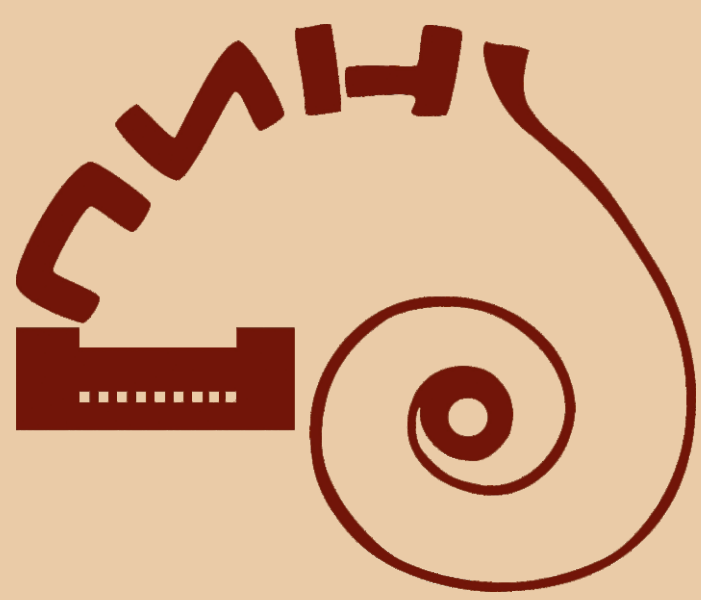




Irregular shell coiling in Paleozoic ammonoids: a review

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The ammonoid shell shape throughout the history of the group could be monomorph or heteromorph. Monomorph shells are planispiral-coiled with touching or overlapping whorls, while in heteromorphs the whorls are non planispirally coiled or are detached. However, some Paleozoic monomorph ammonoids display irregular shell coiling. These are known among representatives of the orders **Clymeniida**, **Tornoceratida** and **Goniatitida** (classification according to Leonova, 2002). Three major types of irregular coiling can be distinguished for Paleozoic ammonoids: (1) triangular, (2) tetragonal and (3) cordate. The first type of coiling can be characteristic of the entire shell or its part (outer or inner whorls), the second type – only for inner whorls, the third – for the last whorl only.

The earliest ammonoids with irregular coiling appeared in the Latest Famennian (Devonian). These are ammonoids from the families Hexaclymeniidae, Wocklumeriidae and Parawocklumeriidae (suborder Gonioclymeniina, order Clymeniida) (Schindewolf, 1937; Bogoslovsky, 1981). Most of them had triangular coiling, while some specimens of *Kamptoclymenia endogona* (order Parawocklumeriidae) had tetragonal coiling of the inner whorls (Schindewolf, 1937). Also, only one species of Late Devonian tornoceratids with triangular coiling on the inner whorls is known – *Mimimitoceras trizonatum* from the family Prionoceratidae (Korn, 1988; Treatise..., 2009). Among the Devonian ammonoids with irregular coiling, there were both common and rare forms. For example, representatives of the genera *Wocklumeria* and *Parawocklumeria* had a reasonably wide paleobiogeographic distribution and orthostratigraphic significance. In contrast, occurrences of the genus *Soliclymenia* are rare.

