed in the phylogenetic schemes of Shimansky (1957) and Kummel (1964). Dzik (1984: 149) explicitly addressed the difficulties of distinguishing between taxa higher than the family level: "For practical purposes, I assign the Early Paleozoic nautiloids to the suborder Centroceratina, the Late Paleozoic and Triassic to the suborder Tainoceratina, and the post-Triassic species to the suborder Nautilina. These suborders cannot be unequivocally diagnosed because of frequent evolutionary convergence."

For comparison with the new classification scheme presented here, the three main historical classifications of the Nautilida are given here:

"*Osnovy Paleontologii*" (Shimansky 1962):
Order Nautilida Agassiz, 1847
- Suborder Rutoceratina Flower, 1950
  - Superfamily Rutocerataceae Hyatt, 1884
    - Family Rutoceratidae Hyatt, 1884
    - Family Neptunoceratidae Shimansky, 1957
  - Superfamily Aipocerataceae Hyatt, 1884
    - Family Litogyroceratidae Shimansky, 1957
    - Family Scyphoceratidae Ruzhencev & Shimansky, 1954
    - Family Dentoceratidae Ruzhencev & Shimansky, 1954
    - Family Aipoceratidae Hyatt, 1884
- Suborder Tainoceratina Shimansky, 1957
  - Superfamily Tainocerataceae Hyatt, 1883
    - Family Tetragonoceratidae Flower, 1945
    - Family Tainoceratidae Hyatt, 1883
      - Subfamily Tainoceratinae Hyatt, 1883
      - Subfamily Pleuronautilinae Hyatt, 1900
    - Family Mosquoceratidae Ruzhencev & Shimansky, 1954

Superfamily Encoilocerataceae Shimansky & Erlanger, 1955
Family Encoiloceratidae Shimansky & Erlanger, 1955
Superfamily Temnocheilaceae Mojsisovics, 1902
Family Temnocheilidae Mojsisovics, 1902
Family Gzheloceratidae Ruzhencev & Shimansky, 1954
Superfamily Rhiphaeocerataceae Ruzhencev & Shimansky, 1954
Family Rhiphaeoceratidae Ruzhencev & Shimansky, 1954
Family Aktubonautilidae Ruzhencev & Shimansky, 1954
Suborder Centroceratina Flower, 1950
Superfamily Trigonocerataceae Hyatt, 1884
Family Trigonoceratidae Hyatt, 1884
Subfamily Trigonoceratinae Hyatt, 1884
Subfamily Aphelaeceratinae Shimansky, 1962
Subfamily Thrincoceratinae Ruzhencev & Shimansky, 1954
Subfamily Knightoceratinae Shimansky, 1962
Family Subclymeniidae Shimansky, 1962
Family Phacoceratidae Shimansky, 1962
Superfamily Centrocerataceae Hyatt, 1900
Family Centroceratidae Hyatt, 1900
Family Grypoceratidae Hyatt, 1900
Subfamily Domatoceratinae Miller & Youngquist, 1949
Subfamily Grypoceratinae Hyatt, 1900
Subfamily Syringonautilinae Mojsisovics, 1902
Subfamily Clymenonautilinae Shimansky, 1962
Family Neothrincoceratidae Shimansky, 1962
Family Permoceratidae Miller & Collinson, 1953
Suborder Liroceratina Flower, 1955
Superfamily Lirocerataceae Miller & Youngquist, 1949
Family Liroceratidae Miller & Youngquist, 1949
Family Ephippioceratidae Miller & Youngquist, 1949
Family Koninckioceratidae Hyatt, 1900
Family Paranautilidae Kummel in Flower & Kummel, 1950
Superfamily Clydonautilaceae Hyatt, 1900
Family Clydonautilidae Hyatt, 1900
Family Gonionautilidae Kummel in Flower & Kummel, 1950
Family Siberonautilidae Popov, 1951
Family Pseudonautilidae Hyatt, 1900
Suborder Nautilina Agassiz, 1847
Superfamily Nautilaceae d'Orbigny, 1840 recte de Blainville, 1825
Family Nautilidae d'Orbigny, 1840
Subfamily Nautilinae d'Orbigny, 1840
Subfamily Pseudaganidinae Kummel, 1956
Family Cymatoceratidae Spath, 1927
Subfamily Cymatoceratinae Spath, 1927
Subfamily Heminautilinae Shimansky, 1962
Family Hercoglossiidae Spath, 1927
Superfamily Aturiaceae Hyatt, 1894
Family Aturiidae Hyatt, 1894 [recte Chapman, 1857]

"*Treatise on Invertebrate Paleontology*" (Kummel 1964):
Order Nautilida Agassiz, 1847
Superfamily Tainocerataceae Hyatt, 1883
Family Tainoceratidae Hyatt, 1883
Family Rutoceratidae Hyatt, 1884
Family Tetragonoceratidae Flower, 1945
Family Rhiphaeoceratidae Ruzhencev & Shimansky, 1954
Family Koninckioceratidae Hyatt, 1900
Superfamily Trigonocerataceae Hyatt, 1884
Family Trigonoceratidae Hyatt, 1884
Family Centroceratidae Hyatt, 1900
Family Grypoceratidae Hyatt, 1900
Family Permoceratidae Miller & Collinson, 1953
Family Syringonautilidae Mojsisovics, 1902
Superfamily Aipocerataceae Hyatt, 1884
Family Aipoceratidae Hyatt, 1884
Family Solenochilidae Hyatt, 1893
Family Scyphoceratidae Ruzhencev & Shimansky, 1954
Superfamily Clydonautilaceae Hyatt, 1900
Family Clydonautilidae Hyatt, 1900
Family Liroceratidae Miller & Youngquist, 1949
Family Ephippioceratidae Miller & Youngquist, 1949
Family Gonionautilidae Kummel in Flower & Kummel, 1950
Family Siberonautilidae Popov, 1951
Superfamily Nautilaceae de Blainville, 1825
Family Nautilidae de Blainville, 1825
Family Pseudonautilidae Shimansky & Erlanger, 1955
Family Paracenoceratidae Spath, 1927
Family Cymatoceratidae Spath, 1927
Family Hercoglossiidae Spath, 1927
Family Aturiidae Chapman, 1857

"*Phylogeny of the Nautiloidea*" (Dzik 1984):
Order Nautilida Agassiz, 1847
Suborder Centroceratina Flower, 1950
Family Uranoceratidae Hyatt, 1900
Family Lechritrochoceratidae Flower, 1950
Family Rhadinoceratidae Hyatt, 1900
Family Trochoceratidae Zittel, 1884
Suborder uncertain
"Superfamily Aipoceratoidea Hyatt, 1884"
Family Aipoceratidae Hyatt, 1883
Family Solenochilidae Hyatt, 1893
Suborder Tainoceratina Shimansky, 1957
Family Trigonoceratidae Hyatt, 1884
Family Phacoceratidae Shimansky, 1962
Family Tainoceratidae Hyatt, 1883
Family Grypoceratidae Hyatt, 1900
Family Clydonautilidae Hyatt, 1900
Family Syringonautilidae Mojsisovics, 1902
Family Liroceratidae Miller & Youngquist, 1949

Suborder Nautilina Agassiz, 1847
Family Paracenoceratidae Spath, 1927
Family Cymatoceratidae Spath, 1927
Family Nautilidae de Blainville, 1825
Family Aturiidae Chapman, 1857

Basics for a new systematic scheme for the Carboniferous and Permian nautiloids

There is currently no generally accepted hierarchical character system for the structure of Late Palaeozoic coiled nautiloids. Comparison with ammonoids shows that the characters used to distinguish orders, families, genera and species are not clearly recognised in nautiloids. Regarding the classification schemes of coiled nautiloids, different approaches to the use of characters have been taken in recent decades.

General conch morphology

The external shape of the conch was considered the classic character for distinguishing the major units within the order Nautilida (e.g., Hyatt 1900; Flower & Kummel 1950). The main criteria were the degree of coiling (cyrtoconic, gyroconic or more or less tightly coiled), the degree of overlap upon the preceding whorl and the shape of the whorl profile.

The general shape of the conch and the shape of the whorl profile in many phylogenetic lineages and taxonomic units of the Nautilida are stable characters that have changed slowly in the course of evolution. This is evident in genera with simple conch geometry, such as *Domatoceras* Hyatt, 1891 and *Liroceras* Teichert, 1940 as well as genera with more complex conch geometry, such as *Tainoceras* Hyatt, 1883, whose representatives have only slightly altered their conch shape over long geological timescales.

On the other hand, there are cases where similar conch geometry does not necessarily reflect phylogenetic relationships. Such examples are the genera *Permonautilus* Kruglov, 1933 (Liroceratina) and *Solenocheilus* Hyatt, 1884 (Solenochilina Flower, 1950), both of which possess very conspicuous, long thorn-like processes on the umbilical wall of a pachyconic or globular adult conch.

Taxa at various levels have often been characterised by changes of their conch morphology during ontogenetic development. However, these characterisations were usually vague and lack quantification, such as “conch rapidly increasing in width and height”. To improve clarity, descriptions in this format can be translated into the ratio of whorl width to whorl height and the whorl expansion rate (WER).

The shape of the whorl profile, specifically the position of the ventrolateral shoulder and the umbilical margin, plays a crucial role in ontogenetic development of Early Carboniferous nautilids (Fig. 3). Phylogenetic reconstructions have to include this character. The evolution of the angular lateral margin can take four paths: remaining in a lateral or ventrolateral position (Fig. 3A, F) in the suborder Temnocheilina Flower, 1963, being replaced by a circular whorl profile, developing into an umbilical margin in the suborders Domatoceratina subordo nov. (Fig. 3B–C, G–H) and Tainoceratina Shimansky, 1957 (Fig. 3D, I), or evolving into both a ventrolateral shoulder and an umbilical margin (Fig. 3E, J) in the suborder Liroceratina Flower, 1955..

Juvenile conch morphology

The morphology of the juvenile conch is an important criterion in differentiating high taxonomic units. The curvature of the first volution and the size of the umbilical foramen are key features that have not been consistently studied. Ruzhencev & Shimansky (1954) conducted a detailed study on the variation in juvenile development using well-preserved Early Permian material from the South Urals. Studies at many other sites have not been conducted due to either fragmented material or the inability to mechanically separate juvenile volutions.

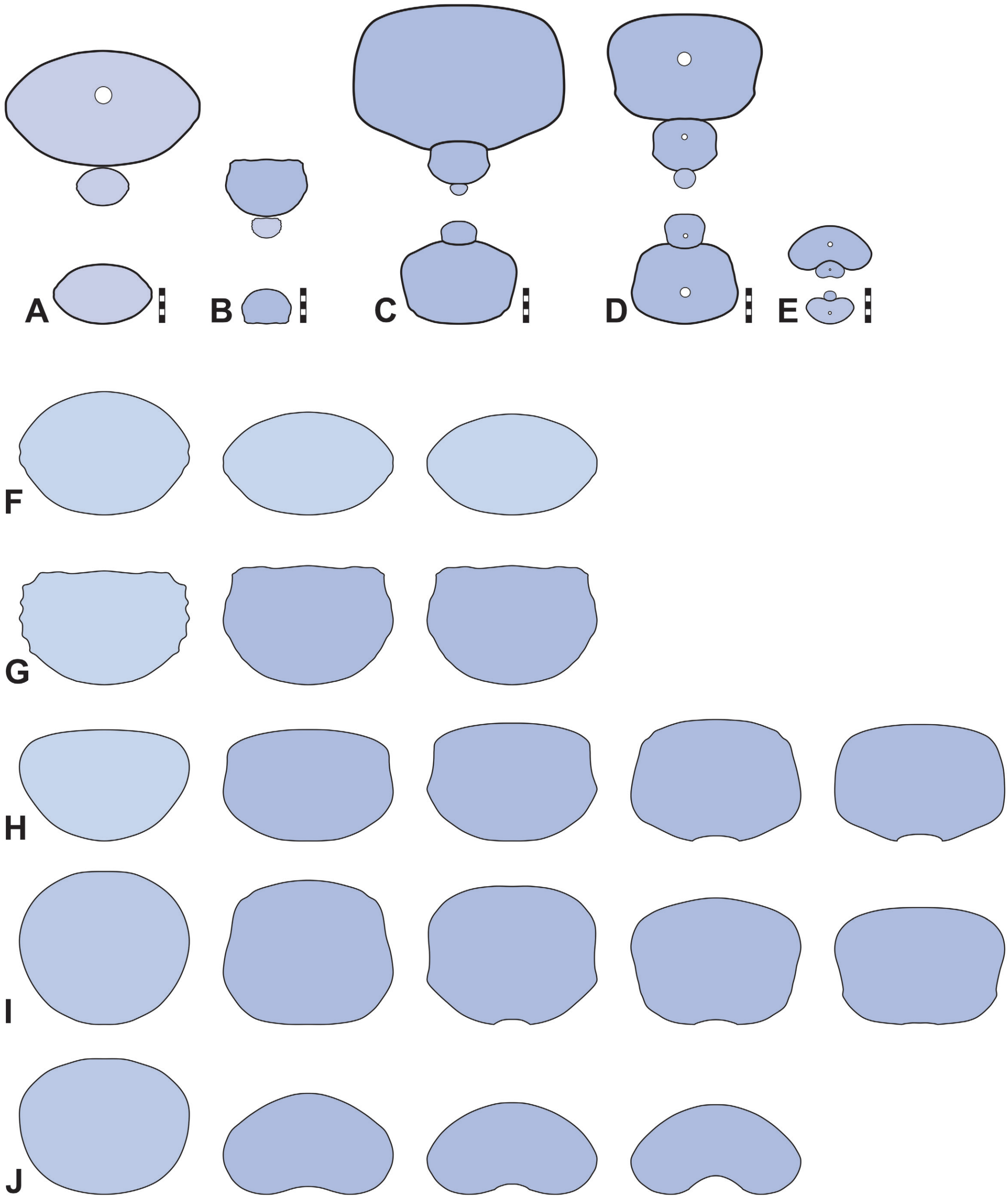

Fig. 3. Ontogenetic and phylogenetic change in the whorl profile of Carboniferous and Permian coiled nautiloids. **A–E**. Conch cross sections (scale bar units = 1 mm). **F–J**. Successions of whorl profiles (re-scaled to uniform width) in steps of half a volution. **A, F**. Suborder Temnocheilina Flower, 1963. *Subvestinautilus kesslerae* (Korn & Klug, 2023), from Korn & Klug (2023). **B, G**. Suborder Domatoceratina subordo nov.. *Stroboceras mane* Korn & Bockwinkel, 2022, from Korn & Bockwinkel (2022). **C, H**. Suborder Domatoceratina. *Epidomatoceras ebbighausenorum* Korn & Klug, 2023, from Korn & Klug (2023). **D, I**. Suborder Tainoceratina Shimansky, 1957. *Serometacoceras dorsoarmatum* (Abich, 1878), from Korn & Ghaderi (in press). **E, J**. Suborder Liroceratina Flower, 1955. *Liroceras bicostatum* Gordon, 1965, from Gordon (1965). Blue shadings refer to ontogenetic stages.

Septal shape and suture line

In contrast to ammonoids, where the suture line is a cardinal character used to distinguish major taxonomic units, its applicability to nautiloids is limited. In the vast majority of Carboniferous and Permian nautiloids, the septal surface is simply domed without marginal inflexions. Therefore, in these cases, the suture line is merely a 'cut-out shape' where the shape of the lobes and saddles and their amplitude reflect the shape of the whorl profile. Conchs with an almost circular whorl profile, such as *Millkoninckioceras* Kummel, 1963 and *Liroceras* Teichert, 1940, have an almost straight suture line. In contrast, conchs with a complex whorl profile, such as *Stroboceras* Hyatt, 1884 and *Tainoceras* Hyatt 1883, have a correspondingly more complex suture line with lobes and saddles produced by the shape of the whorl profile. Only a few deviations from a simple domed septum are known from independent evolutionary lineages. Examples of more complex septal shapes and hence more complex suture lines include *Subclymenia* d'Orbigny, 1849, *Permoceras* Miller & Collinson, 1953 and *Ephippioceras* Hyatt, 1894. Rarely, a small dorsal indentation is present, resulting in an annular process.

Siphuncle construction

The position of the siphuncle plays an important role in Carboniferous and Permian nautilids, as the suborder Solenochilina with a peripheral ventral siphuncle can be clearly distinguished from the other suborders with central or subcentral siphuncles. At a lower taxonomic level, the position of the siphuncle does not seem to be important. Possible differences in the width of the siphuncle have rarely been studied.

Sculpture and shell ornamentation

The presence or absence of shell sculpture, particularly ribs and nodes, is typically a stable morphological character in nautilids that is maintained over long geological periods. For example, members of the genus *Tainoceras* Hyatt, 1883 retained their highly distinctive sculpture of rows of nodes from the Late Carboniferous throughout to the Late Permian.

Stratigraphic occurrence

The phylogeny of Carboniferous and Permian nautiloid species and genera has been reconstructed using their stratigraphic succession and character evolution over time (Ruzhencev & Shimansky 1954; Dzik 1984).

Material and methods

The characterisation of the taxa follows the terminology of conch, ornament and suture line proposed by Korn (2010) and Klug *et al.* (2015) for the characterisation of ammonoids (Fig. 4). The terminology of conch geometry used here largely corresponds to that proposed by Teichert (1964b), but with a new

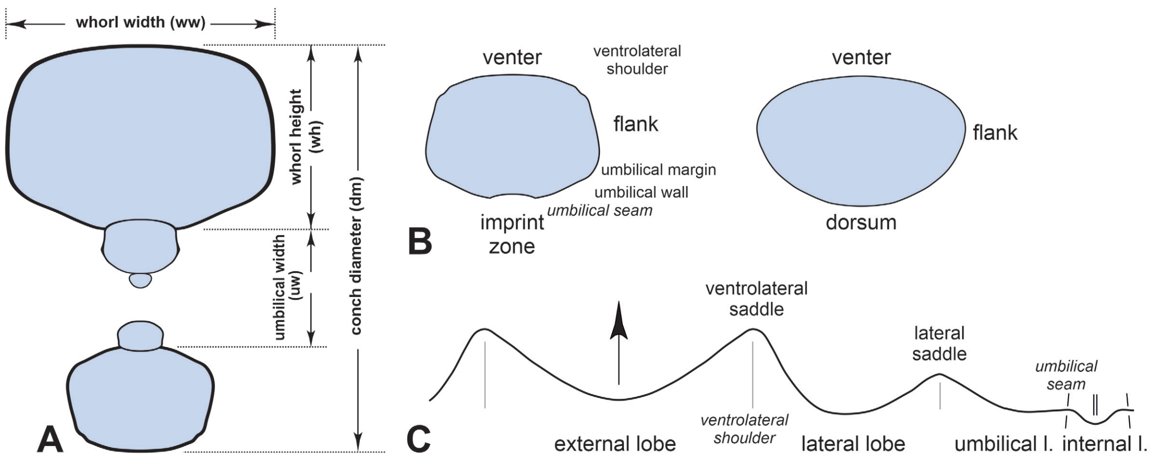

Fig. 4. The conch and suture line parameters used in the taxonomic descriptions. **A**. Conch parameters. **B**. Descriptive terms of whorl profiles. **C**. Suture line terminology (from Korn & Klug 2023).

terminology of whorl profile shapes (Fig. 5). The only differences concern the following terms: umbilical angle or shoulder (= umbilical margin) and umbilical area (= umbilical width).

Lists of the subordinate taxa are given below for each of the higher taxa. These lists cannot claim to be exhaustive. At the same time, it must be emphasised that there are considerable uncertainties, particularly in the classification of some genera. These problems cannot be eliminated within the framework of the present study without a time-consuming examination of the original material. The stratigraphic ranges for the Mesozoic and Cenozoic taxa are from Kummel (1964) and Dzik (1984).

Due to the numerous gaps in our knowledge, the classification presented here can only represent the current state of research. In the future, further revisions will certainly lead to modifications and problematic genera will be assigned to other families or possibly even other superfamilies or subfamilies.

Diagnoses for characterisation and delimitation are provided for all taxa above the genus level. As higher-ranking units in invertebrate palaeontology are rarely explicitly based on apomorphies, character matrices are presented here. The higher taxa are constructed 'accretionally'; lower-ranking taxa are grouped into a higher-ranking taxon based on their morphological similarity. This typically prevents the identification of distinct apomorphies, particularly when morphological reversals or homeomorphies occur.

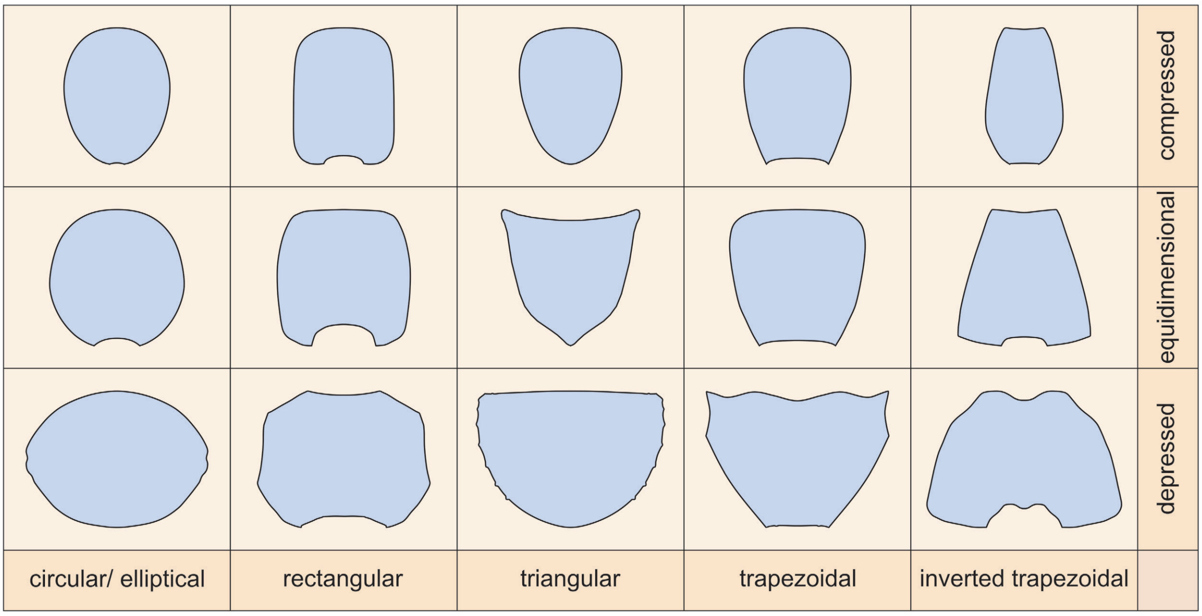

Fig. 5. Descriptive terms for the whorl profiles.

Results

Class Cephalopoda Cuvier, 1795
Subclass Nautiloidea Agassiz, 1847

Order **Nautilida** Agassiz, 1847

Diagnosis

Exogastrically curved or coiled nautiloids with a conch shape ranging from gyroconic or cyrtoconic to more or less tightly coiled. Shell surface smooth or sculptured with a variety of elements (ribs, nodes, spines, longitudinal ridges or lines). Septa simply domed in most species, with the shape of the whorl profile producing suture lines with variable lobes and saddles. Variations in septal shape with inflexions producing deep lobes in some genera. Septal necks short and straight, rarely slightly widened. Connective rings cylindrical or beaded. Siphuncular or cameral deposits absent. Juvenile conch with cup-shaped initial chamber and narrow siphuncle. Morphological evolution includes the degree of coiling, the shape and size of the juvenile and adult conch and the suture line (after Shimansky 1962; emended).

Included suborders

Nautilina Agassiz, 1847 (Late Triassic to Recent).
Solenochilina Flower, 1950 (Early Carboniferous to Late Permian; 16 genera, 77 species).
Liroceratina Flower, 1955 (Early Carboniferous to Late Triassic; 26 Palaeozoic genera, 168 Palaeozoic species).
Rutoceratina Flower, 1950 (Early to Middle Devonian).
Tainoceratina Shimansky, 1957 (Early Carboniferous to Triassic; 55 Palaeozoic genera, 279 Palaeozoic species).
Temnocheilina Flower, 1963 (Late Devonian to Early Permian; 31 genera, 166 species).
Domatoceratina subordo nov. (Early Carboniferous to Triassic; 40 Palaeozoic genera, 201 Palaeozoic species).

Remarks

Shimansky (1962: 115; translated from Russian) characterised the order Nautilida as follows: "Conch nautiliconic, less often gyroceraconic, cyrtoceraconic or trochoceraconic, smooth or sculptured. Suture line variable in structure, often with distinct lobes and saddles, which are usually shallow but sometimes very deep. Septal neck straight, less often slightly widened, as a rule short. Connecting rings from cylindrical to beaded. Siphonal deposits and substantial cameral deposits absent. Embryonic shell with a cuplike initial chamber and a narrow siphuncle which is closed at the base. Development involves mainly the degree of coiling, the form and size of the embryonic and adult shell, and suture line." (translation in Shimansky 1974)

Kummel (1964: K412) gave the following short statement: "Curved to coiled conchs presenting majority of mid-Paleozoic nautiloids. [Tainocerataceae and Trigonocerataceae derived directly or indirectly from Oncocerida; origin of Clydonautilaceae and Aipocerataceae uncertain, probably from Rutoceratidae. Nautilidae stem from Syringonautilidae.]"

Dzik (1984: 149) also gave a short diagnosis: "Exogastrically coiled, moderately elongated shell with narrow, originally subcentral siphuncle (but ventral in *Cenoceras*, and dorsal in *Aturia*); larval development with an egg capsule, without planktonic larval stage."

Suborder **Temnocheilina** Flower, 1963

Diagnosis

Suborder of the order Nautilida, in which a ventrolateral shoulder is formed early in ontogeny; advanced species may regress this character. Conch gyroconic, advolute or tightly coiled; general shape usually discoidal, subevolute or evolute. Juvenile whorl profile depressed elliptical or bicarinate in the early species and more circular in the advanced species. Adult whorl profile rounded triangular, but also rounded trapezoidal or circular in the early species, showing minor modifications during evolution. Dorsal whorl zone very small, if present. Juvenile stage with longitudinal ridges or lines. Septa simply domed. Suture line depending on the whorl profile, with shallow lobes and low saddles. Siphuncle in central or subcentral position.

Included superfamilies

Trigonoceratoidea Hyatt, 1884 (Early Carboniferous to Early Permian; 29 genera, 149 species).
Koninckioceratoidea Hyatt, 1900 (Early Carboniferous to Early Permian; 2 genera, 17 species).

Remarks

Taxonomy

The suborder Temnocheilina was named with some ambiguity, as Flower (1963) used two slightly different spellings. In the first case Flower (1963: 93) postulated: "It would seem that the Tainoceratidae represent a lineage derived from the Tetragonoceratidae; however, unpublished material suggests a close relationship between the Devonian Rutoceratidae and the nodose Temnocheilidae and the smoother whorled Koninckioceratidae. The last two families with possible derivatives are a lineage to which the name Temnochelina may be applied." On the same page, he referred to the publication by Shimansky (1957): "Shimansky (1957), though using only suborders in a too-comprehensive Nautilida, has suggested the addition of Tainoceratina, Solenochilina and Temnocheilina. It would seem that there is a possible advantage in recognizing Rutoceratina and Tainoceratina, though the writer would place the Koninckioceratidae and Temnocheilidae in the Temnochelina, and add Aipoceratina to replace Solenochilina, a taxonomic recognition of the isolated position of that family."

These statements were not critically discussed by Shimansky (1967: 38; translated from Russian): "Almost simultaneously, Flower (1963), in his interesting work on the Permian cyrtocones … speaks in some detail about the families Temnocheilidae and Koninckioceratidae, indicates the likelihood of a common origin and suggests the name Temnocheilina for this group." Later in the article (Shimansky 1967: 42; translated from Russian) he added: "Flower believes that the group can be considered as a suborder Temnocheilina, including the families Temnocheilidae and Koninckioceratidae."

The problem here is that Flower (1963) apparently had no intention of defining a new suborder, and mistakenly assumed that Shimansky (1957) had already established the suborder. It is also not clear whether the name "Temnochelina" used twice was a typographical error; in the supposed reference to Shimansky (1957) he used "Temnocheilina". However, it appears to be clear that Flower advocated a suborder Temnocheilina, albeit to a rather limited extent with the families Temnocheilidae and Koninckioceratidae. Furthermore, it may have been Flower's intention to name the suborder Temnocheilina; therefore this name is used here.

Shimansky (1957, 1962) included the family Temnocheilidae Mojsisovics, 1902 in the suborder Tainoceratina, the families Triboloceratidae Hyatt, 1884, Thrincoceratidae Ruzhencev & Shimansky, 1954 and Phacoceratidae Shimansky, 1962 in the suborder Centroceratina and the family Koninckioceratidae Hyatt, 1900 in the suborder Liroceratina. Later, Shimansky (1967, 1979) changed his opinion; the superfamilies Temnocheilaceae Mojsisovics, 1902, Koninckioceratacea Hyatt, 1900 and Trigonocerataceae Hyatt, 1884 were placed in the suborder Rutoceratina.

Kummel (1964) placed the taxa of the suborder Temnocheilina as understood here in the superfamilies Tainocerataceae Hyatt, 1883 and Trigonocerataceae Hyatt, 1884. Dzik (1984) recognised a closer relationship of genera such as *Vestinautilus* Ryckholt, 1852 and *Temnocheilus* M'Coy, 1844 and placed these genera in the family Trigonoceratidae Hyatt, 1884. From this he directly derived the family Phacoceratidae Shimansky, 1962.

The concept of Dzik (1984) is followed here for the following reasons: the morphology of the initial whorl is similar in all species of the suborder, with a mostly broadly elliptical whorl profile and a sculpture of coarse longitudinal ridges. In many species a prominent ventrolateral shoulder developed from the lateral margin of the initial whorl. The ventrolateral row of nodes characteristic of *Temnocheilus* Mojsisovics, 1902 is not considered to be related to the nodes of members of the suborder Tainoceratina (e.g., *Metacoceras* Hyatt, 1883), but is considered to be an independent development. These nodes are not a continuation of the lateral ribs (as in *Metacoceras*) and are elongated longitudinally; rather, they may be related to the ventrolateral spiral ridges in genera such as *Vestinautilus*.

The concept of the suborder Temnocheilina presented here differs significantly from previously published concepts of comparable taxonomic groups. It contains the majority of the Tournaisian and Viséan coiled nautiloids, which were previously distributed in the suborders Tainoceratina, Centroceratina and Liroceratina (Shimansky 1957, 1962), the suborder Rutoceratina (Shimansky 1967), the superfamilies Tainocerataceae Hyatt, 1883 and Trigonocerataceae Hyatt, 1884 (Kummel 1964) or the family Trigonoceratidae Hyatt, 1884 (Dzik 1984).

Morphology and subdivision

The vast majority of species in the suborder Temnocheilina have a discoidal conch with a widely opened umbilicus. Especially in the stratigraphically older Tournaisian and Viséan species, there is a morphocline ranging from gyroconic, advolute to more or less tightly coiled conchs. The umbilical foramen is quite large in most of the species; it is usually more than 5 mm in diameter, but can be considerably larger. A common character of most early representatives is the triangular adult whorl profile, which is preserved in various variations throughout the phylogeny of the group. This shape evolved from an early ontogenetic depressed oval or bicarinate shape of the whorl profile, in which the initial lateral margin developed into the ventrolateral shoulder (Fig. 3A, F). In later species, the whorl profile of the early ontogenetic stage is usually circular. In the juvenile stage of the early species, the shell is decorated with coarse spiral ridges. These lines evolved in the different evolutionary lineages into either fine spiral ornament (e.g., *Rineceras* Hyatt, 1893) or very coarse ridges (e.g., *Vestinautilus* Ryckholt, 1852), which gave the whorl profile a polygonal shape. More advanced species usually had a pattern of finer spiral lines. Longitudinally elongated ventrolateral nodes are present in the family Temnocheilidae Mojsisovics, 1902.

In this paper, the suborder Temnocheilina is redefined on the basis of a phylogenetic hypothesis based on the shape of the initial whorl and its modification during ontogeny. The suborder Temnocheilina contains the species with the most plesiomorphic characters of the Carboniferous and is the dominant suborder of the Early Carboniferous. The suborder Temnocheilina is divided into two superfamilies, which are characterised as follows:

Trigonoceratoidea Hyatt, 1884. – The whorl profile in the ancestral species is often triangular or trapezoidal with a flat venter; derived species show various modifications leading to circular shapes. During ontogeny, the geometry of the conch changes slightly. The shell is usually ornamented with spiral ridges or spiral lines.

Koninckioceratoidea Hyatt, 1900. – The whorl profile is depressed oval and does not change during ontogeny. The shell surface is largely smooth.

Origin

There are several concepts to explain the evolutionary pathways of curved and coiled nautiloids during the Devonian–Carboniferous transition and thus the origin of the taxa defined here as Temnocheilina. This group was partly named suborder Centroceratina and was interpreted by Shimansky (1957) to start with the Devonian family Centroceratidae Hyatt, 1900; according to this it had been derived from the family Rutoceratidae Hyatt, 1884. At the end of the Triassic, the suborder Centroceratina gave rise to the suborder Nautilina, which includes all Jurassic to Recent coiled nautiloids.

According to the phylogenetic scheme outlined by Dzik (1984), all post-Devonian coiled nautiloids, with the exception of the aipoceratids, form a monophyletic unit with roots in the earliest Carboniferous.

Dzik & Korn (1992) presented *Dasbergoceras* Dzik & Korn, 1992 as a possible ancestor of the Trigonoceratidae and thus the suborder Temnocheilina and with this the majority of post-Devonian coiled nautiloids. *Dasbergoceras alternans* (Tietze, 1871) has an advolute conch with a large umbilical foramen (27 mm) and a trapezoidal whorl profile. It possesses coarse radial ribs terminating in prominent conical nodes on the ventrolateral shoulder. The siphuncle is located close to the venter. Although this species shows some superficial resemblance to species of *Temnocheilus*, it can hardly be considered a direct ancestor; *Temnocheilus* was probably derived from *Subvestinautilus* Turner, 1954, as suggested by Dzik & Korn (1992: 88), and the ventrolateral row of nodes is considered a secondary character.

The ancestry of the Temnocheilina, with or without *Dasbergoceras* included, is an unsolved problem because of several unanswered questions:

(1) What was the morphological inventory of a possible ancestor of the Temnocheilina? – The characters of the almost central siphuncle and the ornamentation with spiral ridges in the early juvenile stage, which are important for the Temnocheilina, are not present in the Devonian nautilids, including *Dasbergoceras*.

(2) Are the Temnocheilina derived from fully coiled or loosely coiled conchs? For example, does *Trigonoceras* M‘Coy, 1844 represent a plesiomorphic form or did the cyrtoconic conch arise by secondary uncoiling? – Intuition, based on knowledge of some other evolutionary lineages in cephalopods, would favour an evolutionary lineage from loosely coiled to fully coiled conchs. However, this observation in some of the groups may not apply in every individual case; some other cases of probable secondary uncoiling are known, for example in *Maccoyoceras* Miller, Dunbar & Condra, 1933 where the terminal whorl separates slightly from the preceding one (Foord 1900; Histon 1999).

(3) Did the oldest representatives of the Temnocheilina undergo a rapid middle and late Tournaisian evolution after the Hangenberg Event at the Devonian–Carboniferous boundary, or was it a slow, long evolutionary process that started already in the Late Devonian, but was hidden without a fossil record? – The ‘nautiloid gap’ spanning most of the Late Devonian and the earliest Carboniferous with the only one known genus *Dasbergoceras* in the latest Devonian is the cardinal obstacle to answering this question. This is related to the general question of possible very different evolutionary rates in nautiloids.

Phylogeny

Gaps in our knowledge mean that the evolutionary pathways within the suborder Temnocheilina are, at least in part, unknown. Several questions concern the degree of involution of the conch, the shape of the whorl profile and the ornamentation:

(1) Do the gyroconic conchs (e.g., *Trigonoceras* M‘Coy, 1844) represent the plesiomorphic state or are they the result of secondary uncoiling? – This is a difficult question to answer as there are only very fragmentary records of the stratigraphically oldest representatives. Moreover, openly coiled conchs are known from both the oldest known assemblages such as *Chouteauoceras* Miller & Garner, 1953 in early Late Tournaisian (Miller & Furnish 1939; Miller & Garner 1953) and from much younger assemblages such as *Trigonoceras* in the Viséan (Maillieux 1925). It is possible that both evolutionary paths, including increased coiling and also secondary uncoiling, were realised in

these Early Carboniferous nautiloids. However, if a form like *Dasbergoceras* was the ancestor, then repeated cases of secondary uncoiling must be assumed.

(2) Does the triangular (e.g., *Trigonoceras* M'Coy, 1844, *Triboloceras* Hyatt, 1884), compressed oval (*Chouteauoceras*), or depressed ovate (e.g., *Rineceras* Hyatt, 1893) whorl profile represent the plesiomorphic condition? – Similar to the general conch shape, the evolutionary pathways of the whorl profile are also not fully understood. For example, in the proposed evolutionary lineage *Triboloceras*-*Vestinautilus*-*Subvestinautilus*, an evolutionary trend can be observed from angular triangular to more rounded triangular and trapezoidal whorl profiles.

(3) Are coarse longitudinal ridges or more delicate spiral lines of the juvenile conch the plesiomorphic state? – Longitudinal ridges in the stratigraphically oldest known species have been reported from several Middle and early Late Tournaisian formations, including the Calcaire de Vaulx and Calonne in Belgium (de Koninck 1878), the Chouteau Formation in Missouri (Miller & Furnish 1939), the Marshall Sandstone in Michigan (Miller & Garner 1953) and the Argiles de Teguentour in central Algeria (Korn & Bockwinkel 2022). At the same time, the coarse spiral ornamentation of the earliest juvenile stage has been reported to have regressed in several species and genera. These records provide good evidence for the hypothesis that the longitudinal ridges represented a plesiomorphic state. In addition, the stratigraphic position of the material also suggests that in one derived evolutionary lineage (family Subclymeniidae Shimansky, 1962 of the suborder Domatoceratina subordo nov.) there was a phylogenetic change in the juvenile ornamentation from coarse spiral ridges (early Late Tournaisian) to fine spiral lines (latest Tournaisian) and finally to the loss of spiral ornamentation (Viséan). In others, the spiral ridges were reduced in number but became much coarser (family Epistroboceratidae fam. nov. of the suborder Domatoceratina) or were gradually reduced (e.g., Vestinautilinae subfam. nov. and Temnocheilidae Mojsisovics, 1902).

Despite these partly unresolved problems, at least some possible phylogenetic lineages can be identified, which are also supported by stratigraphic data. A morphological transformation of the different conch characters can be observed:

(1) General coiling. – Within the genera *Rineceras* and *Vestinautilus* there is an evolutionary trend towards increasingly dense coiling, which could be seen as a general trend among the early representatives of the Temnocheilina.

(2) Whorl profile. – There is a trend from triangular to rounded trapezoidal shapes. This is related to the tighter enclosure of the preceding whorls. However, there is also a trend from an originally concave or at least strongly flattened venter to an increasingly convex rounded venter.

(3) Sculpture. – A general trend can be seen in the decreasing strength of the spiral ridges. Such a trend affects, for example, the number and strength of spiral ridges, as can be seen in *Vestinautilus* and *Subvestinautilus*.

Descendants

According to the current state of knowledge, three further suborders can be derived from the Temnocheilina; these are the Domatoceratina subordo nov., the Tainoceratina and the Liroceratina. The first two are distinguished from the Temnocheilina by the more or less simultaneous early ontogenetic formation of an umbilical margin and a ventrolateral shoulder; the latter developed only an umbilical margin but no prominent ventrolateral shoulder. The demarcation of some of the genera (e.g., *Catastroboceras* Turner, 1965 and *Epidomatoceras* Turner, 1954) placed here in the Domatoceratina is sometimes difficult because it is not always clear whether they already possess an umbilical margin. However, this is formed by the reduction of the spiral ridges present in the early growth stage. The early ontogenetic stage of Tainoceratina, at least those from the Early Permian, apparently does not show a spiral ornament (Ruzhencev & Shimansky 1954).

Superfamily **Trigonoceratoidea** Hyatt, 1884
Figs 6–10

Diagnosis

Superfamily of the suborder Temnocheilina, in which a ventrolateral shoulder is formed early in ontogeny. Conch gyroconic or advolute in some species, but more or less tightly coiled in most of the species; general conch form usually discoidal, subevolute or evolute. Whorl profile depressed elliptical or bicarinate in the initial growth stage of the early species and circular in the advanced species. Conch ontogeny with the widest area of the initial growth stage transforming into a pronounced ventrolateral shoulder. Adult whorl profile often rounded triangular but also rounded trapezoidal, polygonal or circular. Juvenile stage with longitudinal ridges or lines, which are particularly pronounced in the area of the venter and the ventrolateral shoulder of the adult stage. Septa simply domed. Suture line with shallow lobes and saddles; internal lobe absent or very shallow and rarely triangular.

Included families

Trigonoceratidae Hyatt, 1884 (Early Carboniferous to Early Permian; 13 genera, 72 species).
Triboloceratidae Hyatt, 1884 [synonym of Trigonoceratidae].
Rineceratidae Hyatt, 1893 [synonym of Trigonoceratidae].
Rhineceratidae Hyatt, 1900 [nomen nullum, synonym of Trigonoceratidae].
Temnocheilidae Mojsisovics, 1902 (Early Carboniferous to Early Permian; 11 genera, 59 species).
Thrincoceratidae Ruzhencev & Shimansky, 1954 (Early Carboniferous to Early Permian; 4 genera, 17 species).
Knightoceratidae Shimansky, 1962 [synonym of Temnocheilidae].
Neothrincoceratidae Shimansky, 1962 [synonym of Thrincoceratidae].
Dasbergoceratidae fam. nov. (Late Devonian; 1 genus, 1 species).

Remarks

The superfamily Trigonoceratoidea probably originated in a genus similar to *Dasbergoceras* in the latest Famennian (Late Devonian). Along with the superfamily Aipoceratoidea, it is the second evolutionary lineage of coiled nautiloids to cross the Devonian-Carboniferous boundary (Dzik & Korn 1992). There

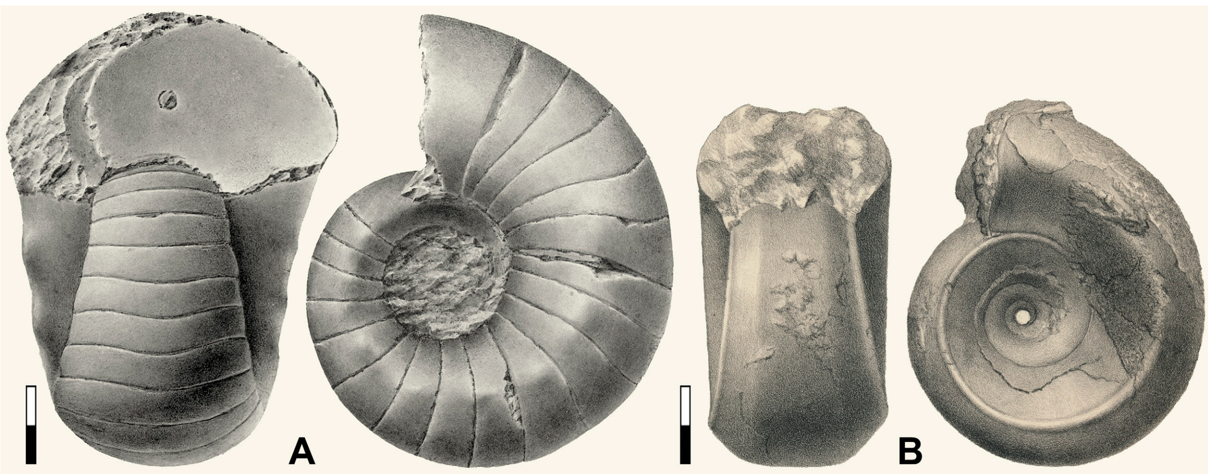

Fig. 6. Representatives of the superfamily Trigonoceratoidea Hyatt, 1884. **A**. Family Temnocheilidae Mojsisovics, 1902. *Endolobus spectabilis* (Meek & Worthen, 1860), from Miller & Youngquist (1949). **B**. Family Trigonoceratidae Hyatt, 1884. *Vestinautilus cariniformis* (Sowerby, 1824), from Foord (1900). Scale bar units = 10 mm.

are as yet no records from the earliest Carboniferous period, the *Gattendorfia* Stufe in the traditional ammonoid stratigraphy. On the basis of current knowledge, it is likely that coiled nautiloids underwent rapid morphological evolution during the Middle Tournaisian, which may be the reason for the great conch and sculpture diversity in the Late Tournaisian.

The adult conch shapes of the Trigonoceratoidea are diverse, ranging from cyrtoconic to subevolute; the latter being the dominant ones (Fig. 6). This is the reason why it is difficult to characterise the superfamily on the basis of the adult conch shape alone. The same is true for the ornamentation. In many species, there are more or less pronounced spiral ridges or spiral lines developed, but this can also be reduced in many advanced species. The course of the suture line is usually strongly dependent on the shape of the whorl profile. This is because the septum is usually uniformly concave in shape. For this reason, the ontogeny of conch shape and ornamentation is used here as a key character to distinguish families and subfamilies.

Four families within the Trigonoceratoidea can be separated on the base of the following principal characters:

Dasbergoceratidae fam. nov. – Ancestral taxa with a triangular whorl profile and a large umbilical foramen. Sculpture with short radial ribs ending in conical ventrolateral nodes. Siphuncle subcentral, close to the venter (Fig. 7).

Trigonoceratidae. – Ancestral taxa with a wide variety of conch shapes ranging from cyrtoconic to more or less tightly coiled. Early juvenile whorl profile depressed oval. Internal lobe shallow, broadly rounded (Fig. 8).

Thrincoceratidae. – Derived taxa with a usually evolute conch shape. Early juvenile whorl profile nearly circular. Internal lobe shallow, broadly rounded (Fig. 9).

Temnocheilidae. – Derived taxa with a subevolute or evolute conch shape. Early juvenile whorl profile strongly depressed oval. Internal lobe deep, funnel-shaped or subtriangular (Fig. 10).

The superfamily Trigonoceratoidea differs from the superfamily Koninckioceratoidea in the shape of the whorl profile, which is triangular or trapezoidal with a flat venter in the ancestral Trigonoceratoidea, but simply oval in the Koninckioceratoidea. In addition, the shell of the Trigonoceratoidea is decorated with coarse, long ridges, whereas that of the Koninckioceratoidea is almost smooth.

Fig. 7. Family Dasbergoceratidae fam. nov. *Dasbergoceras alternans* (Tietze, 1871), from Dzik & Korn (1992). Scale bar units = 1 mm.

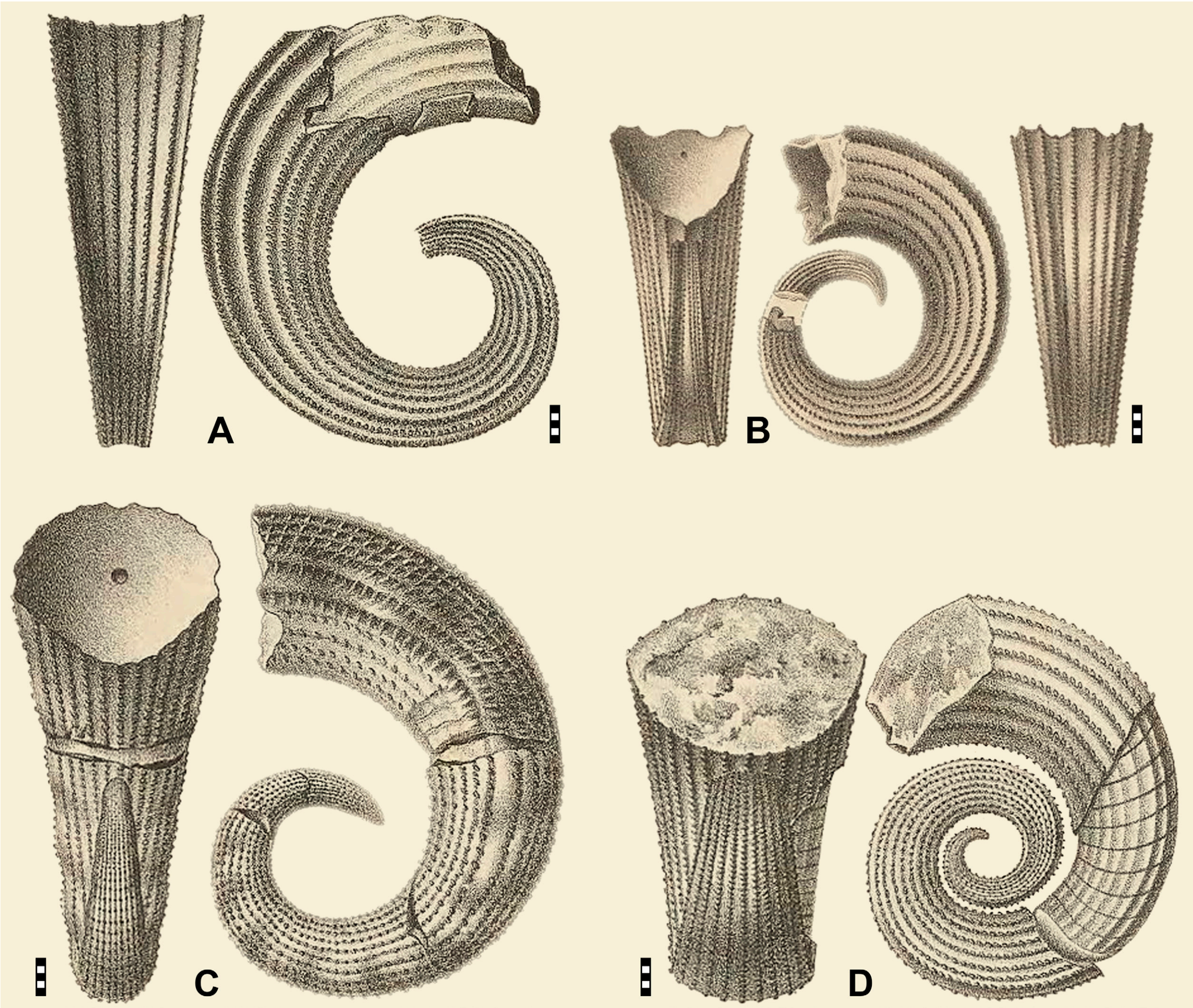

Fig. 8. Representatives of the subfamily Trigonoceratinae Hyatt, 1884; all from de Koninck (1880). **A**. *Triboloceras consobrinum* (de Koninck, 1880). **B**. *Triboloceras serratum* (de Koninck, 1844). **C**. *Rineceras tesselatum* (de Koninck, 1880). **D**. *Rineceras propiquum* (de Koninck, 1880). Scale bar units = 1 mm.

Fig. 9. Family Thrincoceratidae Ruzhencev & Shimansky, 1954. *Thrincoceras hyatti* Foord, 1900, from Foord (1900). Scale bar units = 1 mm.

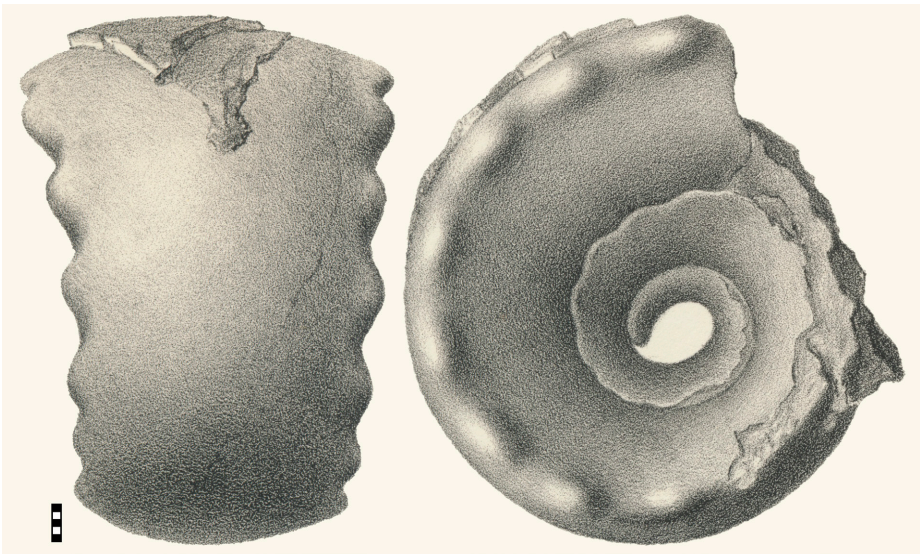

Fig. 10. Family Temnocheilidae Mojsisovics, 1902. *Temnocheilus coronatus* (M‘Coy, 1844), from Foord (1900). Scale bar units = 1 mm.

Family **Dasbergoceratidae** fam. nov.
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Fig. 7

Type genus

Dasbergoceras Dzik & Korn, 1992.

Diagnosis

Family of the superfamily Trigonoceratoidea with a subevolute conch with very small whorl overlap; large umbilical foramen. Whorl profile in the adult stage rounded trapezoidal and depressed oval in the early juvenile stage. Ornament with transverse ribs. Position of the siphuncle closer to the venter than to the centre. Suture line with broadly rounded shallow lobes and low saddles.

Etymology

The family name refers to the type genus.

Included genus

Dasbergoceras Dzik & Korn, 1992 (Famennian; 1 species).

Remarks

Dzik & Korn (1992) devoted a separate paper to the genus *Dasbergoceras* (Fig. 7), discussing the importance of this Late Devonian genus as a link between Devonian and Carboniferous curved and coiled nautiloids. Apparently, no other material has been described since. Therefore, the question of whether *Dasbergoceras* is a direct ancestor of the Carboniferous Trigonoceratoidea or whether it is a side branch of the Trigonoceratoidea cannot be answered unequivocally. *Dasbergoceras* has morphological peculiarities that distinguish it from all other genera of the Trigonoceratoidea. These include the subventrally located siphuncle and the radial ribbing. For this reason, an independent family Dasbergoceratidae fam. nov. is proposed here.

Family **Trigonoceratidae** Hyatt, 1884

Diagnosis

Family of the superfamily Trigonoceratoidea with cyrtoconic to subevolute conch with small whorl overlap if present; large or moderately large umbilical foramen. Whorl profile in the adult stage commonly ranging from triangular to depressed oval, rarely compressed oval or polygonal. Whorl profile usually depressed oval in the early juvenile stage. Ornament with longitudinal ridges or lines, rarely transverse ribs; sometimes the conch is smooth. Position of the siphuncle closer to the centre than to the ventral side. Suture line with broadly rounded shallow lobes and low saddles.

Included subfamilies

Trigonoceratinae Hyatt, 1884 (Early Carboniferous to Early Permian; 7 genera, 38 species).
Chouteauoceratinae subfam. nov. (Early Carboniferous to ? Early Permian; 3 genera, 5 species).
Vestinautilinae subfam. nov. (Early Carboniferous; 3 genera, 29 species).

Remarks

Flower & Kummel (1950: 615) combined the families Triboloceratidae, Trigonoceratidae and Rineceratidae of Hyatt and gave priority to the first of these. Following the idea of Shimansky (1962), the family Trigonoceratidae is divided into several subfamilies here, which differ in the following morphological characteristics:

Trigonoceratinae. – Whorl profile triangular, sculpture with very coarse longitudinal ridges (Fig. 11).

Chouteauoceratinae subfam. nov. – Whorl profile compressed oval, sculpture with numerous longitudinal ridges of the same strength (Fig. 12).

Vestinautilinae subfam. nov. – Whorl profile rounded trigonal or rounded trapezoidal, sculpture with a few coarse longitudinal ridges, usually of different strength (Fig. 13).

Subfamily **Trigonoceratinae** Hyatt, 1884
Fig. 11

Diagnosis

Subfamily of the family Trigonoceratidae with cyrtoconic to evolute or subevolute conch. Whorl overlap small if present. Whorl profile ranging from triangular to depressed oval. Venter flat or rounded. Sculpture in the early species with longitudinal, equidistant ridges throughout ontogeny; advanced species with reduction of spiral ridge number. Suture line with broadly rounded lobes and saddles.

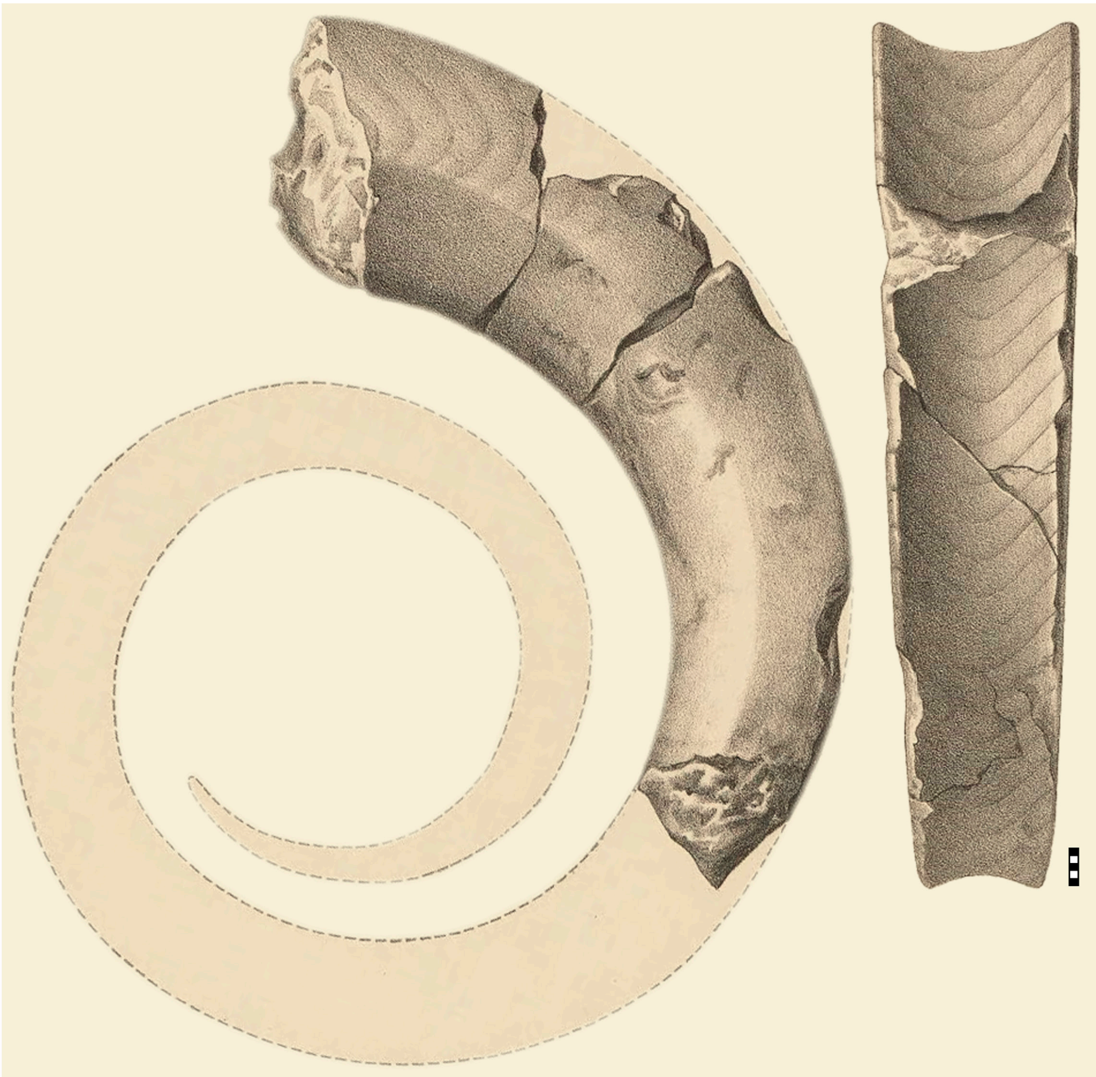

Fig. 11. Subfamily Trigonoceratinae Hyatt, 1884. *Trigonoceras paradoxicum* (Sowerby, 1823), from de Koninck (1880). Scale bar units = 1 mm.

Included genera

Trigonoceras M'Coy, 1844 (Tournaisian to Viséan; 3 species).
Discites M'Coy, 1844 [non Schlotheim, 1813, nec De Haan, 1825; synonym of *Discitoceras*].
Nautiloceras d'Orbigny, 1849 (Tournaisian; 1 species).
Tribolоceras Hyatt, 1884 (Tournaisian to Viséan; 11 species).
Discitoceras Hyatt, 1884 (Tournaisian; 4 species).
Rineceras Hyatt, 1893 (Tournaisian to Viséan; 17 species).
Rhineceras Hyatt, 1900 [synonym of *Rineceras*].
Apogonoceras Ruzhencev & Shimansky, 1954 (Artinskian; 1 species)?
Pararineceras Turner, 1954 [synonym of *Rineceras*].
Strobоrineceras Korn & Bockwinkel, 2022 (Tournaisian to Viséan; 4 species).

Remarks

The cardinal character of the representatives of the subfamily Trigonoceratidae seems to be the slightly depressed oval whorl profile in the early ontogenetic stage and the approximately equidistantly arranged spiral ridges, which are equally developed on the venter as well as on the flanks and dorsum.

The general conch shape is very variable, ranging from cyrtoconic (*Trigonoceras*) to gyroconic (*Tribolоceras*) and advolute (some species of *Tribolоceras* and *Rineceras*) to evolute (most species of *Rineceras*). Almost all species have a more or less triangular or trapezoidal whorl profile.

Subfamily **Chouteauoceratinae** subfam. nov.
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Fig. 12

Type genus

Chouteauoceras Miller & Garner, 1953

Diagnosis

Subfamily of the family Trigonoceratidae with cyrtoconic or gyroconic conch. Whorl profile compressed oval; venter rounded. Sculpture in the early species with longitudinal, equidistant ridges throughout ontogeny; advanced species with a reduction of spiral ridges. Suture line with broadly rounded lobes and saddles.

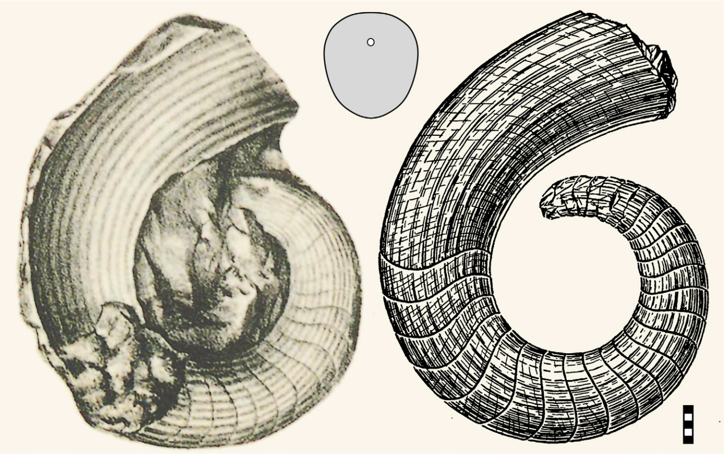

Fig. 12. Subfamily Chouteauoceratinae subfam. nov. *Chouteauoceras americanum* (Miller & Furnish, 1939), from Miller & Furnish (1939) and Miller & Garner (1953). Scale bar units = 1 mm.

Etymology

The subfamily name refers to the type genus.

Included genera

Chouteauoceras Miller & Garner, 1953 (Tournaisian; 3 species).
Ungeroceras Sturgeon & Miller, 1948 (Moscovian; 1 species).
Parachouteauoceras Niko & Ozawa, 1997 (Gzhelian or Asselian; 1 species).

Remarks

The subfamily Chouteauoceratinae subfam. nov. contains genera that are not very well known. It is therefore uncertain whether the other two genera, in addition to the typical genus *Chouteauoceras*, are members of this subfamily. This is particularly true for the enigmatic Late Carboniferous genus *Ungeroceras*, newly described by Sturgeon & Miller (1948). This genus was synonymised by Murphy (1966) with the orthoconic genus *Kionoceras* Hyatt, 1884. Sturgeon *et al.* (1997: 57) discussed the genus, concluding that it is probably a coiled nautiloid, possibly related to the stratigraphically older Tournaisian genus *Chouteauoceras* (Miller & Garner 1953). Loose coiling and a compressed whorl profile are accepted as the most important criteria (Fig. 12). However, further research and new material may substantiate this hypothesis.

Subfamily **Vestinautilinae** subfam. nov.

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Fig. 13

Type genus

Vestinautilus Ryckholt, 1852.