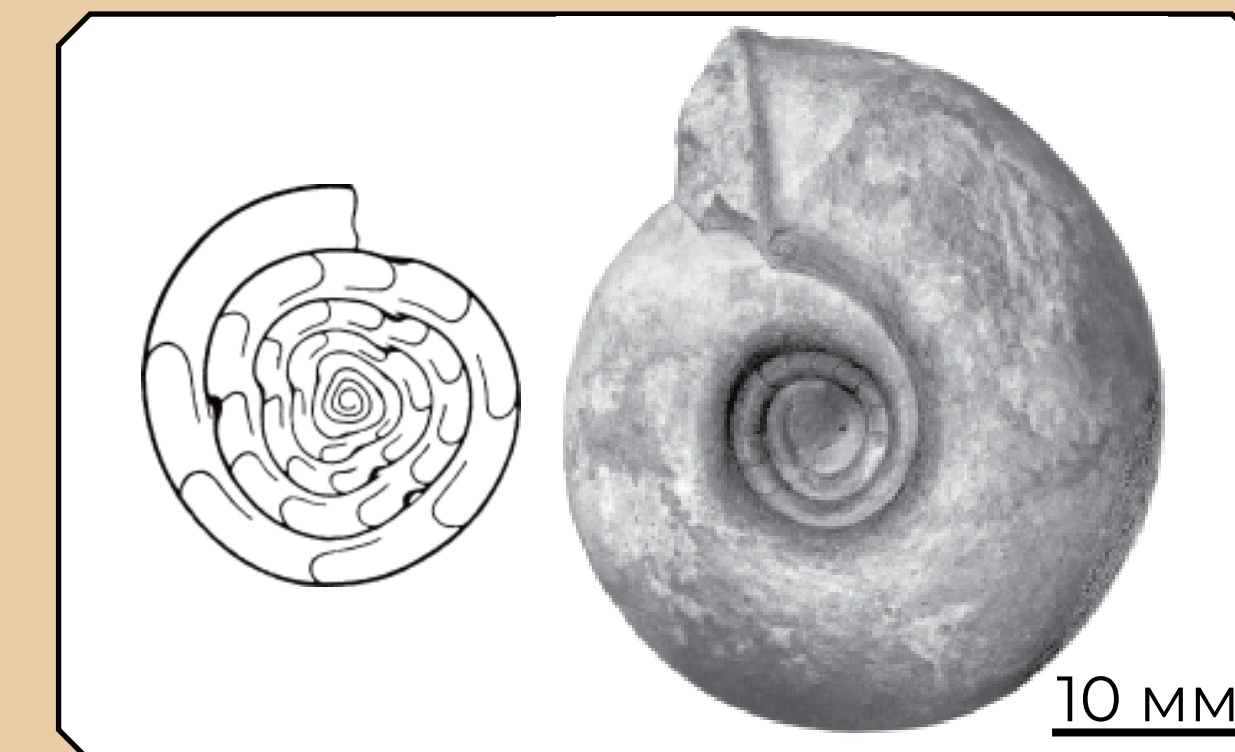
Most Carboniferous ammonoids with irregular coiling were in the order Goniatitida, while only one genus of tornoceratids (*Triimitoceras* from the family Prionoceratidae) had triangular coiling on the inner whorls (Treatise..., 2009). There were seven families of Goniatitida that included forms with irregular coiling: Entogonitidae (tetragonal coiling), Schistoceratidae, Welleritidae, Orulganitidae, Goniatitidae, and Delepinoceratidae (triangular coiling of the inner whorls) (Treatise..., 2009). Most genera with triangular coiling appeared in the Bashkirian (Pennsylvanian). Some of them had a wide paleobiogeographic distribution (e.g., *Diaboloceras*, *Paralegoceras*, etc.), some were endemic (e.g., *Orulganites*, *Mereoceras*, etc.).

Permian ammonoids with irregular coiling are known from the families Marathonitidae (*Cardiella*) and Hyattoceratidae (*Hyattoceras*) of the order Goniatitida and are characterized by a cordate coiling of the last whorl (Leonova, 2002; 2011). These were predominantly Tethyan forms, while *Cardiella* is also known from the Urals, and *Hyattoceras* was also identified from western North America.