Diagnosis

Subfamily of the family Trigonoceratidae with discoidal to pachyconic, subevolute conch. Whorl overlap small. Whorl profile usually rounded triangular or rounded trapezoidal. Venter broadly rounded, flattened or weakly concave. Ornament with longitudinal ridges in most species; younger species show a reduction of the spiral ridges. Suture line with rounded external and lateral lobes, internal lobe shallow.

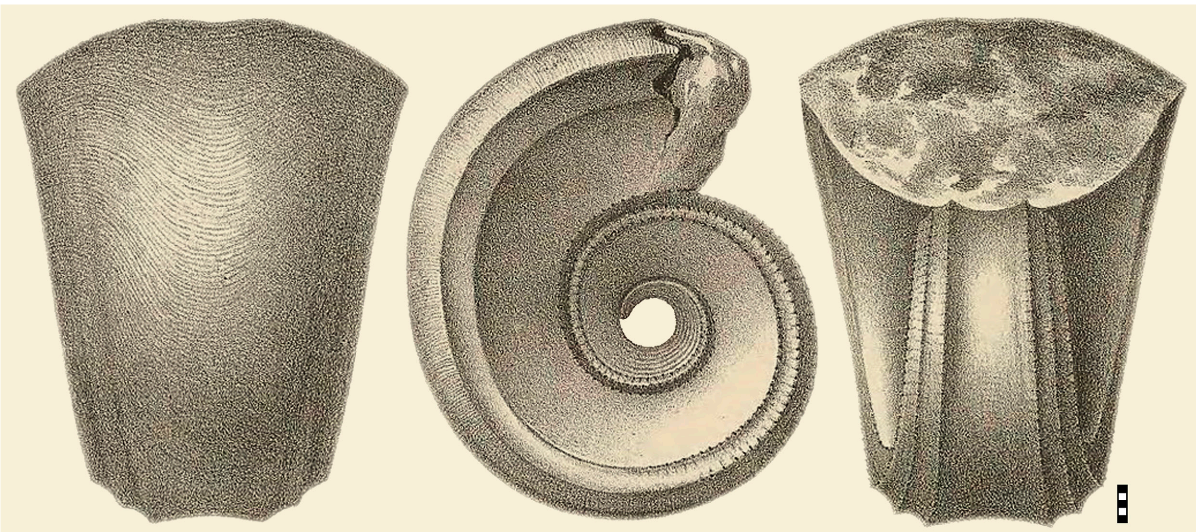

Fig. 13. Subfamily Vestinautilinae subfam. nov. *Vestinautilus koninckii* (d'Orbigny, 1847), from de Koninck (1878). Scale bar units = 1 mm.

Etymology

The subfamily name refers to the type genus.

Included genera

Vestinautilus Ryckholt, 1852 (Tournaisian to Viséan; 20 species).
Edaphoceras Hyatt, 1884 (Viséan; 2 species).
Subvestinautilus Turner, 1954 (Tournaisian to Viséan; 7 species).

Remarks

The Vestinautilinae subfam. nov. are a subfamily that can be easily distinguished from the other subfamilies by their characteristic morphology with a rounded triangular or rounded trapezoidal whorl profile and the presence of coarse longitudinal ridges (Fig. 13).

The origin of the Vestinautilinae subfam. nov. is probably to be found in the subfamily Trigonoceratinae. The stratigraphically oldest species of *Vestinautilus* from the early Late Tournaisian have a conch morphology and shell ornamentation that still closely resemble species from genera such as *Triboloceras* and *Rineceras*. The Vestinautilinae show a morphological evolution with a progressive reduction in the number of longitudinal ridges. These are largely restricted to the ventrolateral shoulder in the younger species. At the same time, the venter changes from a concave to a convex shape.

Family **Thrincoceratidae** Ruzhencev & Shimansky, 1954

Fig. 9

Diagnosis

Family of the superfamily Trigonoceratoidea with discoidal, subevolute to evolute conch; whorl overlap small if present, coiling rate high to extremely high. Whorl profile almost circular in the early juvenile stage. Ornament in the early species with longitudinal, equidistant ridges throughout ontogeny; advanced species with reduction of spiral lines. Suture line with broadly rounded lobes and saddles.

Included genera

Thrincoceras Hyatt, 1893 (Tournaisian to Viséan; 8 species).
Lispoceras Hyatt, 1893 (Tournaisian to Serpukhovian; 5 species).
Diodoceras Hyatt, 1900 (Tournaisian; 1 species).
Neothrincoceras Ruzhencev & Shimansky, 1954 (Artinskian; 3 species).

Remarks

Ruzhencev & Shimansky (1954) established the family Thrincoceratidae for the genera *Thrincoceras*, *Maccoyoceras* and *Neothrincoceras* and had "not the slightest doubt" that this family and the "closely related" family Domatoceratidae Miller & Youngquist, 1949 descended from common ancestors, and not directly from each other (Ruzhencev & Shimansky 1954: 51). A little later, Shimansky (1962) classified the group only as a subfamily with the genera *Discitoceras*, *Stroboceras*, *Thrincoceras*, *Maccoyoceras* and *Epistroboceras* Turner, 1954, while *Neothrincoceras* was placed in the family Neothrincoceratidae within the superfamily Centrocerataceae. Another five years later, Shimansky (1967: 168) reduced the subfamily to the genera *Thrincoceras* and *Neothrincoceras*.

Kummel (1964: K427) considered both the Thrincoceratidae and the Neothrincoceratidae to be synonyms of the Trigonoceratidae. Histon (1999) also included the genus *Thrincoceras* in the Trigonoceratidae. Dzik (1984: 172) included *Thrincoceras*, together with *Discitoceras*, *Pararineceras* and *Maccoyoceras* in *Lispoceras* within the family Trigonoceratidae.

Family **Temnocheilidae** Mojsisovics, 1902
Fig. 10

Diagnosis

Family of the superfamily Trigonoceratoidea with subinvolute or subevolute conch; coiling rate usually very high. Whorl overlap small if present. Adult whorl profile commonly ranging from triangular to trapezoidal with weakly embracing whorls; juvenile whorl profile broadly oval or bicarinate. Ornament with longitudinal ridges or lines in the juvenile stage, adult conch with ventrolateral nodes, spiral ridges or smooth, sometimes with spiral ornament. Position of the siphuncle between centre and venter. Suture line with broadly rounded external and lateral lobes; internal lobe broadly V-shaped; sometimes with an annular process.

Included genera

Temnocheilus M'Coy, 1844 (Viséan to Kasimovian; 10 species).
Endolobus Meek & Worthen, 1865 (Viséan to ? Roadian; 14 species).
Knightoceras Miller & Owen, 1934 (Viséan to Artinskian; 9 species).
Tylodiscoceras Miller & Collinson, 1950 (Serpukhovian; 2 species).
Valhallites Shimansky, 1954 (Viséan to ? Artinskian; 8 species).
Nikenautilus Shimansky, 1962 (Serpukhovian; 2 species).
Kummeloceras Shimansky, 1967 (Artinskian; 1 species).
Temnocheiloides Shimansky, 1967 (Bashkirian to Moscovian; 2 species).
Latitemnocheilus Sturgeon, Windle, Mapes & Hoare, 1982 (Serpukhovian to Asselian; 9 species).
Paravalhallites Shimansky, 1990 (Bashkirian; 1 species).
Alexoceras Leonova & Shchedukhin, 2020 (Asselian or Sakmarian; 1 species).

Remarks

The Temnocheilidae is a family that has been defined in various ways over the years. Originally, it was placed by Mojsisovics (1902: 230) as the fourth family within his higher taxon "Nautilidae" and contained a number of morphologically very different genera such as *Temnocheilus* M'Coy, 1844, *Metacoceras* Hyatt 1883, *Tainoceras* Hyatt 1883, *Foordiceras* Hyatt, 1893, *Pleuronautilus* Hyatt, 1900 and *Germanonautilus* Mojsisovics, 1902. It should be noted that the concept of the family had a different meaning at that time than it does today. Later the family Temnocheilidae was largely ignored and *Temnocheilus* was usually placed in the family Tainoceratidae. Turner (1954) then redefined the family, pointing out the close relationship between *Temnocheilus* and the newly described genus *Subvestinautilus*.

Kummel (1964) did not accept the validity of the family and considered it a synonym of the Koninckioceratidae Hyatt, 1900. This family contained a rather heterogeneous list of genera; *Temnocheilus* stood next to *Millkoninckioceras* Kummel, 1963, *Endolobus* Meek & Worthen, 1865, *Planetoceras* Hyatt, 1893, *Foordiceras* Hyatt, 1893 and *Tylodiscoceras* Miller & Collinson, 1950. In contrast, Shimansky (1967, 1979) distinguished the families Temnocheilidae and Koninckioceratidae; he even considered both groups to be independent superfamilies, each containing only one family. Dzik (1984) placed *Temnocheilus* and related genera in the family Trigonoceratidae and Histon (1999) followed Kummel (1964) in placing *Temnocheilus* in the family Koninckioceratidae.

The typical early representatives of the Temnocheilidae are known from Tournaisian and Viséan strata (Fig. 10), and it is not certain that stratigraphically younger genera really belong to the same group. This is particularly true for the records of *Temnocheilus*-like genera from Late Carboniferous strata of North America, which have usually been placed in the genera *Temnocheilus* and *Latitemnocheilus*. This is also true for *T. annulonodosus* Sturgeon, Windle, Mapes & Hoare, 1982, in which Sturgeon *et al.* (1982)

found the internal lobe to be broadly rounded and shallow with a small annular lobe. However, in Viséan representatives of *Temnocheilus* the internal lobe is broadly V-shaped (Korn & Klug 2023).

It seems worth discussing whether the supposed Late Carboniferous temnocheilids are in fact derived from Early Carboniferous species, or whether they have arisen independently, e.g., by regression of a previously present umbilical margin. Since this cannot be resolved here, these species are provisionally and cautiously placed in the family Temnocheilidae.

Both Turner (1954) and Dzik (1984) suggested that *Temnocheilus* was derived from *Vestinautilus*. The main argument for this was the similar conch geometry; the longitudinal ridges were said to have been transformed into a ventrolateral row of nodes. For this reason, the genera *Vestinautilus* and *Subvestinautilus* are considered here to be the ancestors of the family Temnocheilidae. The material now available allows the reconstruction of a very plausible evolutionary lineage, leading from species of the Trigonoceratidae with conchs completely ornamented with longitudinal lines or ridges (e.g., *Rineceras*) with an increasing reduction of the number of these spiral elements to almost unornamented conchs (e.g., *Knightoceras*).

The position of the genus *Endolobus* has not yet been fully resolved. While Kummel (1964) placed it in the family Koninckioceratidae, Shimansky (1967, 1979) placed it in the family Temnocheilidae. Dzik (1984) saw *Endolobus* as derived from *Vestinautilus* in a parallel evolutionary lineage to *Temnocheilus*. Indeed, the rather narrow and deep internal lobe in *Endolobus* can be seen as a good indicator for a placement within the Temnocheilidae.

Superfamily **Koninckioceratoidea** Hyatt, 1900

Diagnosis

Superfamily of the suborder Temnocheilina, in which the whorl profile shows only minor changes during ontogeny. Conch usually discoidal, subinvolute to evolute. Whorl profile elliptical or almost circular throughout ontogeny. Adult whorl profile depressed oval. Without coarse sculpture. Suture line with shallow lobes and saddles; internal lobe absent or very shallow.

Included family

Koninckioceratidae Hyatt, 1900 (Early Carboniferous to Early Permian; 2 genera, 17 species).

Remarks

Depending on the researcher, the koninckioceratids are a group that has been variously assigned to different phylogenetic lineages. Shimansky (1957, 1962) accepted them as a family within the superfamily Liroceratаceae with the genera *Koninckioceras* Hyatt, 1884, *Lophoceras* Hyatt, 1893 and *Planetoceras* Hyatt, 1893. Later Shimansky (1967, 1979) elevated them to a superfamily within the suborder Rutoceratina, composed of a single family containing the three genera mentioned above.

Kummel (1963, 1964) accepted the koninckioceratids as a family within the Tainocerataceae and included eleven genera (*Millkoninckioceras* Kummel, 1963, *Endolobus* Meek & Worthen, 1865, *Foordiceras* Hyatt, 1893, *Knightoceras* Miller & Owen, 1934, *Subvestinautilus* Turner, 1954, *Temnocheilus* M‘Coy, 1844 and *Tylodiscoceras* Miller & Collinson, 1950); in other words, he combined the koninckioceratids and some of the temnocheilids into one taxon.

The superfamily Koninckoceratoidea is still poorly understood. There are several reasons for this, based on the general rarity and limited morphological inventory. Probably only one specimen of the type species of *Millkoninckioceras* is known, and other species, such as the Early Permian *M. bibbi* (Miller & Kemp, 1947), can only be placed in the genus with reservations. Typically, Carboniferous and Permian nautiloids with a wide umbilicus and a depressed oval whorl profile have been assigned to *Millkoninckioceras* or morphologically similar genera.

The simple morphology (Fig. 14) of the species within the group makes a phylogenetic reconstruction difficult. One hypothesis for their origin is that they descended from fully coiled species in the superfamily Trigonoceratoidea with initially slightly depressed juvenile conchs. However, in contrast to the other evolutionary lineages, there was no ontogenetic change in conch geometry with the formation of a ventrolateral shoulder or an umbilical margin in the koninckioceratids. Instead, members of the Koninckioceratoidea retained the simple juvenile morphology even in the intermediate and adult growth stages.

The species of the superfamily Koninckioceratoidea are distinguished from other Late Palaeozoic nautiloids by their very simple conch morphology, with a wide umbilicus and an unsculptured shell. In contrast to almost all other coiled nautiloids, the conch shows almost no ontogenetic changes.

Family **Koninckioceratidae** Hyatt, 1900
Fig. 14

Diagnosis

Family of the superfamily Koninckioceratoidea with discoidal, subevolute to evolute conch. Whorl profile depressed oval without ventrolateral shoulder or umbilical margin. Dorsal whorl zone always very

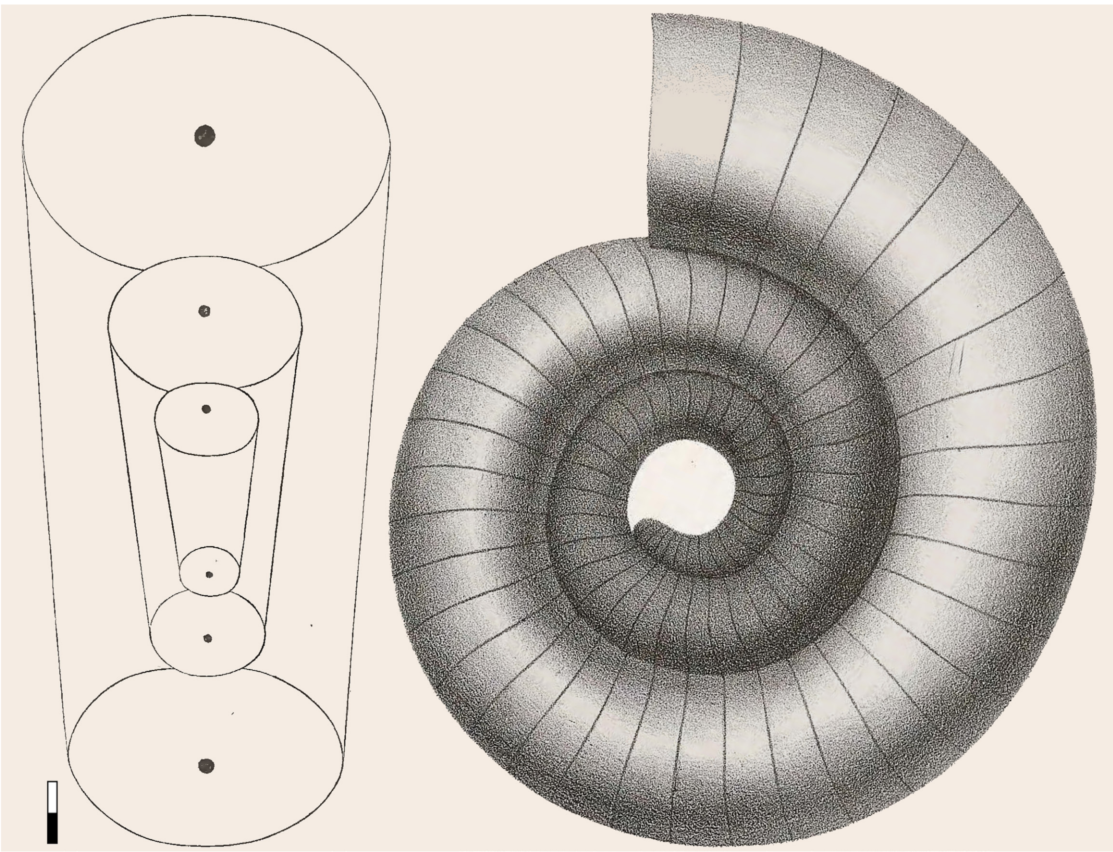

Fig. 14. Family Koninckioceratidae Hyatt, 1900. *Millkoninckioceras konincki* (Miller & Kemp, 1947), from de Koninck (1878). Scale bar units = 5 mm.

small. Shell surface usually not sculptured. Suture line is almost straight or with small lobes and saddles on the outer side of the whorl, with a rounded or funnel-shaped internal lobe. Siphuncle subcentral.

Included genera

Lophoceras Hyatt, 1893 (Viséan to Serpukhovian; 8 species).
Koninckioceras Hyatt, 1884 [nomen dubium].
Koninckoceras Hyatt, 1900 [nomen nullum].
Millkoninckioceras Kummel, 1963 (Viséan to Kasimovian; 9 species).

Remarks

Nomenclatural problems within the Koninckioceratidae were discussed in detail by Kummel (1963). The simple morphology of the conch in the Koninckioceratidae is an obstacle to analysing the origin of the group. Based on the conch morphology, an origin from genera such as *Thrincoceras* seems possible. An alternative would be an origin from a gyroconic or an advolute ancestor.

Suborder **Domatoceratina** subordo nov.

Diagnosis

Suborder of the order Nautilida, in which a ventrolateral shoulder and an umbilical margin are formed early in ontogeny. Conch usually discoidal, subinvolute to evolute. Juvenile whorl profile circular. Adult whorl profile subquadrate or inverted trapezoidal with a distinct ventrolateral shoulder and a distinct umbilical margin in the early species, showing modifications during evolution including a concave venter in some derived species. Dorsal whorl zone always present, but usually very small except for some derived species. Juvenile sculpture sometimes with radial ribs on the flank; adult sculpture is usually lacking except for elongate ventrolateral tubercles in derived species. Septa simply domed in most of the species, with septal inflexion in and corrugated septa in some lineages. Suture line usually depending on the whorl profile, usually with shallow lobes and low saddles, and with distinct lobes in one clade. Siphuncle in central or subcentral position.

Included superfamilies

Grypoceratoidea Hyatt, 1900 (Early Carboniferous to Late Triassic; 22 Palaeozoic genera, 91 Palaeozoic species).
Permoceratoidea Miller & Collinson, 1953 (Early Permian; 2 genera, 2 species).
Subclymenioidea Shimansky, 1962 (Early to Late Carboniferous; 16 genera, 108 species).

Remarks

Taxonomy

Flower & Kummel (1950) placed the Domatoceratidae in the order Centroceratida; the family was interpreted to have descended directly from the family Centroceratidae, and the domatoceratids in turn gave rise to the family Syringonautilidae. Shimansky (1957) had a similar view. He placed the family Domatoceratidae together with the families Centroceratidae, Grypoceratidae, Thrincoceratidae, Syringonautilidae and Permoceratidae in the superfamily Centrocerataceae. The origin of the suborder Domatoceratina subordo nov. was there interpreted to be in the family Centroceratidae. In contrast, Kummel (1964) placed the family Grypoceratidae, in which he included the domatoceratids, in the superfamily Trigonocerataceae. The families Syringonautilidae and Permoceratidae should have been evolved from the Grypoceratidae.

Dzik (1984) presented a very different concept for the family Grypoceratidae; he considered many previously accepted genera to be synonyms and included the genera *Epidomatoceras*, *Stroboceras*, *Subclymenia* and *Permoceras* in the family Grypoceratidae. On the other hand, he placed the genus *Stenopoceras* Hyatt, 1893, previously placed in Domatoceratidae, in the family Phacoceratidae.

Here, the suborder Domatoceratina subordo nov. is separated to include a group of nautilids that appears to be a monophylum, which has an origin in Early Carboniferous trigonoceratids (Dzik 1984), and, therefore, a combination with the Middle Devonian centroceratids is rejected. The suborder is characterised by a rather distinct set of characters. Most importantly, a ventrolateral shoulder and an umbilical margin are formed early in ontogeny (Fig. 3B–C, G–H). This character, together with flattened flanks and a flattened or concave venter, is maintained throughout the evolutionary history of the suborder. Only occasionally, these characters were regressed in side branches.

Morphology and subdivision

The species of Domatoceratina subordo nov. are usually easily recognisable as belonging to the suborder on the basis of their conch morphology and ornamentation. Apart from a few early representatives and some species in advanced side branches, all species are characterised by flattened flanks and an applanate or a more or weakly concave venter. The ventrolateral shoulder is usually subangular or angular and, in some species, skid-like reinforced. Another characteristic of Domatoceratina is the almost complete absence of coarse sculpture.

The following superfamilies are distinguished here:

Subclymenioidea. – Forms with usually quadrate whorl profile with a flattened or concave venter; sculpture absent or with inconspicuous ribs on the flank. Septa sometimes with a ventral inflexion causing a distinct external lobe.

Grypoceratoidea. – Forms with usually quadrate or inverted trapezoidal whorl profile with a more or less strongly flattened or concave venter; sculpture absent or with inconspicuous ribs on the flank.

Permoceratoidea. – Forms with inverted trapezoidal whorl profile with a more or less strongly flattened venter; sculpture absent or with inconspicuous ribs on the flank. Septa corrugated, causing distinct lobes and saddles.

Origin

Dzik (1984: 168) proposed an origin of the grypoceratids from the Early Carboniferous *Epidomatoceras*. He saw *Domatoceras*, the stratigraphically oldest genus of the superfamily, as a direct descendant of *Epidomatoceras* from the Viséan.

Epidomatoceras and the family Subclymeniidae are probably derived from the Thrincoceratidae via the morphologically basal genus *Maccoyoceras*. The formation of the umbilical margin and ventrolateral shoulder could be considered as a new feature for the evolutionary lineage to the domatoceratids.

Phylogeny

Dzik (1984: 168) published a detailed diagram of the proposed phylogenetic relationships within the domatoceratids in the broader sense. Two major lineages can be seen in this diagram. The main lineage extends from *Epidomatoceras* via *Domatoceras* to the Triassic families Grypoceratidae and Syringonautilidae; a secondary lineage branches off from the first and extends via the Late Carboniferous *Titanoceras* Hyatt, 1884 and the Late Permian *Pseudotitanoceras* Shimansky, 1965 to the Triassic genus *Germanonautilus* Mojsisovics, 1902.

Descendants

Shimansky (1957) derived the modern nautiloids (order Nautilina) from the family Domatoceratidae Miller & Youngquist, 1949. Kummel (1964) had a similar view and derived his superfamily Nautilaceae de Blainville, 1825 from the family Domatoceratidae via the family Syringonautilidae Mojsisovics, 1902. Dzik (1984: 175) postulated a continuous evolutionary transition from the Triassic genus *Syringonautilus*

Mojsisovics, 1902 to the Jurassic genus *Cenoceras* Hyatt, 1884. According to the current state of knowledge, two further suborders can be derived from the Domatoceratina subordo nov.

Superfamily **Subclymenioidea** Shimansky, 1962

Diagnosis

Superfamily of the suborder Domatoceratina subordo nov. with discoidal, subinvolute to evolute conch. Whorl profile often subquadrate to polygonal, usually with distinct ventrolateral shoulder and distinct umbilical margin. Derived species show a variation of modifications including a concave or acute venter or an angular or skid-like ventrolateral shoulder. Whorl overlap extremely small to moderate. Sculpture in most species lacking. Septa simply domed but with ventral inflexion in derived species. Suture line usually depending on the whorl profile, with shallow to deep external lobe.

Included families

Apheleceratidae Hyatt, 1893 [nomen nullum].
Subclymeniidae Shimansky, 1962 (Early to Late Carboniferous; 6 genera, 59 species).
Phacoceratidae Shimansky, 1962 (Early to Late Carboniferous; 6 genera, 13 species).
Aphelaeceratidae Shimansky, 1962 [synonym of Subclymeniidae].
Epistroboceratidae fam. nov. (Early to Late Carboniferous; 4 genera, 36 species).

Remarks

The superfamily Subclymenioidea shows a wide range of conch morphologies and sculptures and is therefore difficult to define on the basis of adult morphology. The reason for this is a rapid morphological evolution during the Late Tournaisian and Early Viséan, which produced a high diversity of conch shapes and sculptures known from only a few other clades of nautilids. The common feature of all species is the shape of the whorl profile in the juvenile stage, characterised by sharp longitudinal ridges on a raised umbilical margin.

Three evolutionary lineages can be assumed to form the superfamily Subclymenioidea:

Epistroboceratidae fam. nov. – Forms that retained the polygonal shaped whorl profile once acquired; the whorl profile became more and more compressed during evolution. Whorl profile variable, usually polygonal, sculpture with few very coarse longitudinal ridges of different strength (Fig. 15).

Subclymeniidae Shimansky, 1962. – Forms that developed a flattened or more or less deeply concave venter. Suture line with rather deep external lobe that was caused by a septal inflexion (Fig. 16).

Phacoceratidae Shimansky, 1962. – Forms that developed an extremely compressed whorl profile with a sharp venter (Fig. 17).

Family **Epistroboceratidae** fam. nov.
urn:lsid:zoobank.org:act:88B59168-C65F-4FA4-832A-4E10A6FD9BF9
Fig. 15

Type genus

Epistroboceras Turner, 1954.

Diagnosis

Family of the superfamily Subclymenioidea with usually subevolute conch. Whorl overlap very small. Whorl profile ranging from moderately depressed to moderately compressed, usually with polygonal shape. Venter usually flat. Sculpture with coarse longitudinal ridges and grooves. Suture line with broadly rounded lobes and saddles, strongly dependent on the shape of the whorl profile.

Etymology

The subfamily name refers to the type genus.

Included genera

Stroboceras Hyatt, 1884 (Tournaisian to Bashkirian; 15 species).
Epistroboceras Turner, 1954 (Tournaisian to Serpukhovian; 18 species).
Imonautilus Niko & Mapes, 2007 (Serpukhovian; 1 species).
Trilobitoceras Korn & Bockwinkel, 2022 (Tournaisian; 2 species).

Remarks

The genera *Stroboceras* and *Epistroboceras* have been placed in different families or subfamilies by various authors. Miller & Garner (1953) placed *Stroboceras* in the family Rineceratidae; they derived *Stroboceras* from *Discitoceras*: "*Discitoceras* most probably also gave rise to *Stroboceras* by certain of its longitudinal ridges becoming very large at the expense of others. *Stroboceras*…" (Miller & Garner 1953: 116). Turner (1954) revised *Stroboceras* and proposed the new genus *Epistroboceras*; he placed both in the family Triboloceratidae.

Shimansky (1962) placed *Stroboceras* and *Epistroboceras* in the subfamily Thrincoceratidae and later changed his mind (Shimansky 1967: 134) to assign both genera in the Trigonoceratinae. Earlier, Kummel (1964) had already included both genera in the Trigonoceratidae, without distinguishing between subfamilies. Turner (1965) included *Stroboceras* and *Epistroboceras* in the Thrincoceratinae.

Dzik (1984: 173–174) had a different concept and considered the genera *Stroboceras* and *Epistroboceras* to be not closely related and placing *Stroboceras* in the Grypoceratidae and *Epistroboceras* (as a junior synonym of *Aphelaeceras* Hyatt, 1884) in the Phacoceratidae. Histon (1999) followed Kummel (1964) and considered *Epistroboceras* to be a representative of the Trigonoceratidae.

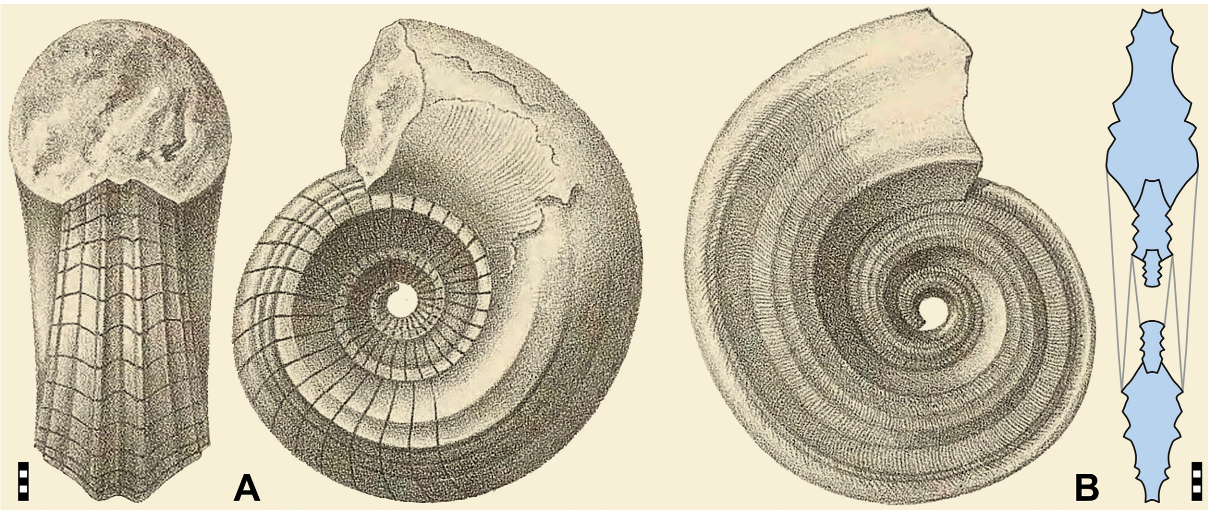

Fig. 15. Representatives of the family Epistroboceratidae fam. nov., both from de Koninck (1878). **A**. *Stroboceras sulciferum* (Leveille, 1835). **B**. *Epistroboceras bisulcatum* (M'Coy, 1844). Scale bar units = 1 mm.

Here, the stroboceratids are distinguished as a separate family, characterised by the presence of prominent longitudinal ridges, which in many species cause a polygonal outline to the whorl profile (Fig. 15). These ridges can be seen as a transfer of the early juvenile sculpture to the adult conch. During phylogeny, these ridges have been secondarily reduced, and in the families Subclymeniidae and Phacoceratidae they are present only in the juvenile stage. Therefore, these are also included in the superfamily Grypoceratoidea.

Family **Subclymeniidae** Shimansky, 1962
Fig. 16

Diagnosis

Family of the superfamily Subclymenioidea with a discoidal, subinvolute to evolute conch; whorl overlap usually very small, coiling rate ranging from moderately high to extremely high. Whorl profile often with a distinct ventrolateral shoulder, a weakly convex, flat or concave venter and a rounded or subangular umbilical margin. Ornament in the early species with spiral lines in the juvenile and preadult stage; advanced species show the reduction of spiral lines. Siphuncle close to the venter. Suture line with a shallow to deep, broadly rounded or V-shaped external lobe that is produced by a ventral inflexion of the septum.

Included genera

Subclymenia d'Orbigny, 1849 (Viséan to Serpukhovian; 7 species).
Aphelaeceras Hyatt, 1884 (Tournaisian to Serpukhovian; 10 species).
Mesochasmoceras Foord, 1900 (Tournaisian; 1 species).
Maccoyoceras Miller, Dunbar & Condra, 1933 (Tournaisian to Viséan; 11 species).
Epidomatoceras Turner, 1954 (Tournaisian to Serpukhovian; 17 species).
Catastroboceras Turner, 1965 (Viséan to Bashkirian; 13 species).
Pseudocatastroboceras Turner, 1965 [synonym of *Catastroboceras*].

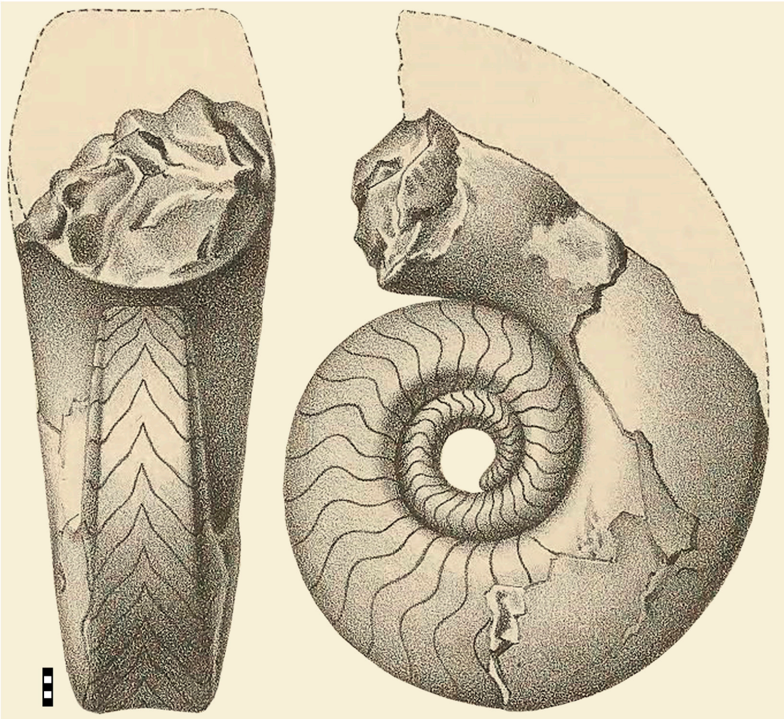

Fig. 16. Subfamily Subclymeniinae Shimansky, 1962. *Subclymenia evoluta* (Phillips, 1836), from de Koninck (1880). Scale bar units = 1 mm.

Remarks

Subclymenia is a remarkable genus because it has a deeply V-shaped external lobe in the suture line (Fig. 16). Unlike many nautiloids, this lobe is not caused by the geometry of the whorl profile alone, but by a ventral inflexion of the septum. Shimansky (1962) based the family Subclymeniidae on this single genus. Kummel (1964) saw *Subclymenia* as a genus belonging to the family Trigonoceratidae and did not accept the family Subclymeniidae.

Turner (1965) downgraded the Subclymeniidae to a subfamily and expanded it to include the genera *Maccoyoceras*, *Epidomatoceras*, *Catastroboceras* and *Pseudocatastroboceras*. He showed that several species of the latter three of these genera also have a slightly angular external lobe. Shimansky (1967: 156) then withdrew the family Subclymeniidae and placed *Subclymenia* in the subfamily Aphelaeceratinae, together with the genera *Aphelaeceras*, *Mesochasmoceras*, *Catastroboceras*, *Epidomatoceras* and *Maccoyoceras*. Dzik (1984: 174) did not accept the systematic independence of a family Subclymeniidae and interpreted *Subclymenia* as a basal representative of the family Grypoceratidae.

In the *Osnovy*, Shimansky (1962) named the subfamily Aphelaeceratinae for the genera *Aphelaeceras* and *Mesochasmoceras* in addition to the family Subclymeniidae. According to the original description by Meek & Worthen (1873: 522), the type species of *Aphelaeceras* has a V-shaped external lobe, indicating that it belongs to the Subclymeniidae. However, it is not clear whether the internal lobe in *Aphelaeceras* is caused by the shape of the whorl profile with a deeply concave venter or by a septal inflexion.

Both Turner (1965) and Shimansky (1967) included *Maccoyoceras* in the subfamily Subclymeniinae. However, typical specimens of *Maccoyoceras* have a broadly rounded external lobe and an almost central siphuncle (Histon 1999); the genus is therefore included here in the Subclymeniidae with reservations.

The Subclymeniidae are treated here as a family because the ventral inflexion of the septum is a very unusual feature. In addition, the position of the siphuncle rather close to the venter is a distinguishing feature from other families in the superfamily Subclymenioidea. The name Subclymeniidae is preferred to Aphelaeceratidae because *Subclymenia* characterises the family much better than *Aphelaeceras*.

In addition to the shape of the septum and the presence of a ventral lobe, a second important feature of the subfamily is the presence of a usually subangular ventrolateral shoulder separating the usually flattened flanks from an equally flattened or concave venter. A third feature is the more or less distinct umbilical margin, which is not present in this form in the other subfamilies of the Trigonoceratidae.

The family Subclymeniidae is not included here in the superfamily Trigonoceratoidea, because its morphological characteristics with a subangular umbilical margin suggests a transitional phylogenetic position leading to the Grypoceratoidea. The close morphological relationship favours placement in the latter superfamily.

Family **Phacoceratidae** Shimansky, 1962
Fig. 17

Diagnosis

Family of the superfamily Subclymenioidea with a usually subinvolute conch; coiling rate usually extremely high; whorl overlap small to moderate. Adult whorl profile extremely compressed with flat flanks and an acute venter. Ornament with longitudinal ridges or lines in the juvenile stage, adult conch smooth or with delicate growth lines. Position of the siphuncle between the centre of the whorl profile and the venter. Suture line without or with a very small external lobe and a broadly rounded lateral lobe.

Included genera

Phacoceras Hyatt, 1884 (Viséan to Serpukhovian; 4 species).
Leuroceras Hyatt, 1893 (Viséan; 1 species).
Diorugoceras Hyatt, 1893 (Viséan to Serpukhovian; 3 species).
Phaceras Teichert & Glenister, 1952 [nomen nullum].
Epiphacoceras Turner, 1966 (Viséan; 1 species).
Askeatonoceras Turner, 1966 (Viséan; 1 species).
Pseudostenopoceras Shimansky, 1967 (Serpukhovian to ? Moscovian; 3 species).

Remarks

The Phacoceratidae are one of the lesser-known families of Carboniferous nautiloids. Kummel (1964) did not accept the family and included *Phacoceras* and similar genera together with some Devonian genera (*Centroceras* Hyatt, 1884, *Carlloceras* Flower & Caster, 1935, *Homaloceras* Whiteaves, 1891, *Strophiceras* Hyatt, 1884) in the family Centroceratidae.

Turner (1966) devoted a special article to the Phacoceratidae and, in discussing their phylogeny, pointed out that some of the genera were monospecific, with type species known from only a few specimens or even only a single specimen. He also saw a close relationship between *Phacoceras* and the Devonian centroceratids and postulated an evolutionary lineage from *Carlloceras* (possibly Late Devonian) through *Diorugoceras* to *Phacoceras*. This scenario is mainly based on the idea that the inverted trapezoidal whorl profile of *Carlloceras* transformed into an oxyconic profile during evolution.

Another hypothesis was proposed by Dzik (1984: 167). He derived the Phacoceratidae, to which he also included the genera *Aphelaeceras* and *Stenopoceras*, from the stroboceratids. This phylogenetic hypothesis is quite plausible, because the morphology of the inner whorl of *Phacoceras* shows a morphology known from *Catastroboceras*, with the pronounced umbilical margin decorated by

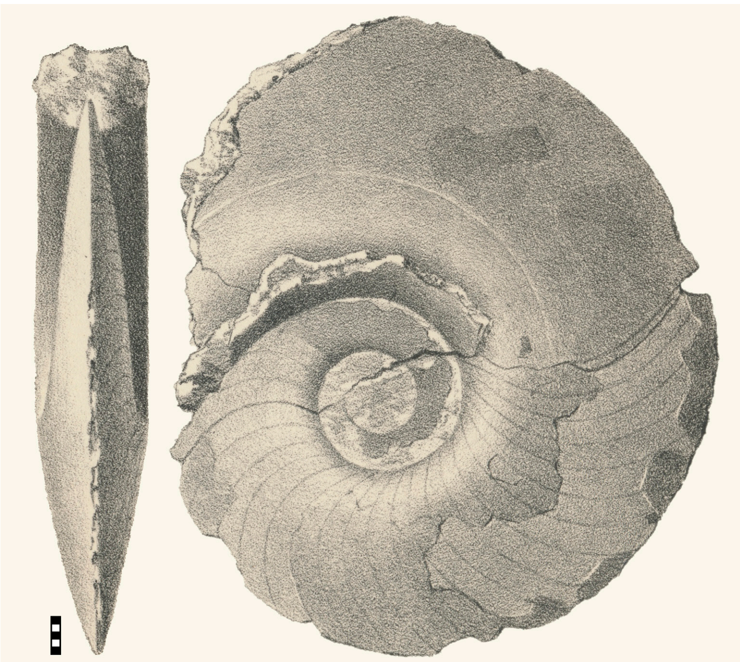

Fig. 17. Family Phacoceratidae Shimansky, 1962. *Phacoceras oxystomum* (Phillips, 1836), from Foord (1900). Scale bar units = 1 mm.

longitudinal ridges, the flattened flanks and the distinct ventrolateral shoulder (Schmidt 1951: pl. 6 fig. 4). It is therefore not necessary to propose a long and hidden evolutionary lineage including survival through the Hangenberg Event, based on poor material.

Poor preservation of type material is a problem when it comes to family composition. The two genera *Epiphacoceras* and *Askeatomoceras* newly described by Turner (1966) and *Diorugoceras* are based on poorly preserved material and are therefore difficult to evaluate.

Superfamily **Grypoceratoidea** Hyatt, 1900

Diagnosis

Superfamily of the suborder Domatoceratina subordo nov. with a discoidal, subinvolute to evolute conch. Whorl profile usually inverted trapezoidal with a distinct ventrolateral shoulder and a distinct umbilical margin. Derived species show a variation of modifications including a concave venter, a skid-like ventrolateral shoulder and an angular umbilical margin. Whorl overlap extremely small to moderate. Sculpture in most species lacking, in some species with short lateral ribs or ventrolateral nodes. Septa simply domed; suture line strongly dependent on the whorl profile, usually with broadly rounded lobes and narrowly rounded or subangular saddles.

Included families

Grypoceratidae Hyatt, 1900 (Early to Late Triassic).
Domatoceratidae Miller & Youngquist, 1949 (Early Carboniferous to Late Permian; 15 genera, 73 species).
Stenopoceratidae fam. nov. (Early to Middle Permian; 3 genera, 11 species).
New family to be described by Korn & Hairapetian (in press) (Late Permian; 4 genera, 7 species).

Remarks

Grypoceras Hyatt, 1883, *Domatoceras* and related genera are characterised by more or less flattened flanks, which are bordered by distinct margins against the venter and the umbilical wall (Fig. 18). Usually, the ventrolateral shoulder is more strongly pronounced than the umbilical margin, being subangular, angular or even raised to form skid-like extensions. A whorl profile with both a pronounced umbilical margin and also a pronounced ventrolateral shoulder is already present in the juvenile conch, i.e., at the end of the first whorl. In this respect, *Domatoceras* and related genera are similar to the metacoceratids. It is worth considering whether these two groups are closely related.

Three Carboniferous and Permian families, which represent evolutionary lineages, can be assigned to the superfamily Grypoceratoidea:

Domatoceratidae Miller & Youngquist, 1949. – Forms that retained usually inverted trapezoidal whorl profile throughout their evolutionary history (Fig. 19).

Stenopoceratidae fam. nov. – Forms that developed a very narrow venter in their evolutionary history (Fig. 20).

New family to be described by Korn & Hairapetian (in press). – Forms that developed a concave venter, partly separated from a skid-like ventrolateral shoulder, in their evolutionary history (Fig. 21).

Family **Domatoceratidae** Miller & Youngquist, 1949
Figs 18A–B–19

Diagnosis

Family of the superfamily Grypoceratoidea with a thinly to thickly discoidal, subinvolute to evolute conch. Whorl profile in the adult stage usually compressed subquadrate or inverted trapezoidal. Umbilical margin distinct or sharp; ventrolateral shoulder nearly rectangular to broadly rounded, rarely skid-like. Ornament consisting of fine growth lines; some species have tubercles on the ventrolateral shoulder. Suture line always with rounded but distinct external, lateral and internal lobes separated by a narrowly rounded or subacute saddles; without annular process.

Included genera

Pselioceras Hyatt, 1884 (Wuchiapingian to Changhsingian; 3 species).
Titanoceras Hyatt, 1884 (Virgilian; 2 species).
Domatoceras Hyatt, 1891 (Moscovian to Changhsingian; 38 species).
Pseudometacoceras Miller, Dunbar & Condra, 1933 [synonym of *Domatoceras* Hyatt, 1891].
Paradomatoceras Delépine, 1937 (Bashkirian; 1 species).
Plummeroceras Kummel, 1953 (Artinskian; 1 species).
Neodomatoceras Ruzhencev & Shimansky, 1954 (Artinskian; 2 species).

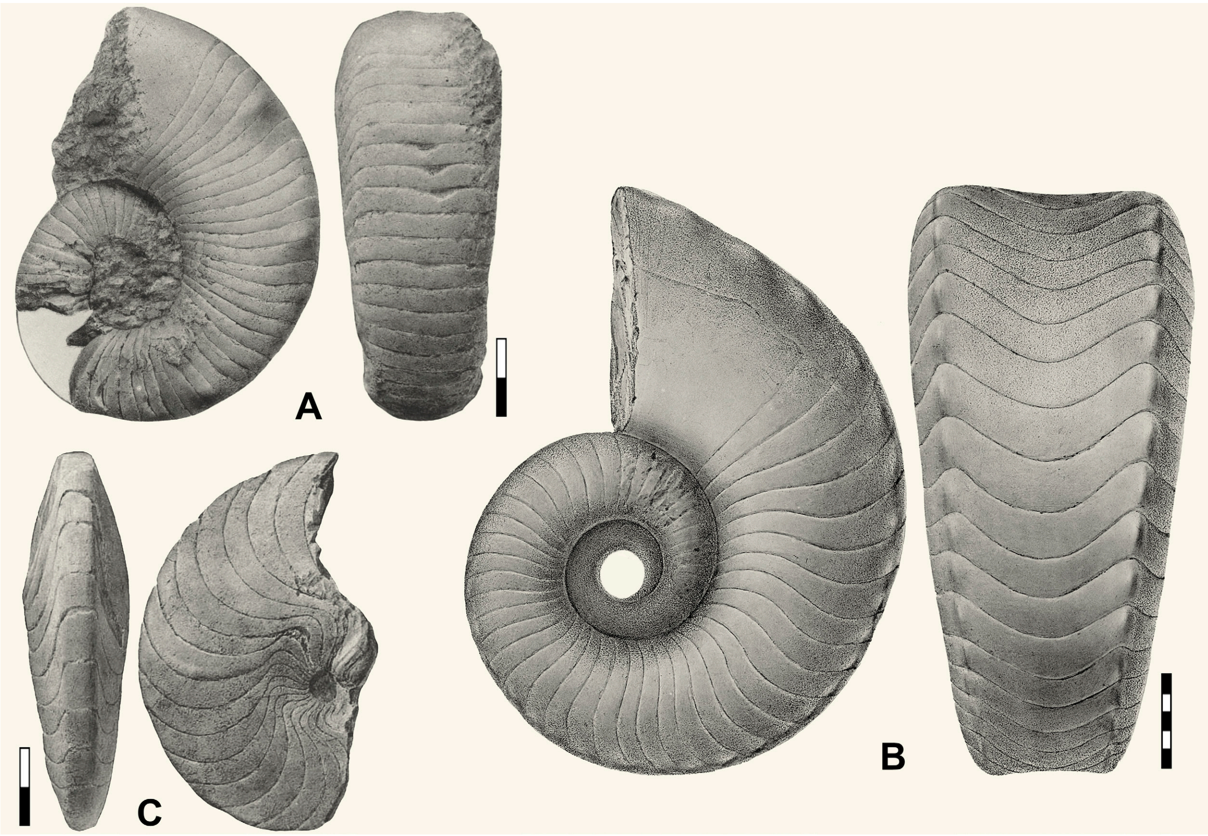

Fig. 18. Representatives of the superfamily Grypoceratoidea Hyatt, 1900. **A**. Family Domatoceratidae Miller & Youngquist, 1949. *Penascoceras northropi* (Miller & Unklesbay, 1942), from Miller & Unklesbay (1942). **B**. Family Domatoceratidae Miler & Youngquist, 1949. *Titanoceras ponderosum* (Meek, 1872), from Miller & Youngquist (1949). **C**. Family Stenopoceratidae fam. nov. *Stenopoceras cooperi* Miller & Unklesbay, 1942, from Miller & Unklesbay (1942). Scale bar units = 10 mm.

Parapenascoceras Ruzhencev & Shimansky, 1954 (Kasimovian to Roadian; 7 species).
Penascoceras Ruzhencev & Shimansky, 1954 (Kungurian to Roadian; 3 species).
Permodomatoceras Ruzhencev & Shimansky, 1954 (Artinskian to Wuchiapingian; 6 species).
Stenodomatoceras Ruzhencev & Shimansky, 1954 (Kasimovian; 4 species).
Virgaloceras Schindewolf, 1954 (Changhsingian; 1 species).
Neostenopoceras Zhao, Liang & Zheng, 1978 (Changhsingian; 1 species).
Shatoceras Leonova & Shchedukhin, 2020 (Asselian; 1 species).
Omorphoceras Leonova & Shchedukhin, 2023 (Asselian or Sakmarian; 1 species).
New genus A to be described by Korn & Ghaderi (in press) (Wuchiapingian to Changhsingian; 2 species).

Remarks

As with other families of Carboniferous and Permian nautilids, the justification and content of the family Domatoceratidae has been the subject of much debate; the views of the various authors were differing widely. When first described, Miller & Youngquist (1949) placed the five genera *Domatoceras*, *Pselioceras*, *Stearoceras* Hyatt, 1893, *Stenopoceras* and *Titanoceras* in the family Domatoceratidae. Kummel (1953) did not accept the family and synonymised it with the family Grypoceratidae. Moreover, he even considered *Domatoceras* to be a subgenus of *Grypoceras*. The genera and subgenera included by him in the Grypoceratidae were *Grypoceras* (*Grypoceras*), *Grypoceras* (*Domatoceras*), *Grypoceras* (*Plummeroceras*), *Gryponautilus* Mojsisovics, 1902, *Stenopoceras*, *Menuthionautilus* Collignon, 1933, *Stearoceras*, *Titanoceras* and *Pselioceras.*

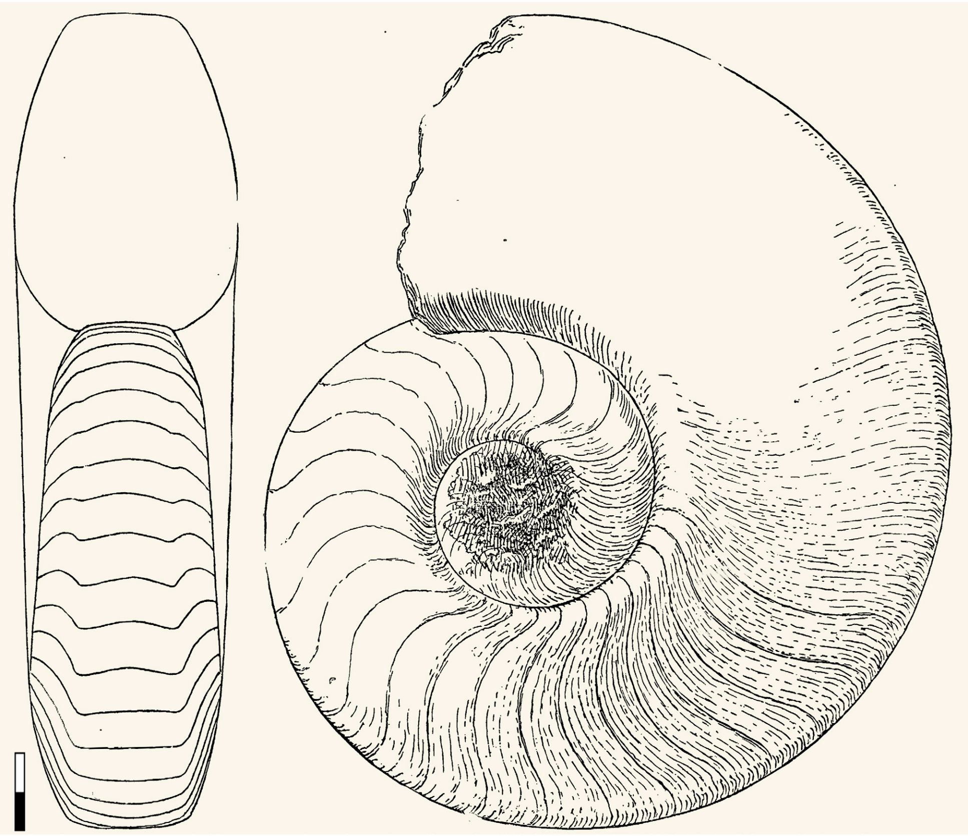

Fig. 19. Family Domatoceratidae Miller & Youngquist, 1949. *Domatoceras umbilicatum* Hyatt, 1891, from Hyatt (1891). Scale bar units = 10 mm.

Ruzhencev & Shimansky (1954) discussed the taxa belonging to this group in detail and included the four already known genera *Domatoceras*, *Titanoceras*, *Pselioceras* and *Stenopoceras* as well as the six newly named genera *Penascoceras*, *Parapenascoceras*, *Permodomatoceras*, *Neodomatoceras*, *Stenodomatoceras* and *Parastenopoceras* Ruzhencev & Shimansky, 1954. In the *Osnovy* (Shimansky 1962), the group was listed only as a subfamily within the family Grypoceratidae. In addition to the ten genera already mentioned, *Paradomatoceras*, *Plummeroceras* (as a subgenus of *Domatoceras*), *Virgaloceras* and *Menuthionautilus* were also included, the latter being the only Triassic genus.

In the *Treatise*, Kummel (1964) reiterated his previously published view and did not accept the Domatoceratidae as a valid family. He considered the genera *Stenodomatoceras*, *Penascoceras* and *Permodomatoceras* newly named by Ruzhencev & Shimansky (1954) to be synonyms of *Domatoceras* and *Parapenascoceras* and *Neodomatoceras* as synonyms of *Stearoceras*. He included the genus *Epidomatoceras* in the family Grypoceratidae.

Sobolev (1989) did not accept the independence of a family Domatoceratidae either and included the corresponding genera in the family Grypoceratidae. However, he accepted the validity of the Permian genera named by Ruzhencev & Shimansky (1954) but did not include *Epidomatoceras* in the family.

As in other Carboniferous–Permian nautilid families, the possible phylogenetic and systematic relationships in the Domatoceratidae (or Grypoceratidae) have been intensively discussed. Ruzhencev & Shimansky (1954) followed the concept that the systematics should be based on phylogeny; they therefore divided the family into a number of genera according to hypothetical evolutionary lineages. This contrasted sharply with other approaches, such as that of Kummel (1953: 45), who had stated: "As an evolutionary unit this family appears to be closely integrated. The extensive variations experimented with in this family keep an over-all unity in both the shape of the conch and sutural development." As a consequence, Kummel (1964) distinguished considerably fewer independent genera than Ruzhencev & Shimansky (1954) and Shimansky (1962).

A reconstruction of the phylogeny was undertaken by Dzik (1984). He derived the species of the family Domatoceratidae (which he included in the Grypoceratidae) from the Early Carboniferous genus *Epidomatoceras* and subdivided it into several long-ranging evolutionary lineages extending from the Carboniferous to the Triassic. Contrary to earlier concepts (Shimansky 1957; Kummel 1964), he placed *Germanonautilus* in the evolutionary lineage of *Titanoceras* and the Syringonautilidae Mojsisovics, 1902 in the lineage of *Domatoceras*. According to this reconstruction, *Stenopoceras* is separated from the Grypoceratidae and is considered a descendant of *Phacoceras* in the family Phacoceratidae.

An unanswered question is still whether certain morphological variations within the family Domatoceratidae occurred only once or iteratively. These characters include (1) the formation of a concave venter, (2) the formation of an angular ventrolateral margin and ventrolateral skids, (3) the formation of an angular umbilical margin, (4) the narrowing (but also widening) of the umbilicus, (5) the change to more compressed or depressed whorl profiles and (6) the development of ventrolateral tubercles. For example, it is not clear whether the separation of the genera *Stenodomatoceras* and *Permodomatoceras* from *Domatoceras*, which was justified by the reduction in umbilical width and whorl height, respectively, actually occurred only once. Therefore, it is not possible to say with certainty whether these genera are monophyletic units.

Family **Stenopoceratidae** fam. nov.
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Figs 18C, 20

Type genus

Stenopoceras Hyatt, 1893.

Diagnosis

Family of the superfamily Grypoceratoidea with an extremely discoidal to thinly discoidal, involute conch. Whorl profile in the adult stage compressed with very narrow venter. Ornament consisting of fine growth lines. Suture line always with rounded and small external lobe and broadly rounded lateral lobe separated by a subacute saddle, without annular process.

Etymology

The family name refers to the type genus.

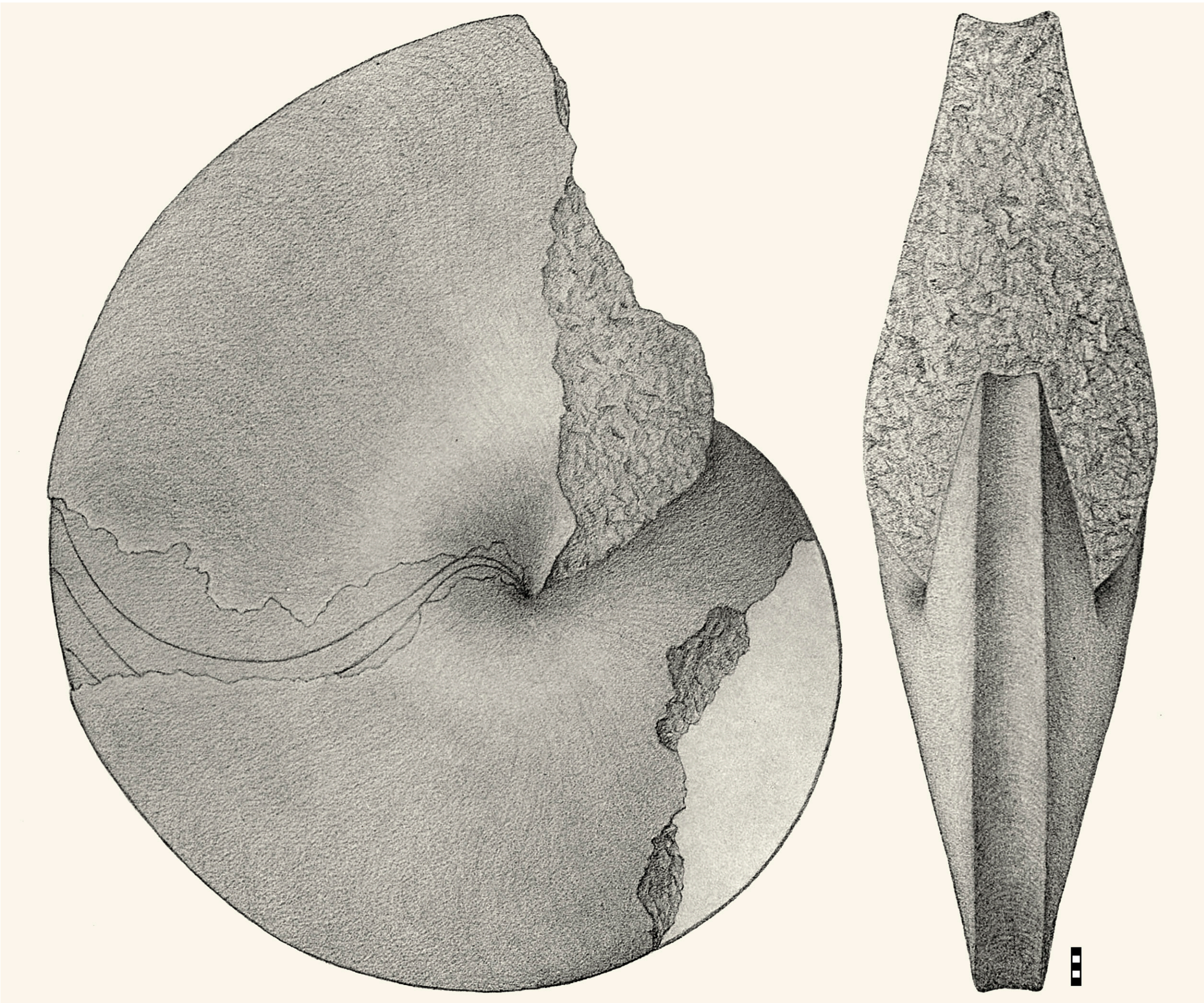

Fig. 20. Family Stenopoceratidae fam. nov. *Stenopoceras abundum* Miller & Thomas, 1936, from Miller & Youngquist (1949). Scale bar units = 1 mm.

Included genera

Stenopoceras Hyatt, 1893 (Bashkirian to Roadian; 9 species).
Parastenopoceras Ruzhencev & Shimansky, 1954 (Artinskian; 1 species).
Leptodomatoceras Leonova & Shchedukhin, 2023 (Asselian or Sakmarian; 1 species).

Remarks

The genera of the family Stenopoceratidae were previously placed in the family Domatoceratidae (Miller & Youngquist 1949; Ruzhencev & Shimansky 1954), in the family Grypoceratidae (Kummel 1953, 1964; Shimansky 1967, 1979), in the subfamily Domatoceratinae (Shimansky 1962) or in the family Phacoceratidae (Dzik 1984). However, Ruzhencev & Shimansky (1954: 51) proposed an evolutionary lineage with *Stenopoceras* as the terminal genus. This separate lineage is used here to name a separate family characterised by increasing compression of the whorl profile, closure of the umbilicus and narrowing of the venter.

New family Korn & Hairapetian (in press)
Fig. 21

Diagnosis

Family of the superfamily Grypoceratoidea with a usually discoidal, subinvolute conch. Whorl profile in the adult stage weakly compressed or weakly depresses; flanks and venter usually separated by a distinct ventrolateral shoulder, venter more or less concave. Umbilical margin usually subangular or angular, rarely rounded; umbilical wall steep, often flattened. Ornament usually consisting of fine growth lines. Septum simple in shape, concavely domed; suture line depending on whorl profile with shallow to V-shaped external lobe and shallow lateral lobe (from Korn & Hairapetian in press: 14).

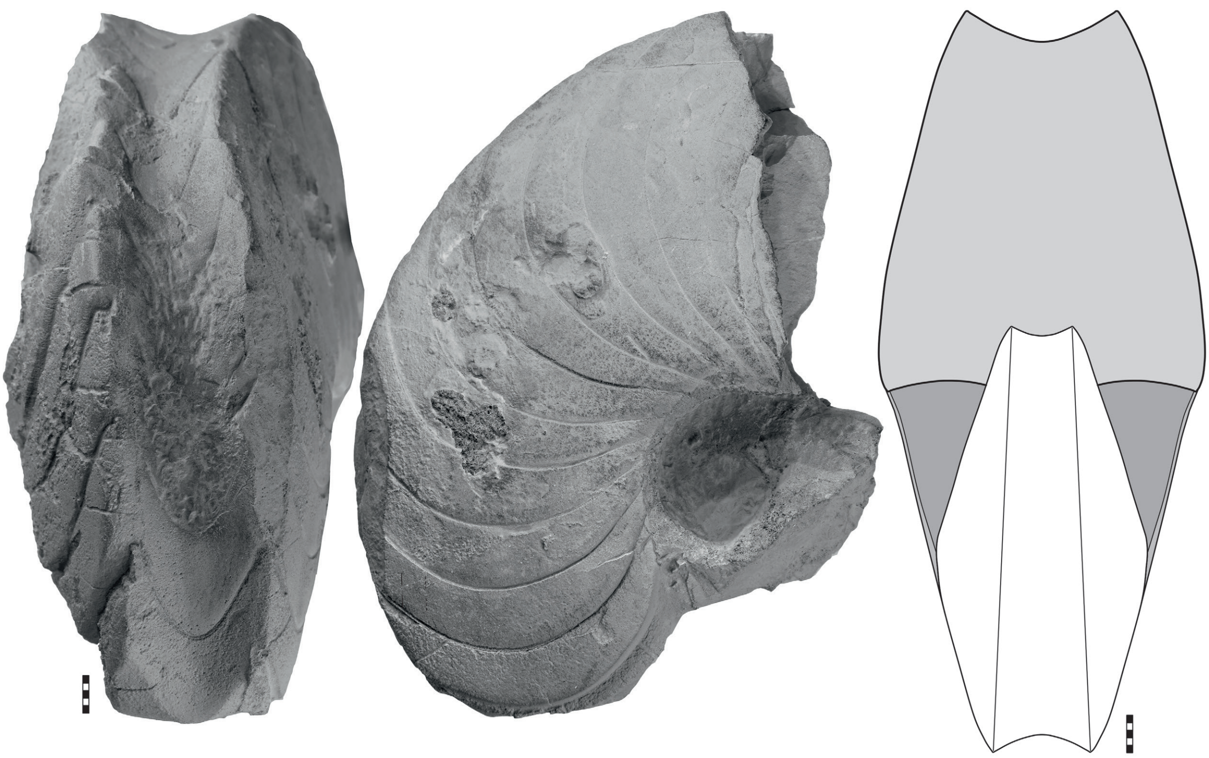

Fig. 21. New family to be described by Korn & Hairapetian (in press). New species to be described by Korn & Hairapetian (in press), ventral and lateral views, reconstruction of apertural view, from Korn & Hairapetian (in press). Scale bar units = 1 mm.