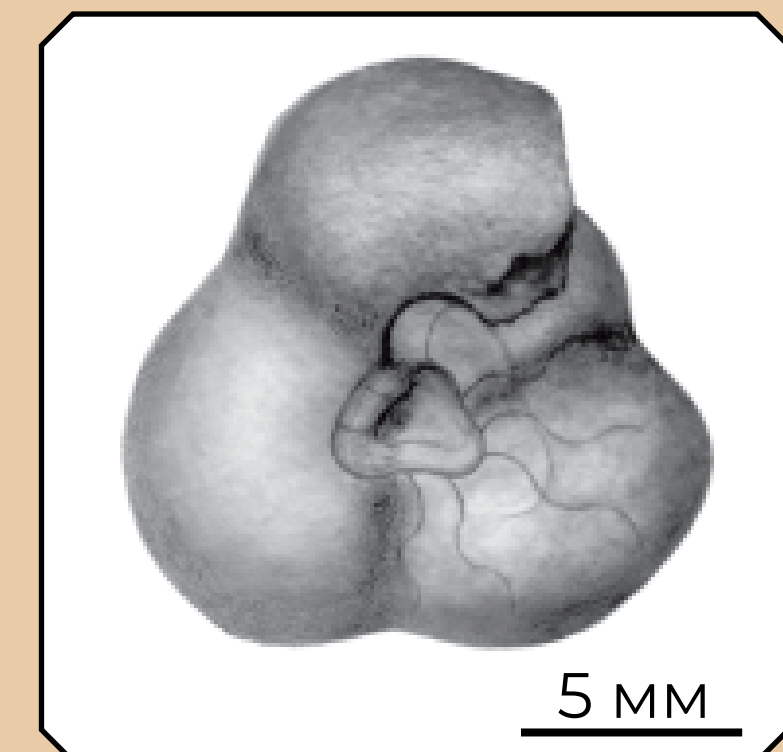
Two peaks of diversity of ammonoids with irregular coiling can be recognized in the Paleozoic. The first of them was in the Latest Famennian, when the number of genera with irregular coiling reached 28.8% of all known Latest Famennian ammonoid genera and 7.7% of all Famennian ammonoid genera. Presumably, this could be associated with events leading to the subsequent Hangenberg crisis near the Devonian-Carboniferous boundary. The second peak was in the Bashkirian (14%) and Moscovian (8%). It could possibly be associated with the earlier Serpukhovian-Bashkirian minor mass extinction. This extinction could have been related to global cooling event and glaciation in Gondwana leading to widespread sea regression, (Alekseev et al., 2001; Koronovsky et al., 2008).



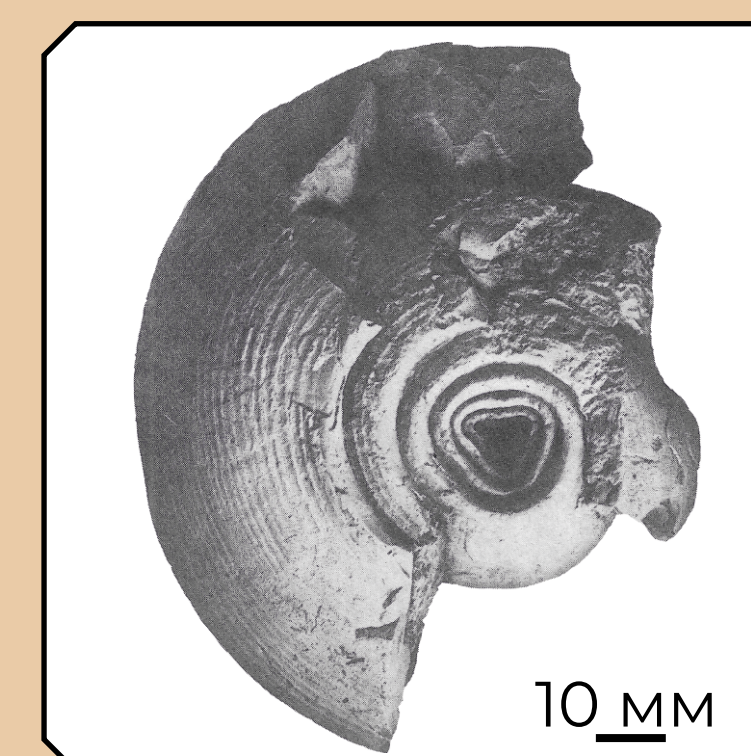
*Soliclymenia
paradoxa* (Münster)
Famennian