Included genera

Pseudotitanoceras Shimansky, 1965 (Wuchiapingian; 1 species).
New genus B to be described by Korn & Ghaderi (in press) (Changhsingian; 2 species).
New genus A to be described by Korn & Hairapetian (in press) (Wuchiapingian; 3 species).
New genus B to be described by Korn & Hairapetian (in press) (Wuchiapingian; 2 species).

Remarks

As Korn & Hairapetian (in press) will outline, grypoceratids with a whorl profile characterised by a concave venter, a pronounced ventrolateral shoulder with skid-like extensions, strongly convergent flanks and an angular umbilical margin occurred iteratively in the Late Carboniferous and Late Permian. It may be discussed whether they are phylogenetically related or belong to independent evolutionary lineages.

The Late Permian species are morphologically closely related; they are characterised by a rather late ontogenetic transformation from a juvenile growth stage with a rounded or flattened venter to an adult stage with a concave venter. Furthermore, the Late Permian species have rather stout conchs (ww/dm between 0.40 and 0.55), whereas the conchs of the Late Carboniferous species are usually much slenderer (ww/dm between 0.30 and 0.35). The umbilical margin is more pronounced in the Late Permian genera. These are probably good reasons to assume that the Late Permian species evolved independently of the Late Carboniferous species.

The family Ocunautilidae is characterised by a transformation of the originally broadly rounded venter into a more or less concave venter in the middle ontogenetic stage. The new family can therefore easily be derived from the family Domatoceratidae, some species of which also show a similar transformation. In addition to the modification of the venter, some members of the family Ocunautilidae show a narrowing of the umbilicus and a subangular or angular shape of the umbilical margin.

Superfamily **Permoceratoidea** Miller & Collinson, 1953
Fig. 22

[nom. transl., ex Permoceratidae Miller & Collinson, 1953.]

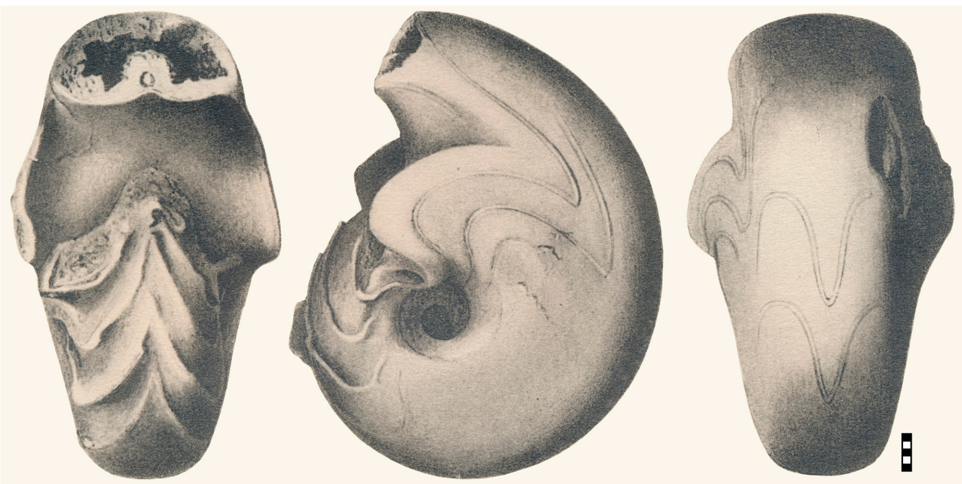

Fig. 22. Family Permoceratidae Miller & Collinson, 1953. *Permoceras bitauniense* (Haniel, 1915), from Haniel (1915). Scale bar units = 1 mm.

Diagnosis

Superfamily of the suborder Domatoceratina subordo nov. with discoidal, involute conch. Suture line with distinct, deeply V-shaped external lateral and internal lobs and two small, rounded umbilical lobes.

Included family

Permoceratidae Miller & Collinson, 1953 (Early Permian; 2 genera, 2 species).

Remarks

Permonautilus, and thus the family Permoceratidae, is based on the species described by Haniel (1915) as "*Nautilus* (*Aganides*) *bitauniensis*" (Fig. 22). According to Haniel (1915) the material comes from the "Bitauni beds", which have a late Early Permian age. Miller & Collinson (1953) discussed this species and created the new genus *Permoceras* and the family Permoceratidae for it. They based this taxonomic classification on the peculiarity of the suture line; in contrast to all other Permian nautilids, *P. bitauniense* has a complex suture with eight lobes. They compared the species with *Pseudonautilus geinitzi* (Oppel, 1865) from Late Jurassic strata in Moravia, a species that is almost identical in both conch geometry and suture line. Nevertheless, Miller & Collinson (1953) decided to create a new genus and family. The reason they gave was the considerable stratigraphic distance between *Permonautilus* and *Pseudonautilus*.

The family Permoceratidae was placed in the superfamily Centrocerataceae by Shimansky (1957, 1962, 1967, 1979) and in the superfamily Trigonocerataceae by Kummel (1964). Dzik (1984) did not recognise the independence of the family and placed *Permoceras* in the family Grypoceratidae. However, the very peculiar suture line, which differs greatly from all other Palaeozoic nautilids, justifies a separation at a high taxonomic level, and the family is therefore elevated to the rank of a superfamily.

The phylogenetic origin of *Permoceras* has long been considered unclear. Dzik (1984: 168, text-fig. 65) linked *Permoceras* as a short evolutionary lineage to *Neodomatoceras*, a genus with comparatively similar conch proportions but a very simple domatoceratid suture. Leonova & Shchedukhin (2023) presented *Foveroceras* Leonova & Shchedukhin, 2023 as a probable transitional form linking *Permoceras* with members of the Domatoceratidae. *Foveroceras* has a discoidal involute conch with a flat venter and is characterised by a deep and narrow outer lobe, a deep blunt lateral lobe, a fairly deep umbilical lobe and a very narrow deep internal lobe.

Family **Permoceratidae** Miller & Collinson, 1953
Fig. 22

Diagnosis

Family of the superfamily Permoceratoidea with a discoidal, involute conch. Suture line with distinct, deeply V-shaped external lateral and internal lobs and two small, rounded umbilical lobes.

Included genera

Permoceras Miller & Collinson, 1953 (Kungurian; 1 species).
Foveroceras Leonova & Shchedukhin, 2023 (Asselian or Sakmarian; 1 species).

Suborder **Tainoceratina** Shimansky, 1957
Fig. 23

Diagnosis

Suborder of the order Nautilida, in which a ventrolateral shoulder and an umbilical margin are formed early in ontogeny in the advanced species. Conch usually discoidal, subinvolute to evolute. Juvenile whorl profile depressed oval or circular. Adult whorl profile depressed oval or reniform in the early species, showing numerous modifications during evolution (inverted trapezoidal, trapezoidal or polygonal whorl profiles or with ventral depression). Dorsal whorl zone always present, but usually very small. Juvenile sculpture with radial ribs on the flank; adult sculpture with radial ribs on the flank, ventrolateral nodes or several rows of nodes in derived species. Septa simply domed, with dorsal inflexion in advanced species. Suture line depending on the whorl profile, with shallow lobes and low saddles. Siphuncle in central or subcentral position.

Included superfamilies

Tainoceratoidea Hyatt, 1883 (Late Carboniferous to Early Triassic; 23 Palaeozoic genera, 89 Palaeozoic species).

Pleuronautiloidea Hyatt, 1900 (Late Carboniferous to Late Triassic; 32 Palaeozoic genera, 190 Palaeozoic species).

Remarks

Taxonomy

A number of different concepts have been published with regard to the taxonomic composition and subdivision of the Tainoceratina. In the concept used here and in contrast to earlier authors, the suborder Tainoceratina is more restricted in size and several taxa of different rank are excluded, such as the Rutoceratidae, the Temnocheilidae and the Koninckioceratidae. Accordingly, the stratigraphic range of the suborder Tainoceratina is considered here from Viséan to Triassic.

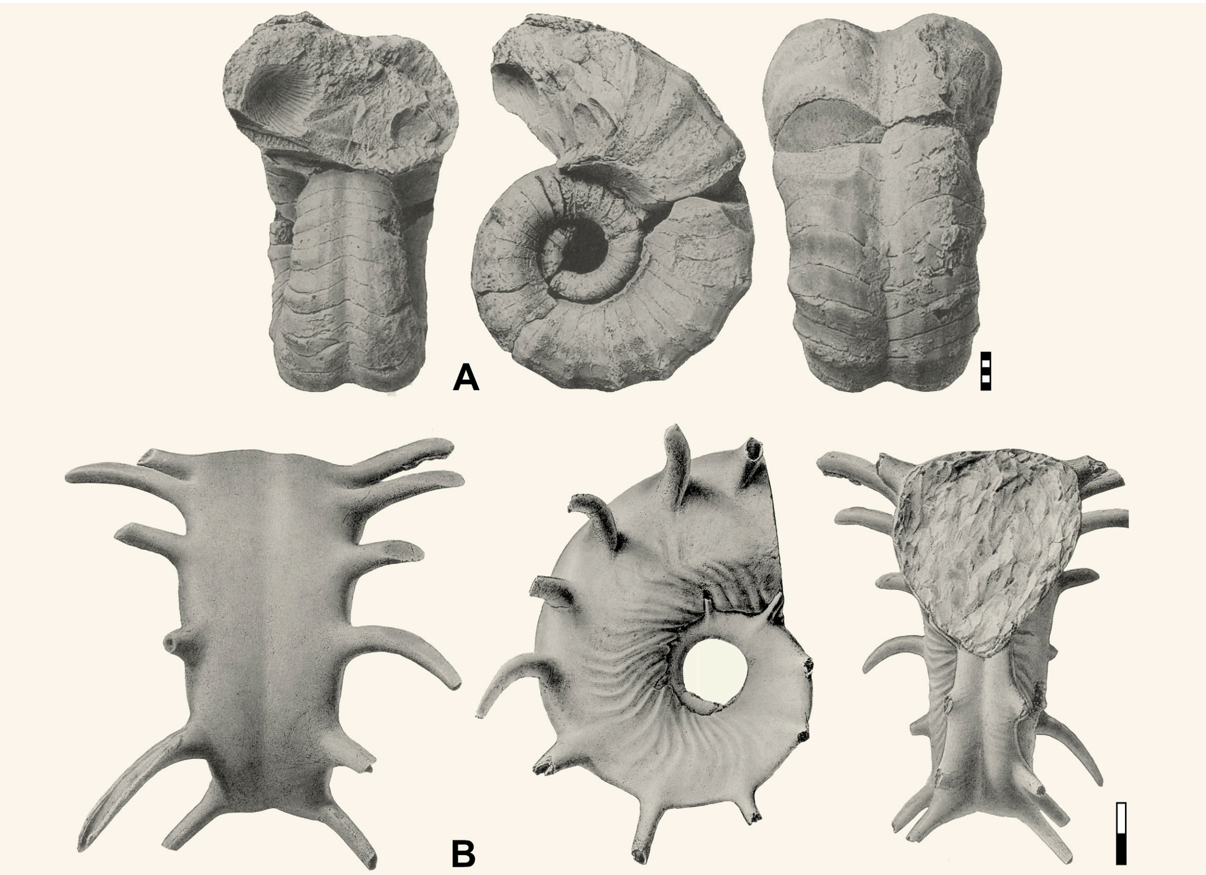

Fig. 23. Suborder Tainoceratina Shimansky, 1957. **A**. Superfamily Tainoceratoidea Hyatt, 1883. *Tylonautilus gratiosus* (Girty, 1909), from Miller & Furnish (1955). **B**. Pleuronautiloidea Hyatt, 1900. *Cooperoceras texanum* Miller, 1945, from Miller & Youngquist (1949). Scale bar units: A = 1 mm; B = 10 mm.

Morphology and subdivision

The phylogenetic scheme proposed by Shimansky (1957, 1962) distinguished four evolutionary lineages, translated in superfamilies within the suborder Tainoceratina: Tainocerataceae Hyatt, 1883, Encoilocerataceae Shimansky & Erlanger, 1955, Temnocheilaceae Mojsisovics, 1902 and Rhiphaeocerataceae Ruzhencev & Shimansky, 1954. According to this scheme, the clade consisting of the superfamilies Tainocerataceae and Encoilocerataceae and the clade consisting of the families Gzheloceratidae Ruzhencev & Shimansky, 1954, Rhiphaeoceratidae Ruzhencev & Shimansky, 1954 and Aktubonautilidae Ruzhencev & Shimansky, 1954 are monophyletic, respectively.

Kummel (1964) included the families Rutoceratidae, Tetragonoceratidae, Tainoceratidae, Rhiphaeoceratidae and Koninckioceratidae in the Tainocerataceae and postulated a Devonian to Triassic range for the superfamily. For the three superfamilies Aipocerataceae, Trigonocerataceae and Clydonautilaceae, he did not provide a clear phylogenetic hypothesis of origin, but suggested that they, like the tainoceratids, were derived from the Rutoceratidae or another ancestral family in the Devonian.

Dzik (1984) used the suborder Tainoceratina for practical reasons to include almost all Late Palaeozoic and Triassic nautiloids; he did not distinguish superfamilies, but rather separated the families Trigonoceratidae, Tainoceratidae, Grypoceratidae, Clydonautilidae, Syringonautilidae and Liroceratidae. It is worth noting that he only included post-Devonian taxa in the Tainoceratina.

Here, the suborder Tainoceratina is reduced to include only the superfamilies Tainoceratoidea and Pleuronautiloidea. This classification is based on phylogenetic considerations based on some key morphological characters. A common morphological feature of the two superfamilies is the early ontogenetic development of both a subangular ventrolateral shoulder and a subangular umbilical margin in the advanced species (Fig. 3D, I). Radial ribs appear in the juvenile conch within several lineages. The general shape of the conch is discoidal and subevolute; subinvolute and evolute conchs are an exception. Tainoceratids are very conservative in this respect; Carboniferous, Permian and Triassic species can have very similar conch morphologies, but the latter probably regularly possess a dorsal inflexion of the septum, causing an annular process.

The two superfamilies are characterised by the following main morphological features:

Tainoceratoidea. – Forms with usually octagonal whorl profile with a more or less deep mid-ventral longitudinal groove; sculpture usually with several rows of nodes (Fig. 23A).

Pleuronautiloidea. – Forms with usually quadrate, trapezoidal or inverted trapezoidal whorl profile with a more or less strongly flattened venter; sculpture usually with ventrolateral nodes and ribs on the flank, sometimes with more or less long spines (Fig. 23B).

Origin

The origin of the suborder Tainoceratina (as interpreted here) is not completely resolved. Ruzhencev & Shimansky (1954) saw the origin of the tainoceratids (in a more general view) in the Devonian family Tetragonoceratidae Flower, 1945 and derived the Tainoceratina from the family Rutoceratidae Hyatt, 1884. Shimansky (1967: 39) stated that the family Gzheloceratidae, which was considered to be the ancestral family from which the family Tainoceratidae and others were derived, arose directly from the family Rutoceratidae.

Dzik (1984: 160) proposed an alternative origin for the tainoceratids. Most importantly, he proposed parallel evolutionary lineages within the group, here separated as the superfamilies Tainoceratoidea and Pleuronautiloidea. Dzik associated *Tainoceras* Hyatt, 1883 with the Viséan to Serpukhovian genus *Tylonautilus* Pringle & Jackson, 1928, which like *Tainoceras* has a polygonal whorl profile with a midventral groove and a sculpture with ribs and rows of nodules or tubercles. This hypothesis would imply a Bashkirian to early Gzhelian interval between the last occurrence of the ancestor *Tylonautilus* and the first of the descendant *Tainoceras*. Dzik also formulated the hypothesis that *Tylonautilus* was derived from the Viséan genus *Celox* Shimansky, 1967.

Dzik saw the origin of the group described here as Pleuronautiloidea in Early Carboniferous representatives of the genus *Gzheloceras* Ruzhencev & Shimansky, 1954, which are now attributed to *Pseudogzheloceras* Dernov, 2021 (Dernov 2021). According to this hypothesis (Dzik 1984: 160), *Gzheloceras* should be derived from the genus *Celox*, which in turn should have been derived from the Tournaisian to Viséan genus *Vestinautilus*. This would mean that the superfamilies Tainoceratoidea Hyatt, 1883 and Pleuronautiloidea Hyatt, 1900 have a common ancestor in the genus *Celox*. At the same time, it means that the angular umbilical margin was acquired independently later in the evolution of the two superfamilies.

This hypothesis for the origin of the tainoceratids in the strict sense, formulated by Dzik (1984), seems to be the most plausible in view of the available data. Within the genus *Vestinautilus* and closely related genera, the transition from the Tournaisian to the Viséan was marked by a progressive simplification of shell ornamentation, with the loss of the original spiral ridges and the strongly pronounced ventrolateral shoulder. Such a morphological trend including the new formation of lateral ribs could have led to genera such as *Celox* and *Pseudogzheloceras*.

As an alternative to a phylogenetic origin in the genus *Vestinautilus*, the tainoceratids could be derived from originally more evolute and discoidal species. Representatives of the family Subclymeniidae, in particular the genera *Maccoyoceras* and *Epidomatoceras*, are possible candidates. This would mean that the Tainoceratina and Domatoceratina subordo nov. are largely sister groups.

Phylogeny

Dzik (1984: text-fig. 62) drew a complex system of relationships with a number of parallel evolutionary lineages within the group, the most important of which are:

(1) *Gzheloceras – Pleuronautilus*: this evolutionary lineage already began in the Early Carboniferous with *Pseudogzheloceras memorandum* Shimansky, 1967 and continued through the Late Carboniferous and Permian with species of *Pseudogzheloceras* and *Gzheloceras*. In the Early Permian, this lineage included species now classified as *Pseudofoordiceras* Ruzhencev & Shimansky, 1954. According to this phylogenetic reconstruction, a separate lineage continued into the Triassic and was represented by *Pleuronautilus trinodosus* Mojsisovics, 1882 and other species of the same genus.

(2) *Gzheloceras – Metacoceras dorashamense*, *M. dorsoarmatum – Pleuronautilus pichleri*: this evolutionary lineage began in the Bashkirian with *Pseudogzheloceras faticatum* Shimansky, 1967 and continued into the Permian via *P. tacitum* Shimansky, 1967 (Moscovian) and *P. maklai* Shimansky, 1967 (Kasimovian). From the Wuchiapingian, the species "*Metacoceras dorashamense*", "*M. dorsoarmatum*" and "*Pleuronautilus dzhulfensis*" belong in this lineage. Survivors into the Triassic formed the species *Pleuronautilus pichleri* author+year and the genera *Encoiloceras* Hyatt, 1900 and *Anoploceras* Hyatt, 1900.

(3) *Pseudotemnocheilus – Tirolonautilus*: this evolutionary lineage began in the Moscovian with *Temnocheiloides acanthicus* (Tzwetaev, 1888) and continued in the Permian with *Pseudotemnocheilus* Ruzhencev & Shimansky, 1954 and *Tirolonautilus* Mojsisovics, 1902. Two side branches were represented by *Cooperoceras* Miller, 1945 and *Articheilus* Ruzhencev & Shimansky, 1954, respectively.

(4) *Metacoceras – Enoploceras*, *Mojsvaroceras*: this evolutionary lineage began in the Kasimovian with *Metacoceras mcchesneyi* Murphy, 1970 and continued throughout the Permian. In the Triassic there was a diversification into different genera (*Enoploceras* Hyatt, 1900, *Mojsvaroceras* Hyatt, 1883).

Superfamily **Pleuronautiloidea** Hyatt, 1900

Diagnosis

Superfamily of the suborder Tainoceratina with a discoidal, subinvolute to subevolute conch. Whorl profile in early species subquadrate with distinct ventrolateral shoulder and distinct umbilical margin. Derived species show a variation of modifications including trapezoidal, inverted trapezoidal or hexagonal whorl profiles with a less angular ventrolateral shoulder and umbilical margin. Whorl overlap is always very small. Sculpture in early species with transverse ribs and ventrolateral nodes, in derived species often with ribs and several rows of nodes. Septa simply domed, in derived species with a dorsal inflexion that produces an annular process. Suture line with broadly rounded lateral lobe and shallow lobe or low saddle on the venter.

Included families

Pleuronautilidae Hyatt, 1900 (Middle Permian to Late Triassic; 1 Permian genus, 10 Permian species).
Gzheloceratidae Ruzhencev & Shimansky, 1954 (Early Carboniferous to Early Permian; 5 genera, 37 species).
Mosquoceratidae Ruzhencev & Shimansky, 1954 (Late Carboniferous to Early Permian; 3 genera, 11 species).
Aktubonautilidae Ruzhencev & Shimansky, 1954 (Early Permian; 2 genera, 2 species).
Rhiphaeoceratidae Ruzhencev & Shimansky, 1954 (Early to Late Permian; 6 genera, 15 species).
Metacoceratidae fam. nov. (Late Carboniferous to Late Permian; 12 genera, 101 species).
Foordiceratidae fam. nov. (Middle to Late Permian; 3 genera, 14 species).

Remarks

Based on the phylogenetic reconstruction that was proposed by Dzik (1984), six families within the superfamily Pleuronautiloidea are distinguished here and briefly characterised as follows:

Metacoceratidae fam. nov. – Ancestral taxa with a commonly subquadrate or weakly depressed whorl profile; sculpture with conical ventrolateral nodes and sometimes with dorsolateral nodes and ribs on the flank (Fig. 24).

Gzheloceratidae Ruzhencev & Shimansky, 1954. – Ancestral taxa with a small conch and an elliptical or reniform whorl profile; sculpture with short ribs or transversely elongated tubercles in the middle of the flank (Fig. 25A).

Aktubonautilidae Ruzhencev & Shimansky, 1954. – Taxa with a semicircular or reniform whorl profile and a broadly rounded venter; sculpture with elongate nodes on the flank (Fig. 25B).

Mosquoceratidae Ruzhencev & Shimansky, 1954. – Taxa with a trapezoidal whorl profile and a convex venter; sculpture with longitudinally elongated tubercles on the outer flank (Fig. 26).

Rhiphaeoceratidae Ruzhencev & Shimansky, 1954. – Taxa with an oval, reniform or trapezoidal whorl profile and a flattened venter; sculpture with short ribs on the flank (Fig. 27).

Foordiceratidae fam. nov. – Derived taxa with a trapezoidal whorl profile and a flattened venter; sculpture with coarse ribs or coarse conical nodes on the outer flank (Fig. 28).

Pleuronautilidae Hyatt, 1900. – Derived taxa with parallel or convergent flanks and rounded ventrolateral shoulder; sculpture with coarse ribs and sometimes with multiple rows of nodes (Fig. 29).

The absence of the midventral groove separates the Pleuronautiloidea from the Tainoceratoidea. In addition, the species of the Pleuronautiloidea usually have a rectangular, trapezoidal or inverted trapezoidal whorl profile, whereas the Tainoceratoidea have a polygonal whorl profile. The sculpture of the Pleuronautiloidea does not have the characteristic rows of nodes typical for the Tainoceratoidea.

Family **Metacoceratidae** fam. nov.
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Fig. 24

Type genus

Metacoceras Hyatt, 1883.

Diagnosis

Family of the superfamily Pleuronautiloidea with an equidimensional or more commonly weakly depressed, trapezoidal to inverted trapezoidal whorl profile. Venter usually flattened, but ranging from slightly convex to slightly concave. Ventrolateral shoulder often prominent, ranging from broadly rounded to subangular. Flanks weakly convergent, parallel or weakly divergent, usually flattened and ranging from weakly convex to weakly concave. Umbilical margin usually pronounced, usually

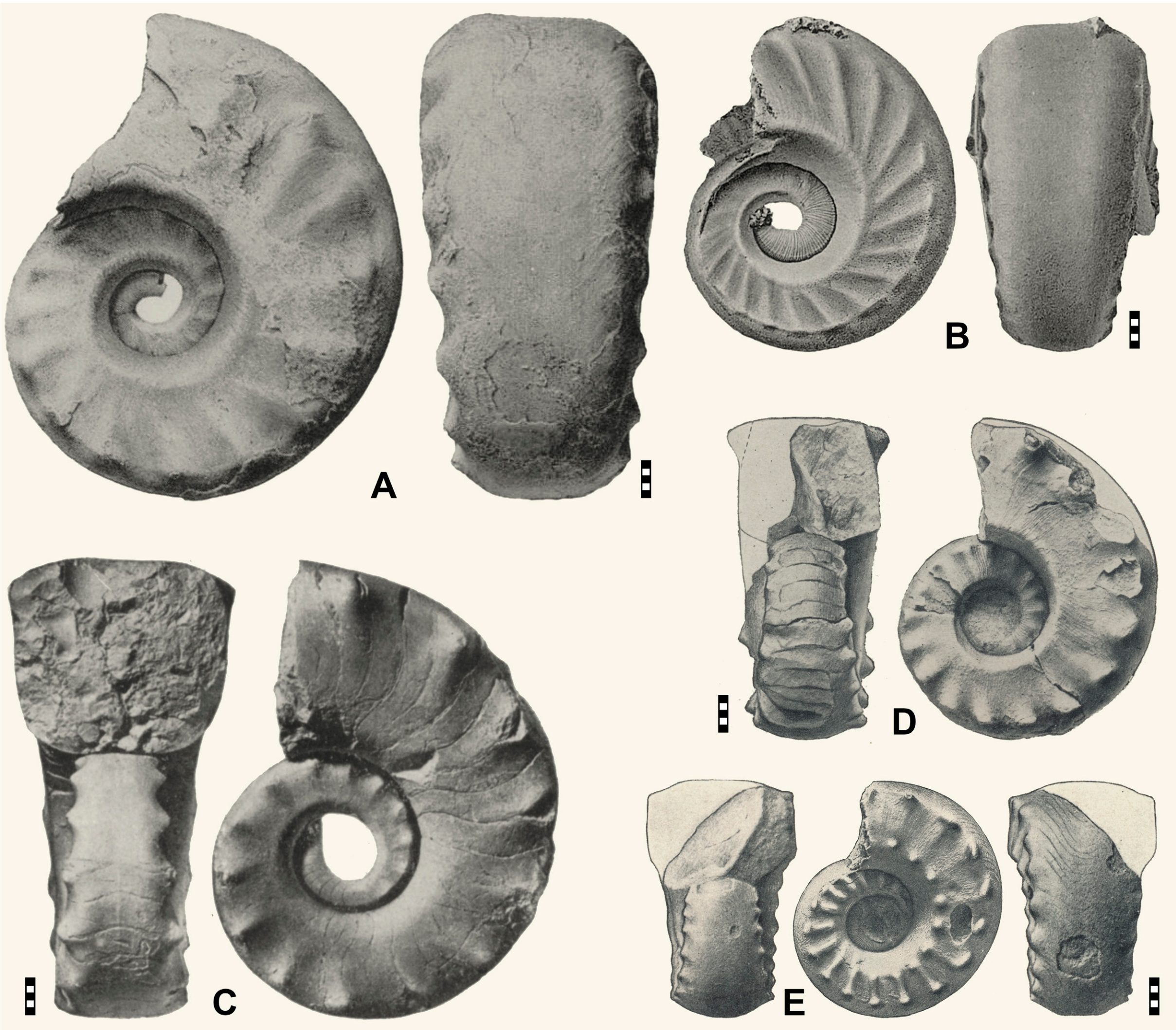

Fig. 24. Family Metacoceratidae fam. nov. **A**. *Pseudofoordiceras cooperi* (Miller, 1945), from Miller (1945). **B**. *Pseudofoordiceras gregarium* (Miller, 1945), from Miller & Youngquist (1949). **C**. *Pseudotemnocheilus artiense* (Kruglov, 1928), from Ruzhencev & Shimansky (1954). **D**. *Metacoceras cornutum* Girty, 1911, from Girty (1915). **E**. *Metacoceras perelegans* Girty, 1911, from Girty (1915). Scale bar units = 1 mm.

subangular in the intermediate growth stage. Sculpture with ventrolateral conical nodes, often with dorsolateral nodes and low ribs on the flank. Suture line with shallow lobes and low saddles. Internal lobe very shallow, without annular process.

Etymology

The family name refers to the type genus.

Included genera

Metacoceras Hyatt, 1883 (Moscovian to Roadian; 45 species).
? *Shansinautilus* Yabe & Mabuti, 1935 (Roadian; 1 species).
Cooperoceras Miller, 1945 (Kungurian; 1 species).
Epimetacoceras Librovitch, 1946 (Carboniferous) (nomen nudum).
Pseudofoordiceras Ruzhencev & Shimansky, 1954 (Artinskian to Kungurian; 7 species).
Pseudotemnocheilus Ruzhencev & Shimansky, 1954 (Artinskian to ? Changhsingian; 11 species).
Tanchiashanites Zhao, 1954 (Roadian; 1 species).
Mahoningoceras Murphy, 1974 (Moscovian; 3 species).
Lichuanoceras Xu, 1977 (Wuchiapingian; 1 species).
Sinotitanoceras Pan, 1983 (Kungurian; 1 species).
Anthodiscoceras Qin, 1986 (Wuchiapingian; 1 species)?
New genus C to be described by Korn & Ghaderi (in press) (Wuchiapingian to Changhsingian; 22 species).
Mojsvaroceras Hyatt, 1883 (Triassic).
Huanghoceras Yin, 1933 (Asselian to Wuchiapingian; 8 species).

Remarks

Miller *et al.* (1933: 166) placed six Pennsylvanian genera from the American Midcontinent in the family Tainoceratidae, namely *Tainoceras*, *Temnocheilus*, *Metacoceras*, *Endolobus*, *Titanoceras* and *Coelogasteroceras* Hyatt, 1893. This list contains a very heterogeneous collection of genera, but the authors were aware of a serious problem: "The classification of the nautiloid cephalopods is not in a satisfactory condition as is that of most of the other major groups of fossil invertebrates." (Miller *et al.* 1933: 38). They discussed an earlier idea expressed by Girty (1915) to subdivide the genus *Metacoceras* into subgenera or genera, but concluded that "… such subdivision, however justifiable it may be from a phylogenic point of view, is so difficult, if not impossible to carry through in practice, that it would lead to endless confusion." Consequently, they listed about 25 Carboniferous taxa at the species level.

Miller & Youngquist (1949: 105) discussed the genus *Metacoceras* including the Permian material and repeated the problems posed by the wide range of variation in conch shape and ornament: "Normally, we would be inclined to regard many of the forms under consideration as varieties of established species, but such a procedure does not seem to be practicable in this case because of the extreme amount of variation in all of the characters involved. Therefore, more or less as a matter of expediency, we are recognizing most of the variants as distinct species." Miller & Youngquist (1949) restricted *Metacoceras* to those species with conical nodes only on the outer flank or the ventrolateral shoulder; species with ventrolateral nodes extending as ribs onto the flank were assigned to *Foordiceras*. Because of this interpretation, they stated that many of the species formerly referred to *Metacoceras* should be better placed in *Foordiceras*.

Kummel (1953: 19) proposed a different concept for the genus *Metacoceras* and understood it with a much wider morphological range. He separated the two subgenera *M*. (*Metacoceras*) and *M*. (*Mojsvaroceras*), the former with nearly 50 species occurring in the Carboniferous and Permian and the latter with 17 species in the Triassic. Kummel did not accept the placement of species with umbilical nodes in *Foordiceras* as done by Miller & Youngquist (1949), instead he stated: "The basic pattern of ornamentation of *Metacoceras* is that of ventrolateral and umbilical nodes." However, at the same time he stated: “The species can be separated into two groups, the first including those that have only ventrolateral nodes, and the second those that have both ventrolateral and umbilical nodes.”

Contrary to Miller & Youngquist (1949), Kummel (1953) saw close relationships between the genera *Metacoceras* and *Pleuronautilus* and transferred a number of Permian species that were previously assigned to *Metacoceras* to *Pleuronautilus*, although they show close affinities to *Metacoceras*. This reduced the number of species of *Metacoceras* but made *Pleuronautilus* a very large genus, spanning the Early Permian to the Late Triassic. Kummel estimated that there may be 58 species in the subgenus *Pleuronautilus* (*Pleuronautilus*), 24 of which are from the Permian. It is worth noting that Kummel argued that many Permian tainoceratid species previously assigned to *Metacoceras* or *Foordiceras* should be placed in *Pleuronautilus* based on the presence of radial ribs: “Many of these species appear to be transitional between *Metacoceras* and the Triassic *Pleuronautilus* and should be placed in the latter genus.” (Kummel 1953: 34). He listed the species, including “*Nautilus dorso armatus*” from Dzhulfa, under *Pleuronautilus* (*Pleuronautilus*).

Ruzhencev & Shimansky (1954) proposed an alternative approach, which was very different from those previously outlined; their approach was based on proposed phylogenetic relationships that should be expressed in the classification of *Metacoceras* and its relatives. These authors had excellently preserved material for study and were therefore able to include the size, shape and ornamentation of early juvenile conch in their phylogenetic analysis. Ruzhencev & Shimansky (1954: 45) postulated that there are two separate evolutionary lineages within *Metacoceras*; the European species (including those from the South Urals) are characterised by a single row of tubercles on the ventrolateral shoulder, whereas the American species possess one row of tubercles on the ventrolateral shoulder and another on the umbilical margin. They reduced the extend of the genus *Metacoceras* by separating the North American Permian species with ribs on the flank as *Pseudofoordiceras*. Furthermore, they accepted the Asian genera *Huanghoceras* and *Shansinautilus*.

In the *Treatise of Invertebrate Paleontology*, Kummel (1964) expressed a much more restrictive view on the tainoceratids. He did not accept the families Gzheloceratidae and Mosquoceratidae that were previously established by Ruzhencev & Shimansky (1954) and included them in the Tainoceratidae. Furthermore, ignoring the family Mosquoceratidae, he synonymised *Mosquoceras* Ruzhencev & Shimansky, 1954 with *Metacoceras* and *Articheilus* and placed *Leonardocheilus* Ruzhencev & Shimansky, 1954 in synonymy with *Temnocheilus*. He also synonymised a number of other genera such as *Huanghoceras* and *Shansinautilus*. In summary, Kummel’s attempt suggested the existence of some long-ranging and geographically widespread genera (*Metacoceras*, *Pleuronautilus*) with a very large number of species.

Shimansky (1965), when describing the Late Permian nautiloids from Dzhulfa, noted the transitional morphology of “*Metacoceras dorsoarmatum*” and “*M. dorashamense*” with “*Pleuronautilus dzhulfensis*”. It seems that Shimansky avoided to name a clear character to separate the two genera.

Metacoceras remained a species-rich genus. Shimansky (1967) listed 34 species, about half of which were from the Late Carboniferous and half from the Permian. He also listed 19 Permian species of *Pleuronautilus*, including some that had been assigned to the genera *Huanghoceras* and *Pseudofoordiceras* in an earlier paper (Ruzhencev & Shimansky 1954). These two genera as well as *Shansinautilus* Yabe & Mabuti, 1935 and *Tungkuanoceras* Hajasaka, 1947 were synonymised with *Pleuronautilus*.

Teichert & Kummel (1973), when describing the nautiloids from the Iranian side of the Aras Valley, accepted the separation of *Metacoceras* (with “*Metacoceras dorsoarmatum*” and “*M. dorashamense*”) and *Pleuronautilus* (with “*Pleuronautilus* sp. indet. 1”) as previously outlined in a similar way by Shimansky (1965). Like Shimansky, they did not provide a clear reason for this choice of separation.

Sturgeon *et al.* (1997: 31) discussed in detail the morphological spectrum of *Metacoceras* and its relationships with other tainoceratid genera. They included Late Carboniferous species with lateral ribs and umbilical nodes in *Metacoceras*.

An alternative division of families within the superfamily Pleuronautiloidea is proposed here. The family Metacoceratidae includes all genera that have a trapezoidal to inverted trapezoidal whorl profile and whose sculpture consists largely of ventrolateral nodes.

The family Metacoceratidae is distinguished from the other families of the superfamily Pleuronautiloidea by the following criteria:

The main difference with the partly rather similar species of the Pleuronautilidae is the sculpture, which in the Pleuronautilidae consists mainly of sharp ribs on the flanks, whereas in the Metacoceratidae it consists mainly of conical nodes and a few low and mostly rounded ribs.

The families Mosquoceratidae and Aktubonautilidae differ from the Metacoceratidae in the very large juvenile whorl; the families Gzheloceratidae and Rhiphaeoceratidae differ from the Metacoceratidae in the more elliptical whorl cross section and, at least partly, in the presence of coarse transverse ribs. The family Foordiceratidae is easily distinguished from the Metacoceratidae by the highly divergent flanks and the absence of an umbilical margin.

Family **Gzheloceratidae** Ruzhencev & Shimansky, 1954
Fig. 25A

Diagnosis

Family of the superfamily Pleuronautiloidea with a rather small conch and a weakly depressed, elliptical or reniform whorl profile. Venter flattened or slightly convex; ventrolateral shoulder, flanks and umbilical margin usually broadly rounded. Sculpture with short ribs or transversely elongated nodes on the flank. Suture line with shallow lobes and low saddles. Internal lobe very shallow, without annular process (after Ruzhencev & Shimansky 1954).

Included genera

Parametacoceras Miller & Owen, 1934 (Bashkirian to Moscovian; 7 species).

Fig. 25. Families Gzheloceratidae Ruzhencev & Shimansky, 1954 and Aktubonautilidae Ruzhencev & Shimansky, 1954; both from Ruzhencev & Shimansky (1954). **A**. *Gzheloceras ellipsoidale* Ruzhencev & Shimansky, 1954. **B**. *Aktubonautilus cruciformis* Ruzhencev & Shimansky, 1954. Scale bar units = 1 mm.

Gzheloceras Ruzhencev & Shimansky, 1954 (Gzhelian to Artinskian; 14 species).
Heurekoceras Ruzhencev & Shimansky, 1954 (Artinskian; 1 species).
Celox Shimansky, 1967 (Viséan to Bashkirian; 3 species).
Pseudogzheloceras Dernov, 2021 (Bashkirian to Kasimovian; 12 species).

Remarks

The evolutionary history of the family Gzheloceratidae seems to have extended from the Viséan of the Early Carboniferous to the Early Permian, if not longer. During this long period, only few morphological changes occurred, both in the shape of the conch and in the sculpture. The species of the family show a very conservative shape of the whorl profile, which is either depressed elliptical or reniform. There is neither an angular umbilical margin nor a prominent ventrolateral shoulder developed. The sculpture consists of simple ribs or nodes on the flank (Ruzhencev & Shimansky 1954).

The shape of the juvenile conch is similar to that of all other members of the superfamily Pleuronautiloidea, with the exception of the family Mosquoceratidae, which have a much larger and stouter initial conch. With an elliptical or strongly rounded trapezoidal whorl profile, the adult conch of the Mosquoceratidae has a different shape to the juvenile. Another difference from the other families is the almost straight suture line in the Gzheloceratidae.

Family **Aktubonautilidae** Ruzhencev & Shimansky, 1954
Fig. 25B

Diagnosis

Family of the superfamily Pleuronautiloidea with a large, stout first whorl. Whorl profile weakly depressed, semicircular or reniform. Venter, flanks and umbilical margin broadly rounded. Sculpture with lateral, transversely elongated nodes. Suture line with a shallow external, a very shallow lateral and a rather deep internal lobe; without annular process (after Ruzhencev & Shimansky 1954).

Included genera

Aktubonautilus Ruzhencev & Shimansky, 1954 (Artinskian; 1 species).
Basleonautilus Ruzhencev & Shimansky, 1954 (Roadian; 1 species).

Remarks

The family Aktubonautilidae is closest to the Rhiphaeoceratidae; there are similarities in the shape of the conch, the course of the suture line and partly in the sculpture. However, both families differ significantly in the morphology of the juvenile conch. The Aktubonautilidae are characterised by a stout first volution, whereas the Rhiphaeoceratidae have a slender, worm-like first volution. In this respect, the Aktubonautilidae are more similar to the Mosquoceratidae; however, this family differs greatly in the type of sculpture and suture line. The sculpture is formed by lateral transverse tubercles or ribs in the Aktubonautilidae but by longitudinal oval tubercles along the ventrolateral shoulder in Mosquoceratidae. In contrast to the Mosquoceratidae, the suture line in the Aktubonautilidae has only very shallow lateral lobes.

Family **Mosquoceratidae** Ruzhencev & Shimansky, 1954
Fig. 26

Diagnosis

Family of the superfamily Pleuronautiloidea with a large, rapidly growing first whorl. Whorl profile weakly depressed, subhexagonal to trapezoidal. Venter broad, weakly convex; ventrolateral shoulder

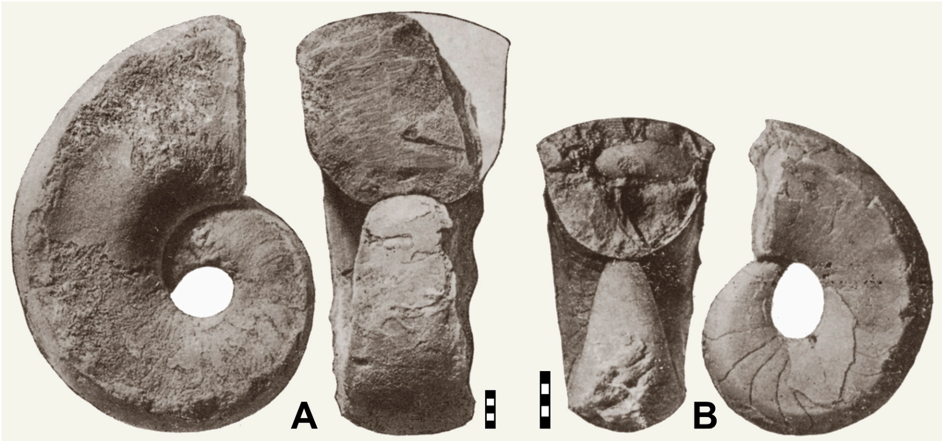

Fig. 26. Family Mosquoceratidae Ruzhencev & Shimansky, 1954, both from Ruzhencev & Shimansky (1954). **A**. *Mosquoceras simense* Ruzhencev & Shimansky, 1954. **B**. *Articheilus luxuriosum* Ruzhencev & Shimansky, 1954. Scale bar units = 1 mm.

angular, flanks convex and strongly divergent; umbilical margin, if present, very weakly developed. Sculpture with ventrolateral, longitudinally elongated nodes. Suture line with a wide external, a narrower lateral and a narrow internal lobe; without annular process (after Ruzhencev & Shimansky 1954).

Included genera

Mosquoceras Ruzhencev & Shimansky, 1954 (Moscovian to Kungurian; 9 species).
Articheilus Ruzhencev & Shimansky, 1954 (Artinskian; 1 species).
Leonardocheilus Ruzhencev & Shimansky, 1954 (Kungurian; 1 species).

Remarks

According to Ruzhencev & Shimansky (1954: 85), the family Mosquoceratidae is closest to Tainoceratidae (which they interpret more broadly than it is currently done). The family Mosquoceratidae differs greatly from most of the other families of the Pleuronautiloidea in the morphology of the first volution, which is large, stout and rapidly growing in the Mosquoceratidae, whereas it is smaller and, above all, much slenderer in the other families. The similarity between these families is evident in both the shape of the conch and the suture lines. There are also sculptural differences. In the Mosquoceratidae, the tubercles are longitudinally elongated and coincide exactly with the ventrolateral shoulder; in the other families, the tubercles are usually rounded conical. The species of the family Aktubonautilidae also possess a large first whorl, but differ in the shape of the whorl profile, which is semicircular or reniform with broadly rounded venter.

Family **Rhiphaeoceratidae** Ruzhencev & Shimansky, 1954
Fig. 27

Diagnosis

Family of the superfamily Pleuronautiloidea with a small, slender first whorl. Whorl profile weakly depressed, elliptical or trapezoidal. Venter broad and weakly convex, flanks convex or slightly flattened, umbilical margin broadly rounded or absent. Sculpture with short ribs on the flank. Suture line with a low external saddle, sometimes with a shallow external lobe, a very shallow lateral and a rather deep funnel-shaped internal lobe; without annular process (after Ruzhencev & Shimansky 1954).

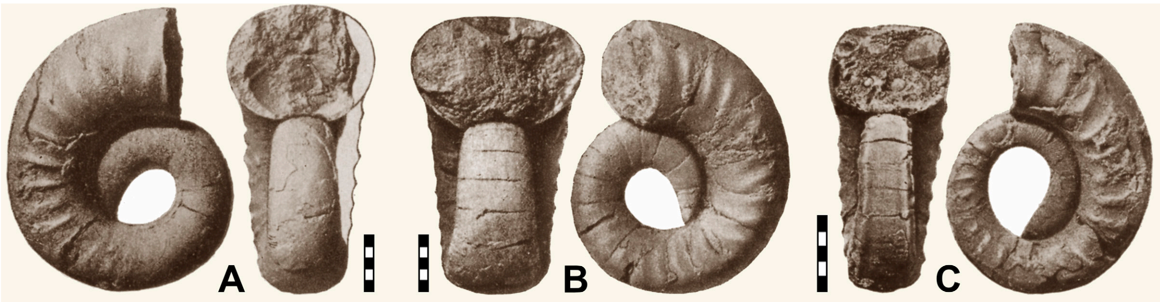

Fig. 27. Family Rhiphaeoceratidae Ruzhencev & Shimansky, 1954, all from Ruzhencev & Shimansky (1954). **A**. *Rhiphaeoceras venustum* Ruzhencev & Shimansky, 1954. **B**. *Pararhiphaeoceras tastubense* Ruzhencev & Shimansky, 1954. **C**. *Sholakoceras bisulcatum* Ruzhencev & Shimansky, 1954. Scale bar units = 1 mm.

Included genera

Rhiphaeoceras Ruzhencev & Shimansky, 1954 (Sakmarian to Artinskian; 2 species).
Pararhiphaeoceras Ruzhencev & Shimansky, 1954 (Asselian to Wuchiapingian; 5 species).
Sholakoceras Ruzhencev & Shimansky, 1954 (Asselian to Artinskian; 4 species).
Rhiphaeonautilus Ruzhencev & Shimansky, 1954 (Artinskian; 1 species).
Eximioceras Shchedukhin, 2022 (Asselian or Sakmarian; 1 species).
New genus D to be described by Korn & Ghaderi (in press) (Wuchiapingian; 2 species).

Remarks

The family Rhiphaeoceratidae can be distinguished from other Permian nautiloids by their suture line with its rather deep internal lobe. The only exceptions are the representatives of the family Aktubonautilidae, but these differ in having a much larger juvenile conch.

Family **Foordiceratidae** fam. nov.

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Fig. 28

Type genus

Foordiceras Hyatt, 1893.

Diagnosis

Family of the superfamily Tainoceratoidea with a trapezoidal whorl profile; ventrolateral shoulder rounded, flanks strongly divergent. Sculpture with ventrolateral conical nodes, sometimes with low ribs on the flank. Suture line with shallow lobes and low saddles. Internal lobe very shallow, without annular process.

Etymology

The family name refers to the type genus.

Included genera

Foordiceras Hyatt, 1893 (Wuchiapingian to Changhsingian; 8 species).
Foordoceras Girty, 1908 [nomen nullum].
Araxonautilus Shimansky, 1979 (Wordian to Wuchiapingian; 3 species).

New genus E to be described by Korn & Ghaderi (in press) (Wuchiapingian to Changhsingian; 3 species).

Remarks

The repeated stratigraphic occurrence of nautiloids with an open umbilicus, a trapezoidal whorl profile and a sculpture with ventrolateral ribs or nodes in the Late Carboniferous (e.g., *Latitemnocheilus*), Early Permian (e.g., *Pseudotemnocheilus*, *Articheilus*) and Late Permian (e.g., *Foordiceras*) is a phenomenon that is not easy to explain. In order to approach this problem, four hypotheses can be discussed:

Hypothesis 1: the species of interest are a monophyletic unit descended from an ancestor with similar conch geometry and sculpture, such as the Early Carboniferous genus *Temnocheilus*. This may be the most parsimonious explanation in terms of morphological evolution, but it would imply a very long and simple evolutionary lineage starting in the Late Viséan and ending in the Changhsingian. It should be noted, however, that this hypothesis is mainly based on adult morphology; the juvenile conch, which is unknown in many species, plays only a minor role. For example, it is not clear whether the genera discussed also possess the characteristic bicarinate juvenile whorl profile, the longitudinal ornamentation and the deep and V-shaped inner lobe of *Temnocheilus*.

Sturgeon *et al.* (1982: 1461; 1997: 48) proposed an origin of *Latitemnocheilus* from *Temnocheilus*, because they found the longitudinal ornament characteristic for *Temnocheilus* also in similar development in two species of *Latitemnocheilus*, but not in *Metacoceras*. As a consequence, they concluded that "… temnocheilids were not the ancestors of, or closely related to, *Metacoceras* as suggested by Miller *et al.* (1933: p. 160), Miller & Owen (1934, p. 221) and Miller & Youngquist (1949, p. 94)".

Hypothesis 2: the species compose a monophyletic unit, descended from a Late Carboniferous genus such as *Metacoceras* by a transformation of the inverted trapezoidal or almost rectangular whorl profile to a trapezoidal shape. This was accompanied by a regression of the angular umbilical margin. After

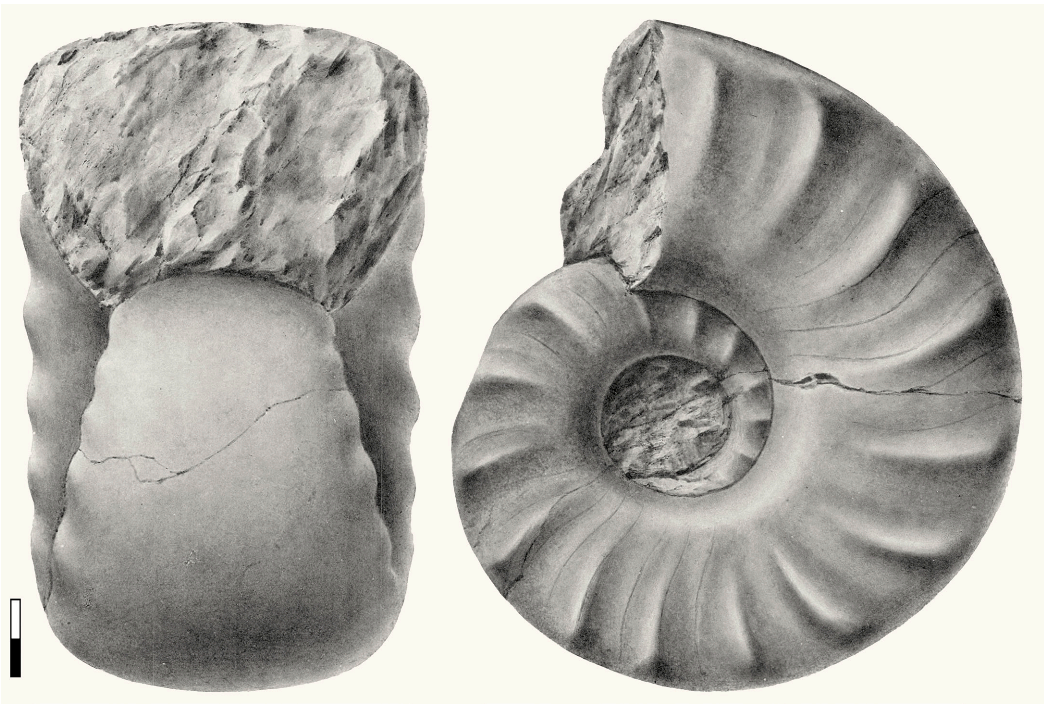

Fig. 28. Family Foordiceratidae fam. nov. *Foordiceras goliathum* (Waagen, 1879), from Miller & Youngquist (1949), after Waagen (1879). Scale bar units = 10 mm.

this initial evolution, the lineage continued with only minor morphological changes throughout the Late Permian.

An origin of *Latitemnocheilus* from *Metacoceras* may be explained by the rather close resemblance of the adult morphology of these two genera, which differ mainly in the presence or absence of a pronounced umbilical margin.

Hypothesis 3: the species do not share the same phylogenetic origin; the Late Carboniferous and Permian nautiloids with trapezoidal whorl profile represent unrelated clades. In this hypothesis, the Early Permian genera such as *Pseudotemnocheilus* independently originated from *Metacoceras* or a similar genus by deflation of the umbilical margin. This scenario was proposed by Ruzhencev & Shimansky (1954: 45). Dzik (1984: 160) suggested to amalgamate the Early Permian species attributed to *Metacoceras* and *Pseudotemnocheilus* by Ruzhencev & Shimansky (1954) in one genus because of the minor morphological differences between the species.

Hypothesis 4: the species repeatedly descended from ancestors with a pronounced umbilical margin in the Late Carboniferous, Early Permian and Late Permian, respectively. This may be the morphologically least parsimonious solution. At the same time, it turns out that in all three cases there are morphoclines in each of the time intervals, which can be used as a good supporting argument for this hypothesis.

The ontogeny of the juvenile conch can provide solid information on the phylogenetic relationships between these species. Although the juvenile conch of the Late Permian genera is poorly known, it appears that it is more similar to the Early Permian genus *Pseudotemnocheilus*, with its more circular whorl profile, than to the Early Carboniferous genus *Temnocheilus*, which has a bicarinate juvenile conch. This may argue for an evolutionary lineage connecting the Permian groups, i.e., a descent of the Foordiceratidae from the metacoceratids.

Family **Pleuronautilidae** Hyatt, 1900
Fig. 29

Diagnosis

Family of the superfamily Pleuronautiloidea with a commonly subquadrate or weakly depressed whorl profile; venter ranging from convex to weakly concave, ventrolateral shoulder and umbilical margin often pronounced, flanks usually weakly convergent. Sculpture with numerous ribs on the flank, sometimes with conical tubercles and more rarely with spiral ridges. An annular process is present in the advanced species.

Included genera

New genus C to be described by Korn & Hairapetian (in press) (Wordian to Changhsingian; 10 species).
Pleuronautilus Mojsisovics, 1882 (Triassic).
Phloioceras Hyatt, 1884 (Triassic).
Anoploceras Hyatt, 1900 (Triassic).
Encoiloceras Hyatt, 1900 (Triassic).
Enoploceras Hyatt, 1900 (Triassic).
Holconautilus Mojsisovics, 1902 (Triassic).
Trachynautilus Mojsisovics, 1902 (Triassic).
Sibyllonautilus Diener, 1915 (Triassic).
Phaedrysmocheilus Shimansky & Erlanger, 1955 (Triassic).
Arctonautilus Sobolev, 1989 (Triassic).
Grumantoceras Sobolev, 1989 (Triassic).

Remarks

Pleuronautilus is a genus that has been the subject of very different opinions in the literature over the last few decades. The genus was established by Mojsisovics (1902) for the very distinctive Triassic species *Pleuronautilus trinodosus*. von Arthaber (1900: 215) also used the genus name for the Late Permian forms similar to the species "*Nautilus dorso armatus*" that was described by Abich (1878) and his newly established species "*Pleuronautilus Verae*"; he considered both to be closely related.

While Miller & Youngquist (1949) did not use the genus name *Pleuronautilus* for Permian nautilids, Kummel (1953: 34) placed 24 Permian species in this genus, together with 34 Triassic species. The reason for this high number is that Kummel also included a number of species in *Pleuronautilus* that had previously been placed in other genera (*Metacoceras*, *Foordiceras*, *Huanghoceras*).

Ruzhencev & Shimansky (1954) reduced the species composition of *Pleuronautilus* by accepting the genera *Huanghoceras* and *Shansinautilus* and by establishing the new genus *Pseudofoordiceras* for some species from the Leonard Formation of Texas, which were previously placed in the genus *Metacoceras* by Miller (1945) and in *Foordiceras* by Miller & Youngquist (1949). However, Shimansky (1967) considered these three genera as being synonyms of *Pleuronautilus*; he listed 19 species belonging to this genus. Kummel (1964), in the *Treatise on Invertebrate Paleontology*, had already before synonymised the genera *Huanghoceras*, *Shansinautilus*, *Tungkuanoceras*, *Basleonautilus* and *Pseudofoordiceras* with *Pleuronautilus*.

It has already been suggested by previous authors that it is difficult to distinguish clearly between genera such as *Metacoceras* and *Pleuronautilus* in the Permian nautiloid assemblages as interpreted at that time (e.g., Kummel 1953: 34). To ensure a monophyletic definition of *Pleuronautilus* and related genera, it is necessary to investigate the possible phylogenetic origin of these genera and their relationships. It also needs to be clarified whether species with *Pleuronautilus*-like conch morphology and sculpture, such as the recently described Late Permian *Serometacoceras* and *Lutonautilus*, could have evolved independently during the Permian.

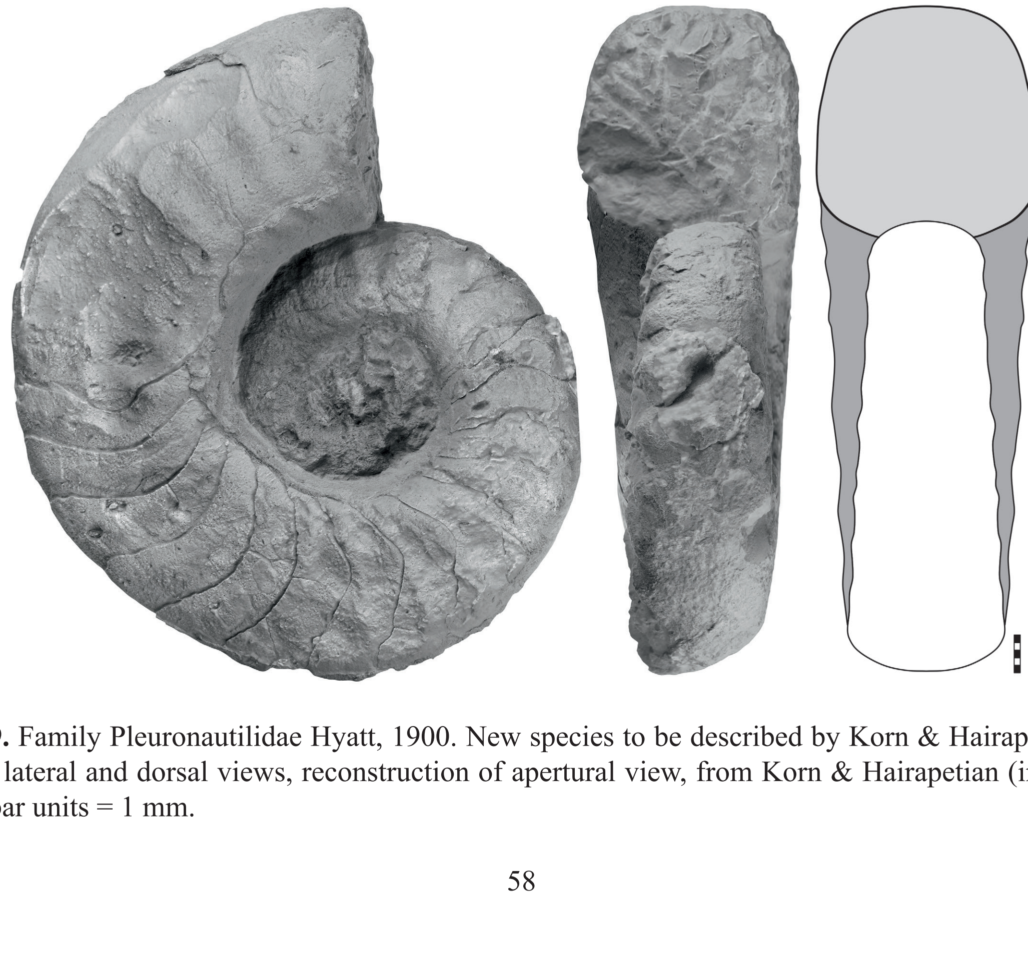

Fig. 29. Family Pleuronautilidae Hyatt, 1900. New species to be described by Korn & Hairapetian (in press); lateral and dorsal views, reconstruction of apertural view, from Korn & Hairapetian (in press). Scale bar units = 1 mm.

Earlier authors had already considered that, starting from the putative ancestral genus *Metacoceras*, lateral branches with strengthened sculpture gave rise to several genera with coarse sculpture, such as *Huanghoceras* from the Taiyuan Series of North China (Yin 1933) and *Pseudofoordiceras* from the Leonard Formation of Texas (Ruzhencev & Shimansky 1954). Apparently, such considerations have not yet been made for the Late Permian species of the Transcaucasus. Both Shimansky (1965) and Teichert & Kummel (1973) assigned the species of this group of species to the two genera *Metacoceras* and *Pleuronautilus*. Such a practice would imply that the latter genus actually has a Late Permian origin. However, the empirical data is hardly sufficient for such a statement.

Here, the family Pleuronautilidae is reduced in its content to the Triassic species, which share some morphological characteristics, such as the rather dense transverse ribbing. Furthermore, they could be united by the presence of an annular process of the suture line, which means that they have a dorsal inflexion of the septum.

There are some Late Permian species that have a very similar shell and sculpture to *Pleuronautilus*, but the apparent lack the annular process. These will shortly be described as new genus C by Korn & Hairapetian (in press) and may be the ancestors of the Triassic pleuronautilids.

Superfamily **Tainoceratoidea** Hyatt, 1883

Diagnosis

Superfamily of the suborder Tainoceratina with a discoidal to pachyconic, subinvolute or subevolute conch. Whorl profile always with midventral longitudinal groove; in early species subquadrate with a distinct ventrolateral shoulder and a distinct umbilical margin, in derived species polygonal with divergent or convergent flanks. Dorsal whorl zone always very small. Sculpture with rows of ventrolateral nodes, in some species with rows of nodes on the flank. Septa simply domed; suture line depending on the whorl profile, usually with shallow lobes and low saddles.

Included family

Tainoceratidae Hyatt, 1883 (Late Carboniferous to Early Triassic; 23 Palaeozoic genera, 89 Palaeozoic species).

Remarks

The superfamily Tainoceratoidea as used here corresponds to the family Tainoceratidae as employed by earlier authors. It is generally regarded as one of the most important Late Carboniferous to Triassic nautiloid clades. Its family composition and internal classification have been discussed repeatedly over the last 90 years, and various concepts for the differentiation of the genera have been presented. As many of the other families of the suborder are placed within the Pleuronautiloidea, only one family is accepted here:

Tainoceratidae Hyatt, 1883 – Forms with usually octagonal whorl profile; sculpture usually with several rows of nodes (Fig. 30).

Family **Tainoceratidae** Hyatt, 1883
Fig. 30

Diagnosis

Family of the superfamily Tainoceratoidea with a discoidal to pachyconic, subinvolute or subevolute conch. Whorl profile always with midventral longitudinal groove; in early species subquadrate with a distinct ventrolateral shoulder and a distinct umbilical margin, in derived species polygonal with divergent or convergent flanks. Dorsal whorl zone always very small. Sculpture with rows of ventrolateral nodes, in some species with rows of nodes on the flank. Septa simply domed; suture line depending on the whorl profile, usually with shallow lobes and low saddles.

Included genera

Tainoceras Hyatt, 1883 (Kasimovian to Changhsingian; 41 species).
Tainionautilus Mojsisovics, 1902 (Wuchiapingian to Early Triassic; 6 species).
Tirolonautilus Mojsisovics, 1902 (Changhsingian; 8 species).
Tylonautilus Pringle & Jackson, 1928 (Serpukhovian to Bashkirian; 6 species).
Aulametacoceras Miller & Unklesbay, 1942 (Roadian; 2 species).
Hexagonites Hayasaka, 1947 (Permian; 1 species)?
Hunanoceras Chao, 1954 (Roadian; 1 species).
Hefengnautilus Xu, 1977 (Roadian; 1 species).
Clavinautilus Zhao, Liang & Zheng, 1978 (Changhsingian; 1 species).
Eulomacoceras Zhao, Liang & Zheng, 1978 (Wuchiapingian; 3 species).
Lirometacoceras Zhao, Liang & Zheng, 1978 (Changhsingian; 1 species).
Neotainoceras Zhao, Liang & Zheng, 1978 (Changhsingian; 5 species).
Paratainonautilus Zhao, Liang & Zheng, 1978 (Changhsingian; 1 species).
Seironautilus Zhao, Liang & Zheng, 1978 (Wuchiapingian; 1 species).
Neoclavinautilus Liang, 1984 (Changhsingian; 1 species).
Nodonautilus Liang, 1984 (Wuchiapingian; 1 species).