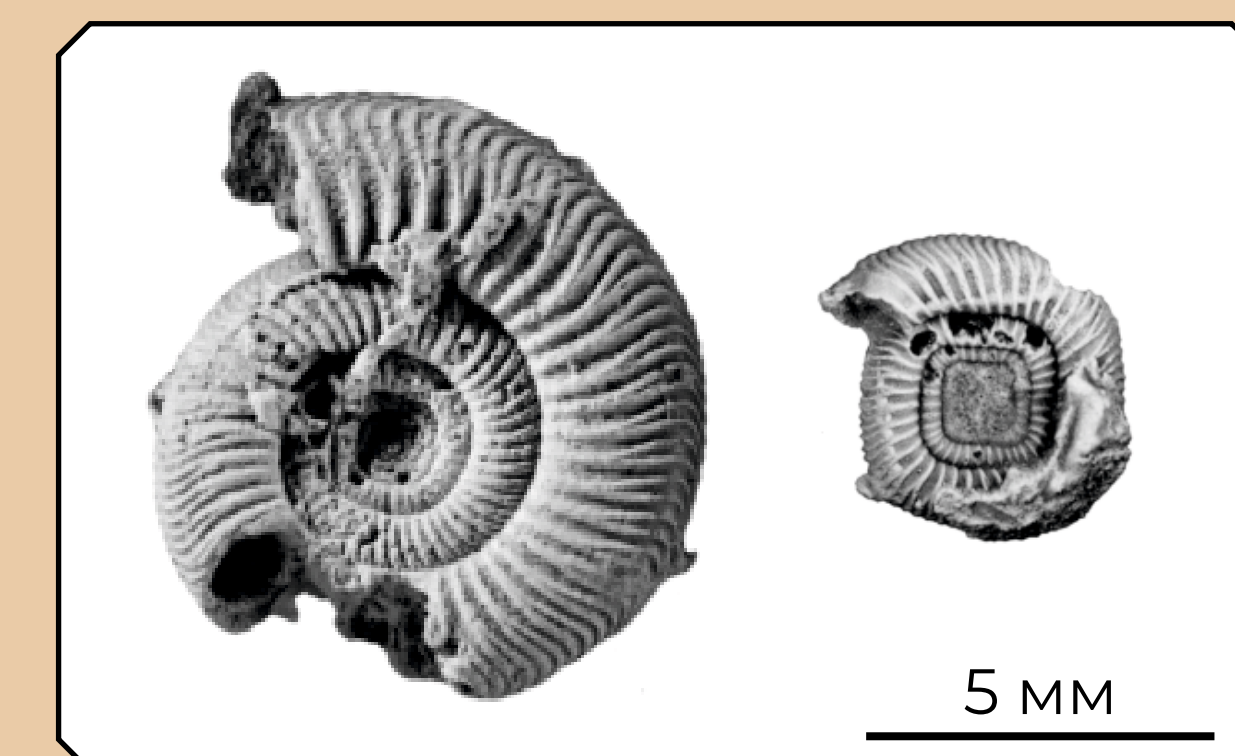
Wocklumeria sphaeroides
(Richter)
Famennian



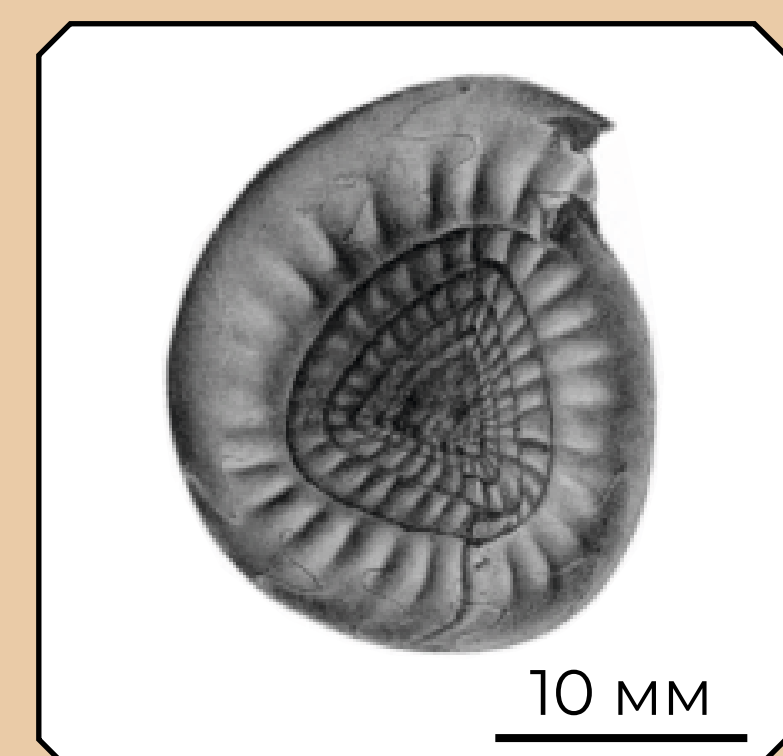
*Parawocklumeria
distorta* (Tietze)
Famennian



*Yanshinoceras
alexandri* Andrianov
Bashkirian



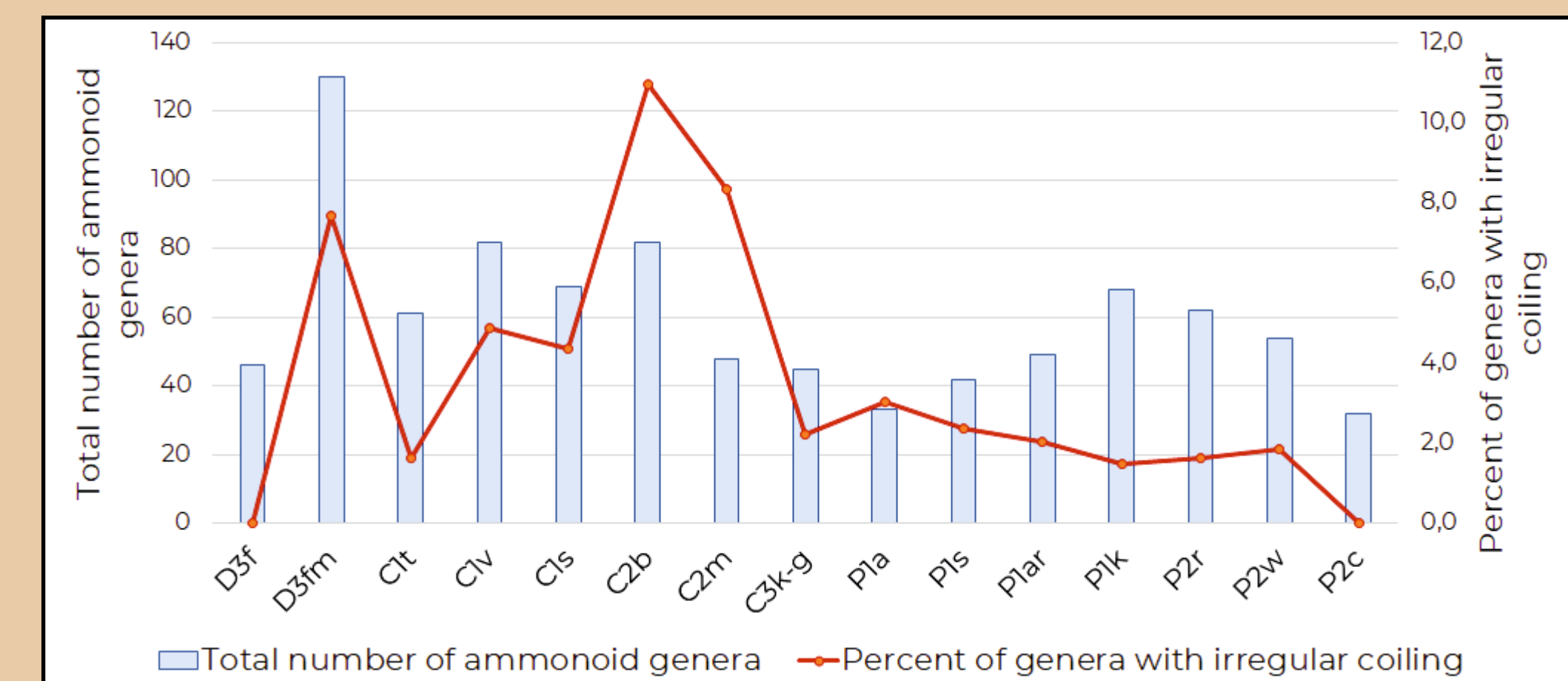
Entogonites saharensis Korn et al.
Viséan



*Paralegoceras
texanum* (Shumard)
Atokan (Moscovian)



Hyattoceras abichi
Gemmellaro
Wordian



Illustrations by Schindewolf, 1937; Miller, Furnish, 1940; Davis, 1972; Andrianov, 1985; Korn et al., 2005