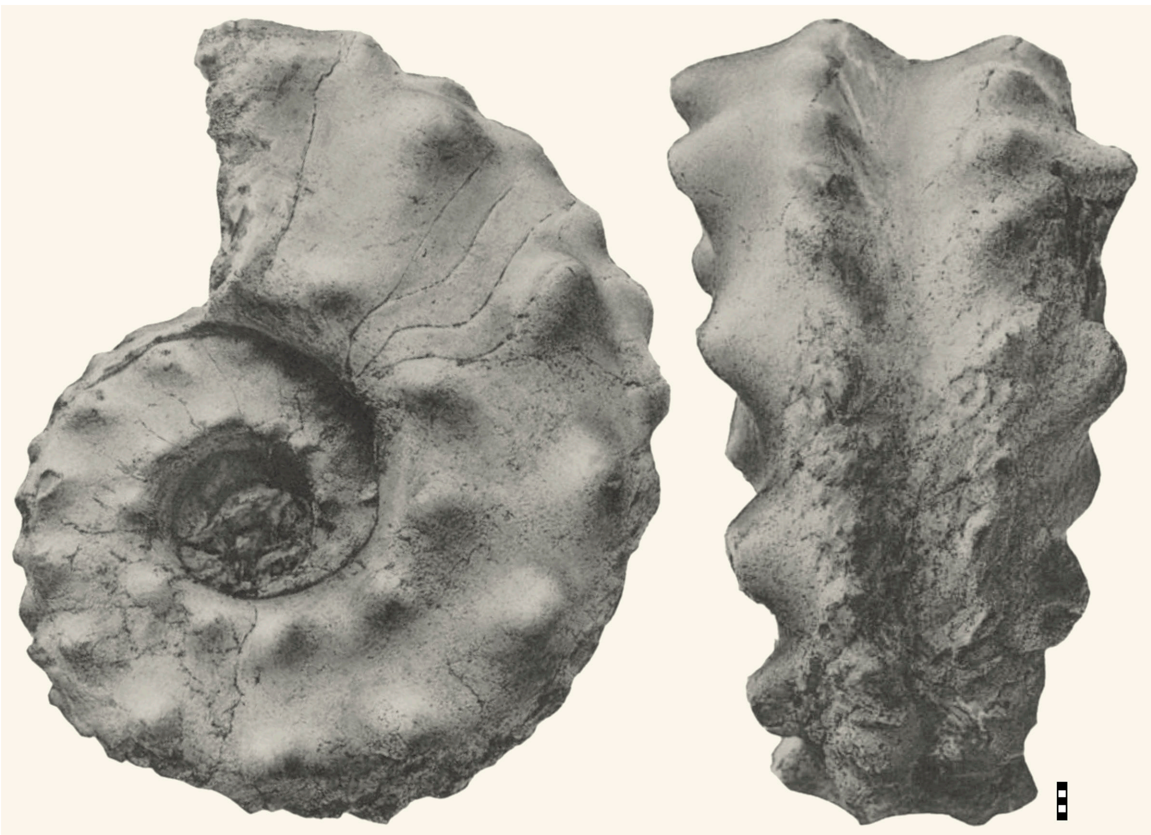

Fig. 30. Family Tainoceratidae Hyatt, 1883. *Tainoceras schellbachi* Miller & Unklesbay, 1942, from Miller & Unklesbay (1942). Scale bar units = 1 mm.

? *Aulagonoceras* Zheng, 1984 (Changhsingian; 4 species).
Nodopleuroceras Zheng, 1984 (Changhsingian; 2 species).
Meixianlingites Qin, 1986 (Wuchiapingian; 1 species).
Paratainoceras Qin, 1986 (Wuchiapingian; 1 species).
Siamnautilus Ishibashi *et al*., 1994 (Changhsingian; 1 species).
Gujiaonautilus Miao *et al*., 2019 (Changhsingian; 1 species).
New genus F to be described by Korn & Ghaderi (in press) (Wuchiapingian; 1 species).
New genus D to be described by Korn & Hairapetian (in press) (Wuchiapingian; 2 species).

Remarks

The Tainoceratidae are a fairly well-defined family characterised by the presence of a prominent midventral groove; most of the species possess at least two rows of ventral or ventrolateral nodes. Additional rows of nodes may be developed on the flanks and ventrolateral shoulder. However, there is a reduction in the number of nodes in some derived Late Permian genera.

Ruzhencev & Shimansky (1954) stated that *Tainoceras* appears to be derived from *Metacoceras*. An argument in favour of this hypothesis could be the stratigraphic co-occurrence of the oldest species of the two genera in Late Carboniferous cephalopod assemblages. However, this hypothesis implies a significant leap in morphological evolution towards *Tainoceras*. It should be noted that *Metacoceras* and related genera usually have inverted trapezoidal or rectangular whorl profiles, in contrast to the polygonal whorl profiles of *Tainoceras*. *Metacoceras* and its close relatives also lack a midventral groove. Finally, *Metacoceras* does not have a sculpture with rows of nodes on the venter; the sculpture elements are restricted to the flanks.

The family Tainoceratidae became diverse in the latest Carboniferous Gzhelian stage, when the single genus *Tainoceras* was geographically widespread with a number of species (e.g., Sturgeon *et al.* 1982, 1997). The family persisted with this single genus throughout most of the Permian (e.g., Miller *et al.* 1933; Miller & Unklesbay 1942; Miller & Youngquist 1949). It continued into the Late Permian, when a large number of new species had evolved, particularly in the Late Permian shelf seas of southern China. To date, more than twelve tainoceratid genera have been described from this single region (Chao 1954; Xu 1977; Zhao *et al.* 1978; Liang 1984; Zheng 1984; Qin 1986; Miao *et al.* 2021). This is far more than in any other region where tainoceratids occur at the same time, such as Europe with the Dolomites (Prinoth & Posenato 2007), the Bűkk Mountains (Schréter 1974) and Serbia (Simić 1933). Transcaucasia (Korn & Ghaderi in press) and central Iran (Korn & Hairapetian in press) are also relatively poor in tainoceratids compared to southern China.

There is a very asymmetric distribution of species composing the genera of the family Tainoceratidae. Of the 22 genera, 14 are monospecific and four have two or three previously known species. The most species-rich genera *Tainoceras* (41 species), *Tirolonautilus* (8 species) and *Tainionautilus* (6 species) are, interestingly or significantly, the first described genera of the family (Hyatt 1883–1884; Mojsisovics 1902).

Suborder **Liroceratina** Flower, 1955

Fig. 31

Diagnosis

Suborder of the order Nautilida, in which an umbilical margin is formed early in ontogeny; advanced species may regress this character. Conch usually pachyconic and rarely discoidal or globular, subinvolute to involute. Juvenile whorl profile circular. Adult whorl profile usually circular or depressed oval without distinct ventrolateral shoulder in the early species, showing modifications during evolution (inverted trapezoidal with convergent flanks and flattened venter). Dorsal whorl zone always present, small to moderately deep. Juvenile sculpture with spiral lines that may be restricted to the umbilical area in the early species; adult sculpture usually lacking except for spiral lines in some species. Septa simply domed in the early species, with dorsal inflexion in advanced species and with corrugated septa in two derived clades. Suture line depending on the whorl profile, usually with shallow lobes and low saddles, with distinct lobes in two clades. Siphuncle in central or subcentral position.

Included superfamilies

Liroceratoidea Miller & Youngquist, 1949 (Early Carboniferous to Late Triassic; 23 Palaeozoic genera, 142 Palaeozoic species).
Ephippioceratoidea Miller & Youngquist, 1949 (Early Carboniferous to Early Permian; 3 genera, 26 species).
Clydonautiloidea Hyatt, 1900 (Middle to Late Triassic).

Remarks

Taxonomy

The suborder Liroceratina was interpreted by Shimansky (1957) as consisting of the superfamily Lirocerataceae Miller & Youngquist, 1949 with the mostly Palaeozoic families Koninckioceratidae, Liroceratidae Miller & Youngquist, 1949, Ephippioceratidae Miller & Youngquist, 1949 and Paranautilidae Kummel in Flower & Kummel, 1950 and the fully Mesozoic superfamily Clydonautiloidea

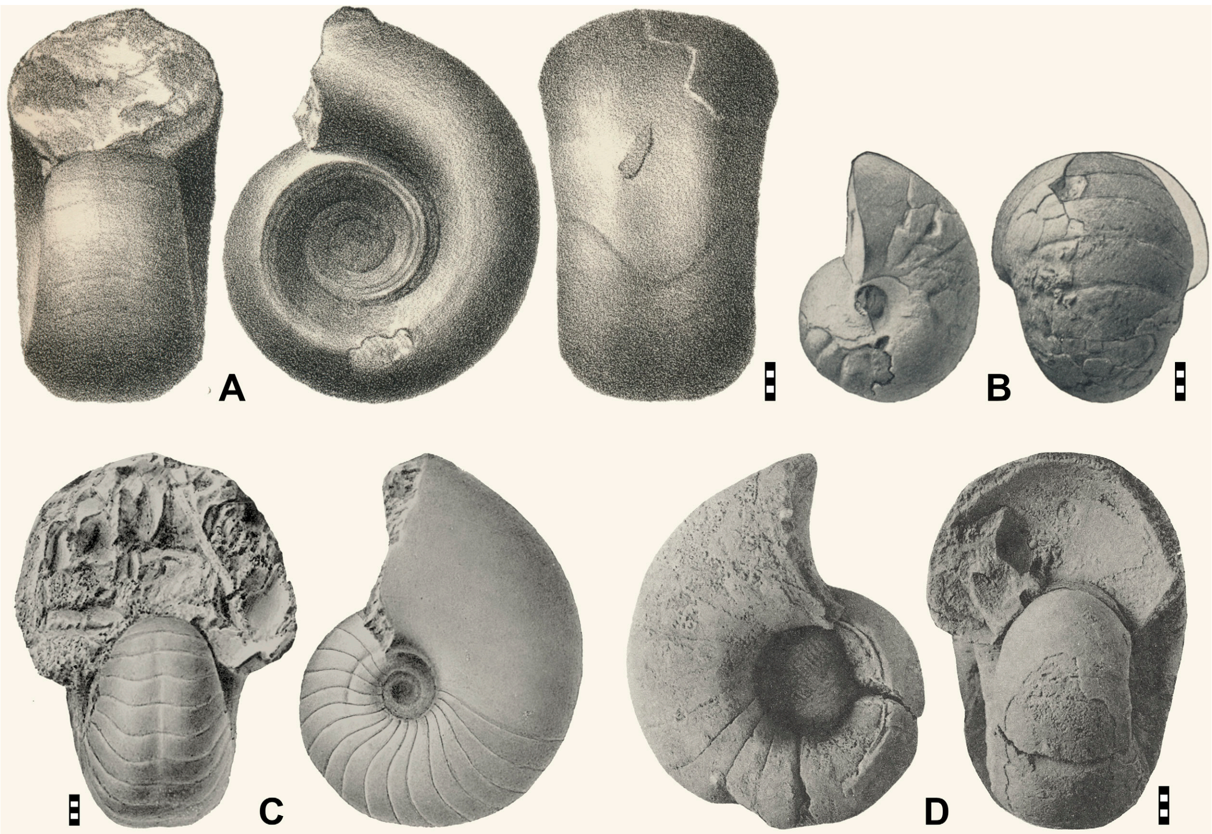

Fig. 31. Family Liroceratidae Miller & Youngquist, 1949. **A**. *Bistrialites bistrialis* (Phillips, 1836), from Foord (1900). **B**. *Liroceras liratum* (Girty, 1912), from Girty (1915). **C**. *Coelogasteroceras canaliculatum* (Cox, 1857), from Miller & Youngquist (1949). **D**. *Potoceras dubium* Hyatt, 1894, from Kummel (1963). Scale bar units = 1 mm.

Hyatt, 1900. Kummel (1964) included the families Liroceratidae, Ephippioceratidae, Clydonautilidae, Gonionautilidae Kummel in Flower & Kummel, 1950 and Siberionautilidae Popov, 1951 in his superfamily Clydonautilaceae.

Morphology and subdivision

Almost all Carboniferous and Permian genera of the suborder Liroceratina, which all belong to the superfamilies Liroceratoidea and Ephippioceratoidea, are easily recognised by their stout, narrowly umbilicate conch. All have either a very simple, almost straight suture line (Liroceratoidea) or a suture line with a high ventral saddle (Ephippioceratoidea). Only the Triassic descendants (superfamily Clydonautiloidea) show a modification of the conch by lateral compression and complete closure of the umbilicus. These species show a complication of the suture line with the formation of lateral lobes; they are the nautiloids with the most complex suture lines.

The suborder Liroceratina represents a large group of species that differ in their conch morphology from the other nautiloid suborders of the Late Palaeozoic and Triassic. The liroceratids are predominantly pachyconic or globular with a narrow or completely closed umbilicus (Fig. 31). The whorl profile is usually reniform, the flanks and venter often merging into a more or less uniformly convex arch. In stratigraphically older genera (e.g., *Bistrialites* Turner, 1954, *Liroceras*) the umbilical margin is usually uniformly rounded and the umbilical wall convex; in derived species the umbilical margin may be subangular and the umbilical wall flattened. Some derived genera (*Coelogasteroceras* Hyatt, 1893, *Permonautilus* Kruglov, 1933 and members of the Clydonautiloidea) show a longitudinal depression on the venter or a galeate form (*Callaionautilus* Kieslinger, 1924).

The suborder Liroceratina consists of three superfamilies, which differ mainly in the morphological evolution of the septal shape and the suture lines:

Liroceratoidea. – Forms with a simple suture line extending almost straight across the umbilical wall, the flanks and the venter. The dorsal suture is also usually almost straight. Some genera (e.g., *Paranautilus* Mojsisovics, 1902) have an annular process, but this may occur only intermittently during ontogeny (Sobolev 1989: 18).

Ephippioceratoidea. – Forms with a highly elevated ventral saddle created by a striking division of the septal surface by a prominent ventrodorsal ridge into two broadly arched domes.

Clydonautiloidea. – Forms with a highly elevated ventral saddle, which is flat (*Styrionautilus* Mojsisovics, 1902) or divided by an external lobe (*Proclydonautilus* Mojsisovics, 1902). There may be several secondary external lobes (*Siberionautilus* Popov, 1951) or extensive separation of the entire suture line (*Yakutionautilus* Arkhipov & Barskov, 1970) (Arkhipov & Barskov 1970; Sobolev 1989). The internal lobe is shallow; an annular process may be present.

Origin

The liroceratids were considered by Flower & Kummel (1950) to be the basal representatives of the order Nautilida (corresponding to the suborder Nautilina in current understanding), which, like the three other nautiloid orders of the Carboniferous and Permian accepted by them, should have originated in the Devonian family Barrandeoceratidae Foerste, 1925. Shimansky (1957) derived the suborder Liroceratina (as he used it) from the Devonian family Litogyroceratidae Shimansky, 1957 (suborder Rutoceratina). Kummel (1964) also saw the origin of his superfamily Clydonautilaceae (which corresponds to the Liroceratina of Shimansky) in the Devonian; he assumed that the group originated from the order Oncocerida Flower.

The assumption that the liroceratids originated in the Devonian is probably based on the problematic genus *Potoceras* Hyatt, 1894. The only species, *P. dubium* Hyatt, 1894, was based on a single specimen that was poorly illustrated by Hyatt. Kummel (1963) gave a detailed description and a good photographic illustration of the holotype. Hyatt (1894: 538) did not know the provenance or stratigraphic position of the specimen and believed it to be Devonian. This was confirmed by Charles Schuchert, who suggested the Iberg in the Harz Mountains as the locality, based on a spiriferid brachiopod attached to the nautilid. Kummel (1963: 356) had this information checked by G.A. Cooper, who concluded that it was probably a Viséan brachiopod. If the specimen indeed comes from the Iberg, which is by no means certain, it could actually be a specimen from the well-known Early Carboniferous Neptunian dykes, in which cephalopods and spiriferids have been identified (e.g., Schindewolf 1951).

The conch morphology of the holotype of *Potoceras dubium* is very similar to the typical Early Carboniferous representatives of *Liroceras* or *Bistrialites*, such as those described by Foord (1891) and Turner (1954) from northern England, by Trenkner (1868) and Schmidt (1951) from the Harz Mountains, and by Korn & Klug (2023) from the Anti-Atlas of Morocco. For this reason, too, it is reasonable to assume that the stratigraphic age of *Potoceras dubium* is Early Carboniferous. *Potoceras* may even be a senior synonym of *Bistrialites* or *Liroceras*, but this problem cannot be solved at present because of the limited data available.

Dzik (1984: 168) proposed a fundamentally different hypothesis in which the family Liroceratidae (which he defined more broadly than the other authors) was derived from an Early Carboniferous group of nautilids, that is the family Trigonoceratidae. He based this hypothesis on the juvenile ornament with spiral ridges present in both *Liroceras* and *Vestinautilus* and postulated that both genera were related through *Bistrialites* Turner, 1954. There are several reasons for accepting this suggestion. An evolution from *Vestinautilus* to *Liroceras* would mainly involve a narrowing of the umbilicus, although this would be mainly due to an expansion of the ventral zone (Fig. 3E, J). Therefore, the spiral ridges are still located in the area of the (topographic) ventrolateral shoulder in *Vestinautilus*, in the middle of the flank in *Bistrialites* and in the (topographic) umbilical margin in *Liroceras*.

Phylogeny

Several scenarios have been developed to clarify the phylogeny within the liroceratids. Shimansky (1957, 1962) proposed three independent evolutionary lineages, the first of which (Koninckioceratidae) is placed here in the suborder Temnocheilina. The superfamily Clydonautilaceae was derived from the Lirocerataceae by Shimansky. This phylogenetic scheme was supported by Kummel (1964).

Descendants

Flower & Kummel (1950) linked, albeit with a question mark, the families that are now considered part of the suborder Nautilina Agassiz, 1847 (e.g., Nautilidae de Blainville, 1825, Aturiidae Chapman, 1857) to the family Paranautilidae, which they accepted as valid. This view was not shared by later authors (Shimansky 1962; Kummel 1964; Dzik 1984).

Superfamily **Liroceratoidea** Miller & Youngquist, 1949

Diagnosis

Superfamily of the suborder Liroceratina with a pachyconic and rarely discoidal or globular, subinvolute to involute conch. Whorl profile usually circular or depressed oval without distinct ventrolateral shoulder; in some species with a pronounced but rounded ventrolateral shoulder. Dorsal whorl zone usually small to moderately deep. Juvenile sculpture in the early species with spiral lines that may be restricted to the umbilical area; derived species are often smooth. Suture line very simple, almost straight across flanks and venter.

Included families

Liroceratidae Miller & Youngquist, 1949 (Early Carboniferous to Late Permian; 17 Palaeozoic genera, 118 Palaeozoic species).
Coloceratidae Hyatt, 1893 [homonym; synonym of Liroceratidae Miller & Youngquist, 1949].
Paranautilidae Kummel in Flower & Kummel, 1950 (Early to Late Triassic).
Permonautilidae Barskov & Shilovsky, 2014 (Middle to Late Permian; 1 genus, 10 species).
Planetoceratidae fam. nov. (Early to Late Carboniferous; 1 genus, 9 species).
New family to be described by Korn & Ghaderi (in press) (Late Permian; 3 genera, 5 species).

Remarks

The species of the Liroceratoidea can easily be distinguished from the species of the other superfamilies of the Liroceratina by the simple septal shape and thus the very simple, almost straight suture line.

The Palaeozoic families are characterised as follows:

Liroceratidae Miller & Youngquist, 1949 – Ancestral forms with involute or subinvolute conch, umbilical wall usually rounded (Fig. 32).

Planetoceratidae fam. nov. – Ancestral forms, in which the terminal whorl detaches from the preceding whorl (Fig. 33).

Permonautilidae Barskov & Shilovsky, 2014 – Advanced forms, which possess a prominent thorn-like umbilical process in the adult stage (Fig. 34).

New family to be described by Korn & Ghaderi (in press) – Ancestral forms with a pronounced umbilical margin and a flattened umbilical wall; the venter has the tendency to become flattened or weakly concave (Fig. 35).

Family **Liroceratidae** Miller & Youngquist, 1949
Fig. 32

Diagnosis

Family of the superfamily Liroceratoidea with a usually pachyconic or globular, subinvolute to subevolute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter form a continuous arch in the early species, the venter can be flattened or concave in advanced species. Umbilical margin rounded; umbilical wall usually convex. Ornament usually consisting of fine growth lines; spiral lines occur in some genera. Septum simple in shape, concavely domed; suture line very simple, almost straight across flanks and venter or with small lobes and saddles.

Included genera

Solenoceras Hyatt, 1884 [homonym of *Solenoceras* Conrad, 1860; objective synonym of *Coelogasteroceras*].
Coelogasteroceras Hyatt, 1893 (Bashkirian to Changhsingian; 11 species).
Coloceras Hyatt, 1893 [homonym of *Coloceras* Taschenberg, 1882; synonym of *Liroceras*].
Stearoceras Hyatt, 1893 (Serpukhovian to Changhsingian; 10 species).
Peripetoceras Hyatt, 1894 (Serpukhovian to Changhsingian; 22 species).
Potoceras Hyatt, 1894 (? Viséan; 1 species).
Nannoceras Hyatt, 1894 [nomen nullum; synonym of *Peripetoceras*].
Conradiceras Cossmann, 1900 [objective synonym of *Coelogasteroceras*].
Cyclonautilus Hind, 1910 [synonym of *Peripetoceras*].
Liroceras Teichert, 1940 (Viséan to Changhsingian; 47 species).
Condraoceras Miller, Lane & Unklesbay, 1947 (Kasimovian to Artinskian; 3 species).
Periptoceras Chao, 1954 [nomen nullum; synonym of *Peripetoceras*].
Hemiliroceras Ruzhencev & Shimansky, 1954 (Bashkirian to Artinskian; 6 species).

Bistrialites Turner, 1954 (Viséan to Serpukhovian; 5 species).
Pseudophacoceras Turner, 1966 (? Viséan; 1 species).
Neobistrialites Tucker, Mapes & Aronoff, 1978 (Moscovian; 1 species).
Jianoceras Ma, 1997 (Permian; 1 species).
Nemdoceras Barskov & Shilovsky, 2014 (Roadian; 3 species).
Paraliroceras Barskov & Shilovsky, 2014 (Roadian to Changhsingian; 2 species).
Tatianautilus Barskov & Shilovsky, 2014 (Roadian; 1 species).
Leniceras Leonova & Shchedukhin, 2020 (Asselian or Sakmarian; 1 species).
Shikhanonautilus Leonova & Shchedukhin, 2020 (Asselian or Sakmarian; 1 species).
Thyoceras Leonova & Shchedukhin, 2020 (Asselian or Sakmarian; 1 species).
New genus G to be described by Korn & Ghaderi (in press) (Wuchiapingian; 1 species).
Perunautilus Crick & Sobolev, 1994 (Triassic).
Tomponautilus Sobolev, 1989 (Triassic).

Remarks

The Liroceratidae are probably the family with the longest stratigraphic range among the Palaeozoic Nautilida, extending from the Early Carboniferous to the Triassic. It can be regarded as a morphologically very stable clade in which morphological changes occurred only very rarely. Some of

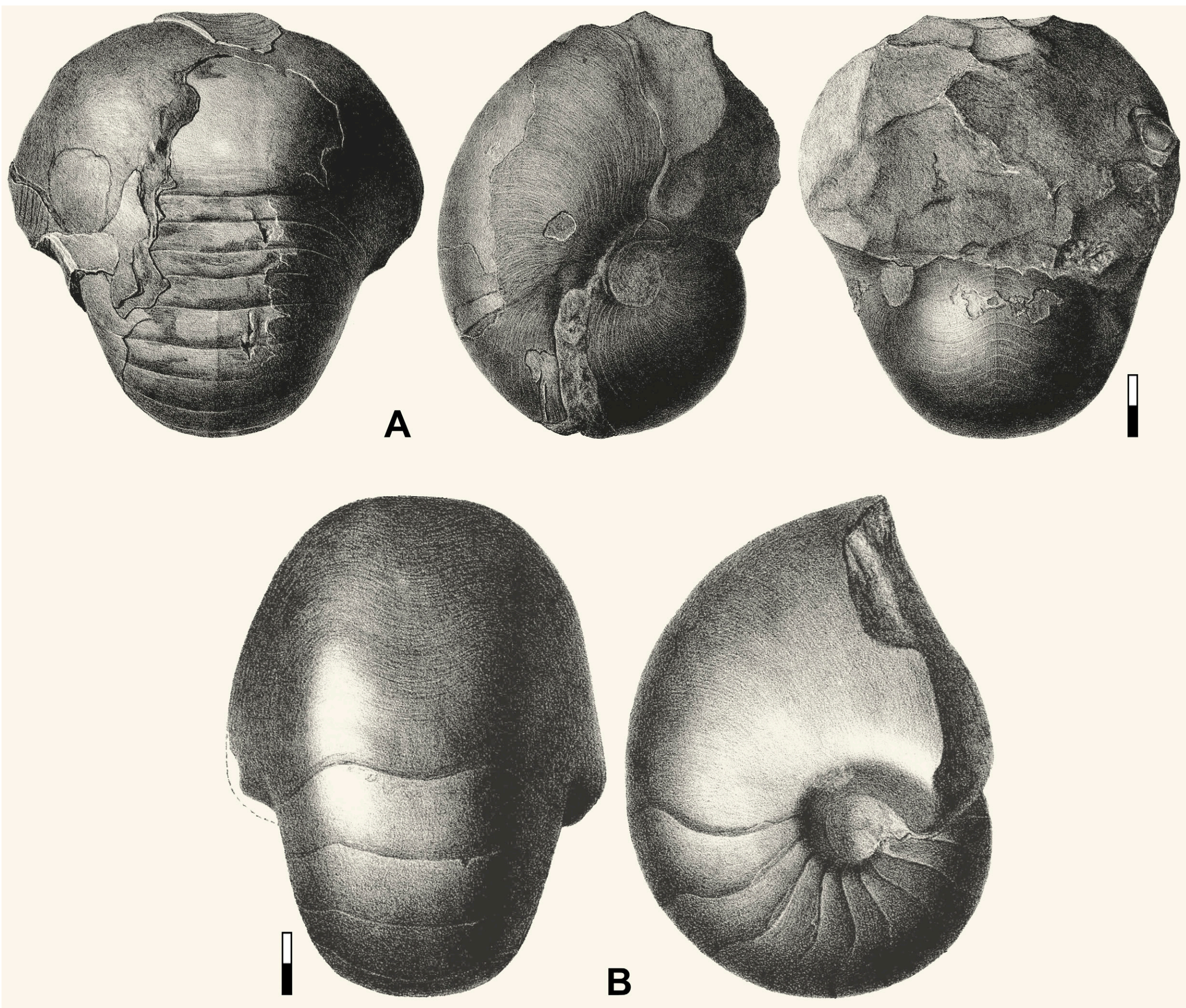

Fig. 32. Family Liroceratidae Miller & Youngquist, 1949, both from Hind (1910). **A**. *Liroceras globosum* (Hind, 1910). **B**. *Peripetoceras umbilicatum* (Hind, 1910). Scale bar units: A = 10 mm; B = 5 mm.

the new morphological developments have been separated as independent families (Permonautilidae, Paranautilidae), so that the Liroceratidae represent the conservative stem group.

The distribution of species among the 18 Palaeozoic genera within the Liroceratidae shows a very asymmetric picture. Nine genera are represented by only one species, while *Liroceras* and *Peripetoceras* are very diverse with 47 and 22 species, respectively. In addition, many species are known from only one specimen. As with many other groups of Nautilida, a revision is necessary and will probably change the picture so that fewer genera and species can be accepted.

Family **Planetoceratidae** fam. nov.
urn:lsid:zoobank.org:act:F919D8AF-4002-4CFE-BD02-0E8CFFC2EE66
Fig. 33

Type genus

Planetoceras Hyatt, 1893.

Diagnosis

Family of the superfamily Liroceratoidea with a pachyconic, usually subinvolute conch; the terminal portion of the conch is detached from the preceding whorl. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter form a continuous arch, umbilical margin pronounced, umbilical all flat and steep. Ornament consisting of fine growth lines. Septum simple in shape, concavely domed; suture line very simple, almost straight across flanks and venter or with small lobes and saddles.

Etymology

The family name refers to the type genus.

Fig. 33. Family Planetoceratidae fam. nov. *Planetoceras globatum* (Sowerby, 1824), from Foord (1900). Scale bar units = 1 mm.

Included genus

Planetoceras Hyatt, 1893 (Tournaisian to Kasimovian; 9 species).

Remarks

The placement of *Planetoceras* was problematic. *Planetoceras retardatum* Hyatt, 1893 and *P. globatum* (Sowerby, 1824) from early Late Tournaisian limestones of Belgium and Ireland have a peculiar conch morphology with a terminal whorl, which is depressed and oval in profile, and is detached from the preceding whorl. It is not possible to conclude whether the detached final volution in *Planetoceras* is due to increased coiling or secondary uncoiling.

Contrary to previous authors, a separate family is established for the genus *Planetoceras* and it is placed in the superfamily Liroceratoidea. Kummel (1964) placed *Planetoceras* in the then very heterogeneous family Koninckioceratidae. Shimansky (1967) also placed it together with the genera *Millkoninckioceras* and *Lophoceras* in the family Koninckioceratidae, which consisted of only three genera.

The shape of the inner volutions and their sculpture argue against placement in the Koninckioceratidae. *Planetoceras* has a distinct umbilical margin, with some coarse longitudinal ridges, giving it a morphology that is much closer to that of early liroceratids. Another common feature with the liroceratids is the expansion of the flank and venter area. In contrast to liroceratids, the umbilical wall of *Planetoceras* is flattened and steep. However, the most important distinguishing feature is the detachment of the adult whorl spiral.

Family **Permonautilidae** Barskov & Shilovsky, 2014
Fig. 34

Diagnosis

Family of the superfamily Liroceratoidea with a pachyconic or globular, usually subinvolute to subevolute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter form a continuous arch in the early forms, the venter can be flattened or concave in advanced forms. Terminal aperture with long lateral shell processes emerging from the umbilical margin. Ornament

Fig. 34. Family Permonautilidae Barskov & Shilovsky, 2014. *Permonautilus cornutus* (Golovkinsky, 1869), from Barskov *et al.* (2014). Scale bar units = 5 mm.

consisting of fine or coarse growth lines. Septum simple in shape, concavely domed; suture line very simple, almost straight across flanks and venter or with small lobes and saddles.

Included genera

Permonautilus Kruglov, 1933 (Roadian to Wuchiapingian; 10 species).
Alexandronautilus Shimansky, 1962 [synonym of *Permonautilus* Kruglov, 1933].

Remarks

The family Permonautilidae was introduced by Barskov & Shilovsky in Barskov *et al.* (2014) on the basis of virtually one character to separate it from the Liroceratidae, namely the presence of long lateral shell processes emerging from the umbilical margin. Such a process is apparently absent in the other genera of the superfamily Liroceratoidea. Very similar processes are only known from the family Solenochilidae (suborder Solenochilina), which is not related to the Permonautilidae. Barskov & Shilovsky in Barskov *et al.* (2014: 1391) clarified that the Permonautilidae are separated from the Solenochilidae by the position of the siphuncle, which is subcentral or centrodorsal in the Permoceratidae and subventral in the Solenochilidae.

The occurrence of the long shell processes in the Early to Late Carboniferous Solenochilidae and the Middle to Late Permian Permonautilidae is indeed a very interesting phenomenon, as both families belong to two unrelated evolutionary lineages that were probably separated already in the Devonian (Dzik 1984). Although the distinction between the two families Liroceratidae and Permonautilidae is based on only one character, the separation is still accepted here with reservations.

New family Korn & Ghaderi (in press)

Fig. 35

Diagnosis

Family of the superfamily Liroceratoidea with a usually pachyconic, subinvolute to involute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter usually separated by distinct ventrolateral shoulder, venter or concave. Umbilical margin subangular or angular; umbilical wall steep, flattened. Ornament usually consisting of fine growth lines. Septum simple in shape, concavely domed; suture line with shallow lobes on venter and flank (from Korn & Ghaderi in press: 98).

Included genera

New genus H to be described by Korn & Ghaderi (in press) (Changhsingian; 2 species).
New genus E to be described by Korn & Hairapetian (in press) (Wuchiapingian; 2 species).
New genus F to be described by Korn & Hairapetian (in press) (Wuchiapingian; 1 species).

Remarks

The new family is characterised by a combination of characters not found in any other family of Palaeozoic nautilids. This is the combination of a rather stout conch with a very pronounced umbilical margin and also a sometimes pronounced ventrolateral shoulder. While the first character suggests a placement in the superfamily Liroceratoidea, the second and third characters show a closer morphological relationship to the superfamilies Pleuronautiloidea and Grypoceratoidea. Unfortunately, the early ontogenetic development of the conch in the species of the new family is not known. However, the material shows that the pronounced umbilical margin is present early in ontogeny and that this feature can therefore be considered apomorphic, whereas the ventrolateral shoulder does not assume a subangular shape until a late ontogenetic stage, if at all. Therefore, these genera are included here as a new family of the superfamily Liroceratoidea (from Korn & Ghaderi in press: 98).

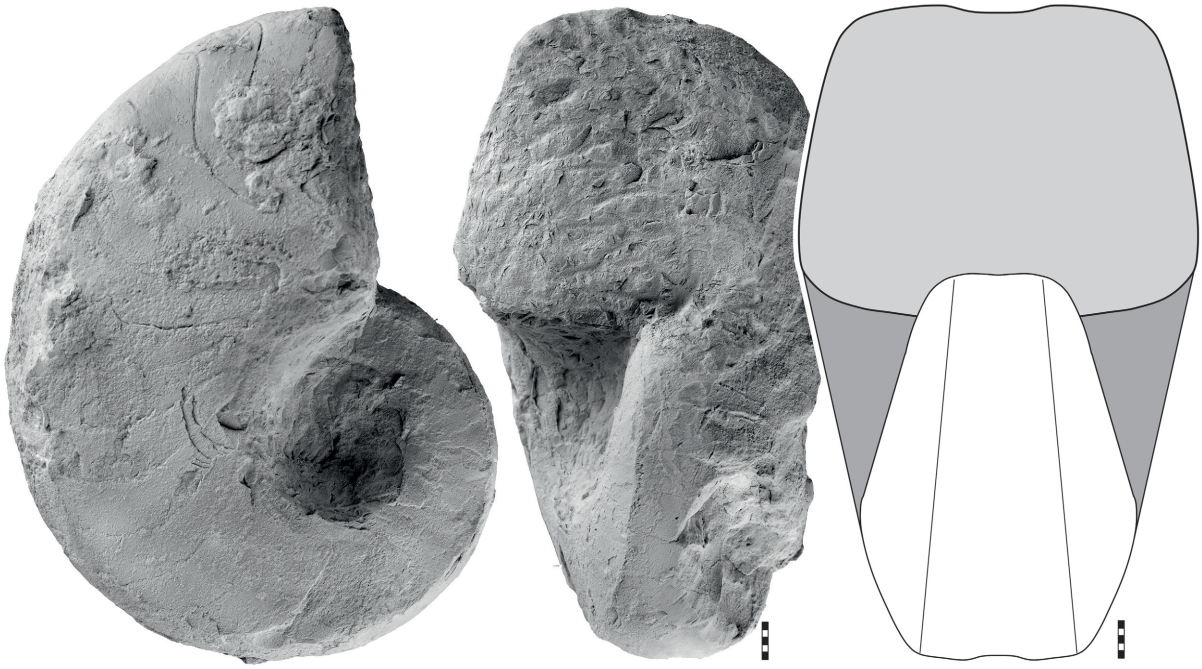

Fig. 35. New family to be described by Korn & Ghaderi (in press). New species to be described by Korn & Ghaderi (in press), lateral and apertural views, reconstruction of apertural view, from Korn & Ghaderi (in press). Scale bar units = 1 mm.

Superfamily **Ephippioceratoidea** Miller & Youngquist, 1949

Diagnosis

Superfamily of the suborder Liroceratina with a pachyconic or globular, involute to subinvolute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter form a continuous arch. Ornament usually consisting of fine growth lines; some species have spiral lines or fine ribs. Septum strikingly bilobate; suture line with high external saddle.

Included family

Ephippioceratidae Miller & Youngquist, 1949 (Early Carboniferous to Early Permian; 3 genera, 26 species).

Family **Ephippioceratidae** Miller & Youngquist, 1949
Fig. 36

Diagnosis

Family of the superfamily Ephippioceratoidea with a pachyconic or globular, involute to subinvolute conch. Whorl profile in the adult stage usually more or less strongly depressed; flanks and venter form a continuous arch. Ornament usually consisting of fine growth lines; some species have spiral lines or fine ribs. Septum strikingly bilobate; suture line with high external saddle.

Included genera

Ephippioceras Hyatt, 1894 (Viséan to Roadian; 16 species).

Megaglossoceras Miller, Dunbar & Condra, 1933 (Bashkirian to Asselian; 9 species).
Arthuroceras Shimansky, 1962 (Bashkirian; 1 species).

Remarks

The composition of the family Ephippioceratidae proposed here agrees with that outlined by Shimansky (1962) and Kummel (1964), while Dzik (1984) included the genera *Ephippioceras* and *Megaglossoceras*, together with *Styrionautilus* and others, in the family Liroceratidae.

The members of the family Ephippioceratidae cannot be confused with other nautiloids if the shape of the septa is preserved. *Ephippioceras* and *Megaglossoceras* are characterised by a very conspicuous bilobate septal surface, the peculiar shape of which is produced by a high ventrodorsal ridge dividing the entire septum (Fig. 36). There are apparently no known species that could be considered as intermediates between *Bistrialites* or *Liroceras* and *Ephippioceras*.

Dzik (1984: 169) discussed the origin of *Ephippioceras* and suggested *Stearoceras* as a possible ancestor. The reason for this suggestion was that the suture line of *Stearoceras* has a ventral undulation, which may have developed into the conspicuous external saddle. According to Dzik (1984), *Ephippioceras* gave rise to *Megaglossoceras*, which is the ancestor of the Triassic genus *Styrionautilus*. This assumption is based on the superficially similar sutures with a ventral saddle. However, it overlooks the fact that the ventral saddle in *Ephippioceras* and *Megaglossoceras* was produced by the bilobate deformation of the entire septum by a high ridge, which is not present in *Clydonautilus* Mojsisovics, 1882 and related genera. Therefore, a phylogenetic lineage from the Liroceratidae to the Clydonautilidae is preferred here.

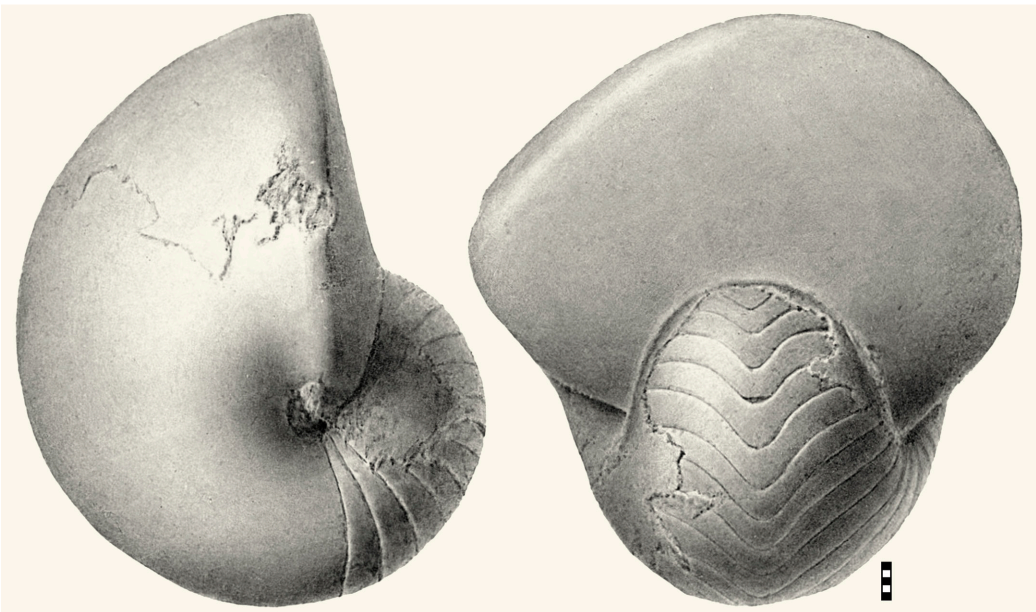

Fig. 36. Family Ephippioceratidae Miller & Youngquist, 1949. *Ephippioceras ferratum* (Cox, 1858), from Miller & Youngquist (1949). Scale bar units = 1 mm.

Suborder **Solenochilina** Flower, 1950

Diagnosis

Suborder of the order Nautilida, in which the conch form ranges from cyrtoconic, gyroconic to nearly involute with extraordinarily high coiling rate. Dorsal whorl zone missing or very small. Shell surface usually smooth. Suture line nearly straight with a small external lobe. Siphuncle in marginal ventral position.

Included superfamilies

Aipoceratoidea Hyatt, 1884 (Early Carboniferous to Early Permian; 7 genera, 54 species).
Scyphoceratoidea Ruzhencev & Shimansky, 1954 (Early Carboniferous to Early Permian; 9 genera, 23 species).

Remarks

Taxonomy

The position of the solenochilids within the order Nautilida has been very unstable over the decades, with different authors expressing sometimes very different opinions. Flower & Kummel (1950) presented them as an isolated order Solenochilida, derived (with a question mark) from the family Barrandeoceratidae Foerste, 1925.

Shimansky (1957) placed the superfamily Solenochilaceae, to which he included the families Litogyroceratidae Shimansky, 1957, Scyphoceratidae, Dentoceratidae and Solenochilidae, in the suborder Rutoceratina. Later, Shimansky (1962, 1967) modified this scheme only in the minor detail of giving priority to the names Aipoceratidae and Aipocerataceae over the names Solenochilidae and Solenochilaceae.

Furnish & Glenister (in Kummel 1964: K440) interpreted the superfamily Aipocerataceae, to which they assigned the families Aipoceratidae, Solenochilidae and Scyphoceratidae, as an independent evolutionary lineage, which possibly derived from the superfamily Tainocerataceae (Kummel 1964: K385).

Dzik (1984) considered the families Aipoceratidae and Solenochilidae to belong to an uncertain suborder. He suppressed the family Scyphoceratidae that was recognised by the other authors and placed the genera belonging to it in the orthoceratid family Cycloceratidae Hyatt, 1900 (Dzik 1984: 130).

Due to the lack of new information, little can be contributed here to the two competing systematic interpretations. However, on the basis of the somewhat marginal position of the siphuncle, the family Scyphoceratidae is provisionally retained in the suborder Solenochilina.

Morphology and subdivision

The suborder Solenochilina is characterised by two main features, which are the ventrally located siphuncle and the very high coiling rate. Two superfamilies are recognised here:

Aipoceratoidea Hyatt, 1884. – Conch cyrtoconic, gyroceraconic to subinvolute or involute, pachyconic to globular with a very mall whorl overlap zone.

Scyphoceratoidea Ruzhencev & Shimansky, 1954. – Conch from nearly orthoconic to cyrtoconic.

Phylogeny

The origin of the suborder Solenochilina has been discussed several times in the literature and cannot yet be considered sufficiently resolved. Flower (1955: 256) interpreted all Carboniferous coiled nautiloids as derived from rutoceratids and explicitly included the solenochilids: “Probably the small Late Paleozoic order the Solenochilida has its origin also in the Rutoceratida”. This concept was supported by Shimansky

(1957, 1962, 1967), Kummel (1964) and Flower (1964: 5). Flower (1964: 12), however, stated that the solenochilids were "almost certainly" allied to the order Oncoceratida.

Dzik (1984: 156) was not sure whether the two families, Aipoceratidae and Solenochilidae, were phylogenetically related and suggested the Devonian genera *Geitonoceras* Zhuravleva, 1974 and *Cranoceras* Hyatt, 1884 as possible ancestors. According to Dzik (1984: 157), the data suggest that solenochilids "... are much more closely related to the Oncoceratidae than to the Nautilida". But at the same time, he suggested that "... it is more reasonable to retain the Aipocerataceae in the Nautilida until their systematic position is known". That view is shared here.

Superfamily **Aipoceratoidea** Hyatt, 1884
Fig. 37

Diagnosis

Superfamily of the suborder Solenochilina, in which the conch form ranges from gyroconic to nearly involute with extraordinarily high coiling rate. Whorl profile laterally compressed to weakly depressed.

Included families

Aipoceratidae Hyatt, 1884 (Early Carboniferous to Early Permian; Permian; 5 genera, 18 species).
Solenochilidae Hyatt, 1893 (Early Carboniferous to Middle Permian; 2 genera, 36 species).

Remarks

A very apt characterisation of the superfamily Aipoceratoidea was given by Shimansky (1967: 39) (translated from Russian): "The origin of the peculiar Late Palaeozoic nautiloids, grouped in the superfamily Aipocerataceae and characterised by a smooth conch of various shapes, a ventral position of the siphuncle and an almost straight suture line, is not very clear. There seems to be no doubt about

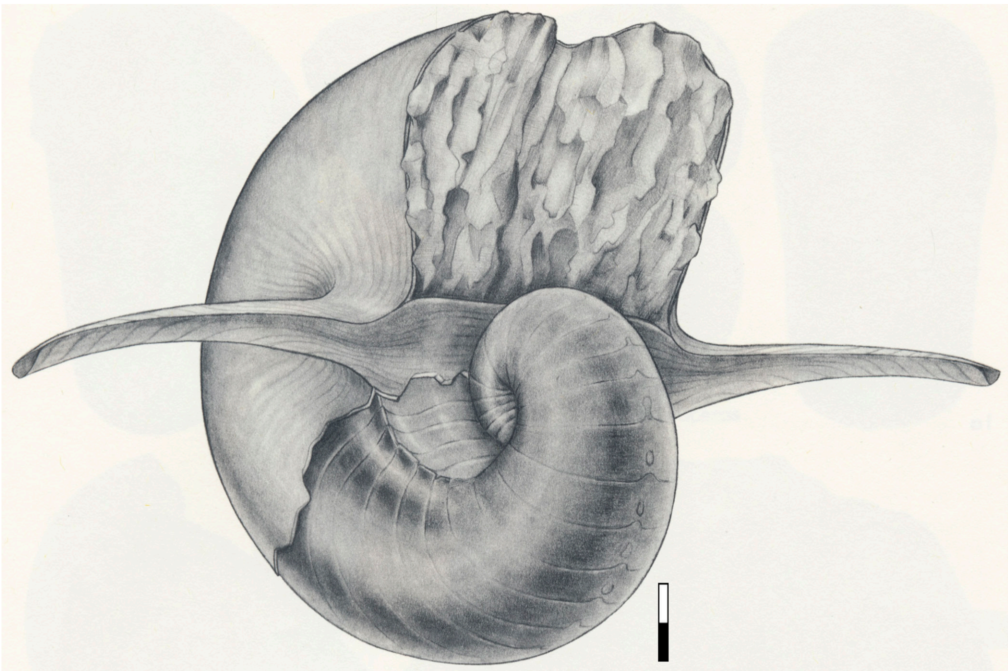

Fig. 37. Family Solenochilidae Hyatt, 1893. *Solenochilus springeri* (White & St. John, 1868), from Furnish & Glenister in Kummel (1964). Scale bar units = 10 mm.

the unity of the group, even though its representatives differ greatly in the shape of their conchs. Some have conchs with completely free whorls (*Aipoceras*), others with touching whorls (*Asymptoceras*) and others with slightly overlapping whorls (*Solenochilus*). In most representatives, the shell rapidly increases in width and height, sometimes becoming almost spherical (*Solenochilus*, *Acanthonautilus*) and forming lateral ear-like projections (Fig. 37). American authors differentiate between the families Aipoceratidae and Solenochilidae, which we agree with, since both groups of genera (*Asymptoceras*, *Aipoceras*, *Librovitschiceras*, on the one hand, and *Solenochilus*, *Acanthonautilus*, on the other) are very different. There is no doubt that the former are closer to the ancestral forms, most likely Rutoceratidae, and the latter are descended from the former."

This is similar to what was given by Furnish & Glenister (in Kummel 1964) before: "Conch rapidly expanding, cyrtoconic to coiled, whorls rounded to flattened or possibly impressed dorsally; shell surface smooth to ribbed; modified mature aperture known in most forms; sutures nearly straight; siphuncle marginal and ventral; septal necks orthochoanitic on ventral surface and orthochoanitic to cyrtochoanitic on dorsal side."

The two families are characterised as follows:

Aipoceratidae Hyatt, 1884. – Ancestral forms with a gyroconic conch; whorl profile usually laterally compressed (Fig. 38).

Solenochilidae Hyatt, 1893. – Derived forms with a subinvolute or involute conch; whorl profile circular or depressed (Fig. 39).

Family **Aipoceratidae** Hyatt, 1884
Fig. 38

Diagnosis

Family of the superfamily Aipoceratoidea with a gyroconic conch. Whorl profile usually laterally compressed.

Included genera

Asymptoceras Ryckholt, 1852 (Tournaisian to Serpukhovian; 6 species).
Aipoceras Hyatt, 1884 (Tournaisian to Viséan; 7 species).
Oncodoceras Hyatt, 1893 (Tournaisian; 3 species).
Librovitschiceras Shimansky, 1957 (Moscovian; 1 species).
Barskoceras Leonova & Shchedukhin, 2020 (Asselian or Sakmarian; 1 species).

Remarks

Of the genera of the family Aipoceratidae, only the two genera *Aipoceras* and *Asymptoceras* can be considered well known (e.g., Foord 1900; Miller & Furnish 1939). They show a continuous evolution in the degree of coiling, ending in the genera *Acanthonautilus* Foord, 1896 and *Solenochilus* Meek & Worthen, 1870. At the same time there is a continuous evolution towards a more depressed whorl profile.

Librovitschiceras appears as a foreign item in the list of genera; this is due to the very different conch morphology with a wide umbilicus and low coiling rate (Fig. 38). The genus has been placed in the family Aipoceratidae because of the marginal ventral position of the siphuncle (Shimansky 1957, 1962, 1967, 1979; Kummel 1964), while Dzik (1984: 173) placed the genus in the Tainoceratidae with question mark. Kummel (1964) did not accept the validity of *Librovitschiceras* and synonymised the genus with *Knightoceras*, while Furnish & Glenister (in Kummel 1964, in the same *Treatise* volume) listed it among the superfamily Aipocerataceae. This controversy cannot be resolved at present.

Fig. 38. Family Aipoceratidae Hyatt, 1884. *Aipoceras compressum* Foord, 1900, from Foord (1900). Scale bar units = 5 mm.

Family **Solenochilidae** Hyatt, 1893
Fig. 39

Diagnosis

Family of the superfamily Aipoceratoidea with a subinvolute or involute conch. Whorl profile circular or depressed. Umbilical wall with long, spine-alike outgrows in the adult stage.

Included genera

Solenochilus Meek & Worthen, 1870 (Tournaisian to hanghsingian; 35 species).
Solenocheilus Hyatt, 1884 [synonym of *Solenochilus*].
Acanthonautilus Foord, 1896 (Tournaisian; 1 species).

Remarks

The family Solenochilidae contains only two genera, *Solenochilus* and *Acanthonautilus*, which, according to Kummel (1964: K441), differ only in the shape of the septal necks. As this character has

Fig. 39. Family Solenochilidae Hyatt, 1893. *Acanthonautilus bispinosus* Foord, 1900, from Foord (1900). Scale bar units = 5 mm.

not been studied in most species, little can be said about the clear delimitation of the two genera. It is therefore uncertain whether the very asymmetric distribution of the species described so far, one from *Acanthonautilus* and about 35 from *Solenochilus*, will be confirmed in the necessary revision. Mikesh & Glenister (1966) considered it possible that many of the Early Carboniferous species of the family might be better assigned to *Acanthonautilus*. However, they also admitted that a detailed study of the species, some of which are poorly known, would be necessary for a definitive clarification.

The species of these two genera are characterised by a peculiar conch morphology, the combination of which is not known in any other group of cephalopods. On the one hand, the conch grows very rapidly in width and height, with a circular or depressed oval whorl profile, and on the other hand, the formation of very conspicuous, long outgrowths on the umbilical wall (Fig. 39).

Interestingly, very similar umbilical processes also occur in the family Permonautilidae, a genus of the superfamily Liroceratoidea, which is not closely related to *Solenochilus*. *Permonautilus* also has a stout conch like *Solenochilus*, but usually differs from *Solenochilus* in having a much lower coiling rate (WER ~ 2.60) than *Solenochilus* (WER ~ 2.80–5.50). The most important difference is the position of the siphuncle, which is almost central in *Permonautilus* and slightly ventral in *Solenochilus*.

Superfamily **Scyphoceratoidea** Ruzhencev & Shimansky, 1954
Fig. 40

Diagnosis

Superfamily of the suborder Solenochilina, in which the conch is cyrtoconic and rapidly increasing in width and height, with a round or somewhat angular whorl profile. Body chamber large, phragmocone chambers small. Sculpture of transverse ribs or missing. Siphuncle adjacent to the ventral side or close to it. Suture line straight or with small lobes (after Shimansky 1967).

Included families

Scyphoceratidae Ruzhencev & Shimansky, 1954 (Early Carboniferous to Early Permian; 6 genera, 14 species).
Dentoceratidae Ruzhencev & Shimansky, 1954 (Late Carboniferous to Early Permian; 1 genus, 5 species).
Neptunoceratidae Shimansky, 1957 (Late Carboniferous; 2 genera, 4 species).

Remarks

The superfamily Scyphoceratoidea is so far only very poorly known because its representatives are generally very rare and have only been discovered in a few localities. In addition, the individual occurrences are of isolated stratigraphic age and are therefore difficult to integrate into a phylogenetic scenario. It is not even clear whether the genera grouped together in the superfamily actually form a monophyletic unit.

In the "*Osnovy*", Shimansky (1962: 117) placed the family Neptunoceratidae in the superfamily Rutocerataceae, while he included the families Scyphoceratidae and Dentoceratidae in the superfamily Aipocerataceae, both belonging to the suborder Rutoceratina. Later (Shimansky 1967, 1979) he combined the three families into the superfamily Rutocerataceae.

Meanwhile, Flower (1963) discussed these problems in detail and outlined the various possible origins of the scyphoceratids and related cephalopods. However, he did not present a clear phylogenetic scenario.

Kummel (1964: K442) merged the Dentoceratidae with the Scyphoceratidae and placed them in the superfamily Aipocerataceae. Teichert (1964a: K484) included the family Neptunoceratidae among the "doubtful taxa". This was mainly due to the discussion by Furnish *et al.* (1962), who suggested that the specimens of *Tetrapleuroceras* and *Neptunoceras* were merely growth stages of *Brachycycloceras* Miller, Dunbar & Condra, 1933 and therefore belonged to their family Brachycycloceratidae (Furnish *et al.* 1962).

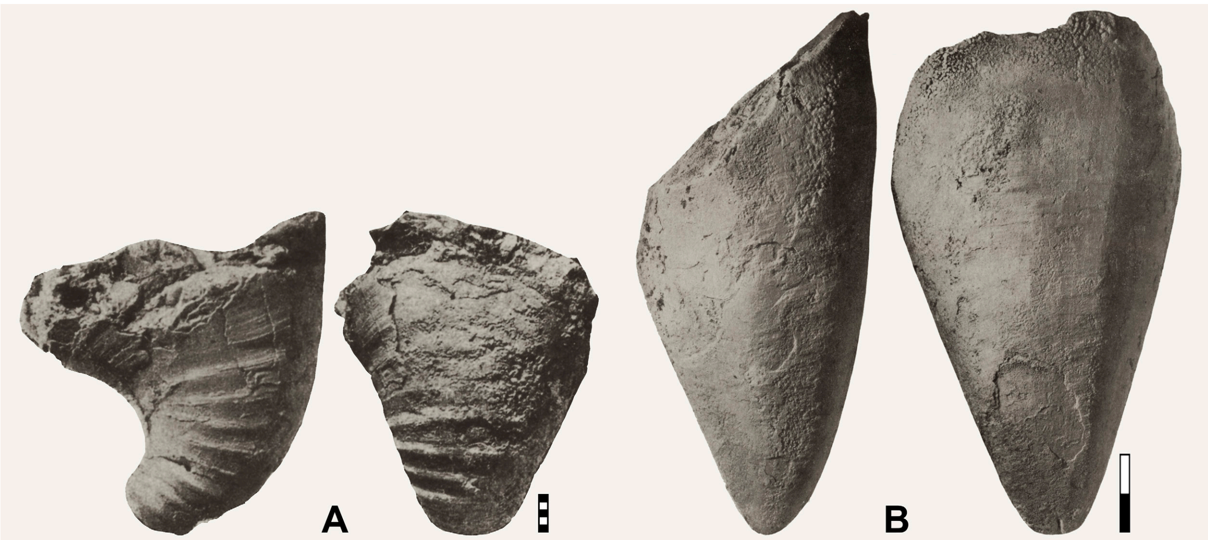

Fig. 40. Families Scyphoceratidae Ruzhencev & Shimansky, 1954 and Dentoceratidae Shimansky, 1957, both from Ruzhencev & Shimansky (1954). **A.** *Scyphoceras dionysi* Ruzhencev & Shimansky, 1954. **B.** *Dentoceras magnum* Ruzhencev & Shimansky, 1954. Scale bar units: A = 1 mm; B = 10 mm.

This hypothesis was also taken up by Dzik (1984: 130), who considered not only the Neptunoceratidae but also the Scyphoceratidae to be synonymous with the Cycloceratidae Hyatt in Zittel, 1900. He only accepted the two genera *Neptunoceras* and *Scyphoceras* as valid.

Niko & Mapes (2011) discussed the systematic position of the Neptunoceratidae; they concluded that the family does not fit into either the order Nautilida or the family Cycloceratidae due to its combination of characters. They therefore rejected the classification schemes advocated by Shimansky (1967) and Dzik (1984) and left the systematic classification in uncertainty. King & Evans (2019: 71) discussed the similarity of *Brachycycloceras* and *Texanoceras* Niko & Mapes, 2011 and suggested that both genera may be better assigned to the Nautilida.

Due to the lack of new material, the problems identified cannot be resolved at present. Therefore, the families (Fig. 40) in question are tentatively placed in the Aipoceratoidea without further discussion.

Family **Neptunoceratidae** Shimansky, 1957

Diagnosis

Family of the superfamily Scyphoceratoidea with a slightly cyrtoconic conch. Whorl profile subtriangular. Sculpture with transverse ribs. Siphuncle between the centre and the convex side (after Shimansky 1962).

Included genera

Tetrapleuroceras Shimansky, 1949 (Gzhelian; 3 species).
Neptunoceras Shimansky, 1949 [synonym of *Tetrapleuroceras* Shimansky, 1949].
Texanoceras Niko & Mapes, 2011 (Gzhelian; 1 species).

Family **Scyphoceratidae** Ruzhencev & Shimansky, 1954

Diagnosis

Family of the superfamily Scyphoceratoidea with a cyrtoconic conch with large body chamber and small phragmocone. Whorl profile oval. Without sculpture or with transverse ribs. Siphuncle at the convex side (after Shimansky 1967).

Included genera

Scyphoceras Ruzhencev & Shimansky, 1954 (Serpukhovian to Artinskian; 6 species).
Mariceras Ruzhencev & Shimansky, 1954 (Kungurian; 3 species).
Venatoroceras Ruzhencev & Shimansky, 1954 (Artinskian; 1 species).
Sorinoceras Flower, 1963 (Kungurian; 1 species).
Cherokeeoceras Windle, 1973 [nomen nudum; Carboniferous; 2 species].
Arcuatoceras Niko, Mapes & Yacobucci, 2009 (Serpukhovian; 1 species).

Family **Dentoceratidae** Shimansky, 1957

Diagnosis

Family of the superfamily Scyphoceratoidea with a conical, almost straight conch. Whorl profile rounded (after Shimansky 1962).

Included genus

Dentoceras Ruzhencev & Shimansky, 1954 (Bashkirian to Artinskian; 5 species).

Discussion

Classification schemes for the Carboniferous and Permian coiled nautiloids were controversially discussed in the 1940s to 1980s, but have rarely been a topic in the paleontological literature since then. Depending on the respective affiliation with regard to the research domain, either the schemes published in the *Osnovy Paleontologii* (Shimansky 1962) or in the *Treatise on Invertebrate Paleontology* (Kummel 1964) were used. New findings from the last 40 years now make it possible to draw a more differentiated picture of the phylogeny of these nautilids.

A new classification scheme is presented here, which is based on the integration of as many characters as possible, such as the general conch shape and its ontogeny, the shell sculpture and the shape of the septum. In addition, the stratigraphic sequence of the genera was taken into account.

- Order Nautilida Agassiz, 1847
  - Suborder Temnocheilina Flower, 1963
    - Superfamily Trigonoceratoidea Hyatt, 1884
      - Family Trigonoceratidae Hyatt, 1884
        - Subfamily Trigonoceratinae Hyatt, 1884
        - Subfamily Chouteauoceratinae subfam. nov.
        - Subfamily Vestinautilinae subfam. nov.
      - Family Triboloceratidae Hyatt, 1884 [synonym of Trigonoceratidae]
      - Family Rineceratidae Hyatt, 1893 [synonym of Trigonoceratidae]
      - Family Rhineceratidae Hyatt, 1900 [synonym of Trigonoceratidae]
      - Family Temnocheilidae Mojsisovics, 1902
      - Family Thrincoceratidae Ruzhencev & Shimansky, 1954
      - Family Knightoceratidae Shimansky, 1962 [synonym of Temnocheilidae]
      - Family Neothrincoceratidae Shimansky, 1962 [synonym of Thrincoceratidae]
      - Family Dasbergoceratidae fam. nov.
    - Superfamily Koninckioceratoidea Hyatt, 1900
      - Family Koninckioceratidae Hyatt, 1900
  - Suborder Domatoceratina subordo nov.
    - Superfamily Subclymenioidea Shimansky, 1962
      - Family Subclymeniidae Shimansky, 1962
      - Family Phacoceratidae Shimansky, 1962
      - Family Aphelaeceratidae Shimansky, 1962 [synonym of Subclymeniidae]
      - Family Epistroboceratidae fam. nov.
    - Superfamily Grypoceratoidea Hyatt, 1900
      - Family Grypoceratidae Hyatt, 1900
      - Family Domatoceratidae Miller & Youngquist, 1949
      - Family Stenopoceratidae fam. nov.
      - New family to be described by Korn & Hairapetian (in press)
    - Superfamily Permoceratoidea Miller & Collinson, 1953
      - Family Permoceratidae Miller & Collinson, 1953
  - Suborder Tainoceratina Shimansky, 1957
    - Superfamily Tainoceratoidea Hyatt, 1883
      - Family Tainoceratidae Hyatt, 1883

Superfamily Pleuronautiloidea Hyatt, 1900
Family Pleuronautilidae Hyatt, 1900
Family Gzheloceratidae Ruzhencev & Shimansky, 1954
Family Mosquoceratidae Ruzhencev & Shimansky, 1954
Family Aktubonautilidae Ruzhencev & Shimansky, 1954
Family Rhiphaeoceratidae Ruzhencev & Shimansky, 1954
Family Metacoceratidae fam. nov.
Family Foordiceratidae fam. nov.
Suborder Liroceratina Flower, 1955
Superfamily Liroceratoidea Miller & Youngquist, 1949
Family Liroceratidae Miller & Youngquist, 1949
Family Permonautilidae Barskov & Shilovsky, 2014
Family Paranautilidae Kummel in Flower & Kummel, 1950
Family Planetoceratidae fam. nov.
New family to be described by Korn & Ghaderi (in press)
Superfamily Ephippioceratoidea Miller & Youngquist, 1949
Family Ephippioceratidae Miller & Youngquist, 1949
Superfamily Clydonautiloidea Hyatt, 1900
Suborder Solenochilina Flower, 1950
Superfamily Aipoceratoidea Hyatt, 1884
Family Aipoceratidae Hyatt, 1884
Family Solenochilidae Hyatt, 1893
Superfamily Scyphoceratoidea Ruzhencev & Shimansky, 1954
Family Scyphoceratidae Ruzhencev & Shimansky, 1954
Family Dentoceratidae Ruzhencev & Shimansky, 1954
Family Neptunoceratidae Shimansky, 1957

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