

PALEOZOIC FORAMINIFERA: CURRENT STATE OF THE CLASSIFICATION AND PERSPECTIVES

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Abstract. An updated classification of Paleozoic foraminifera is proposed, consisting of three classes. Calcareous Paleozoic foraminifera are mainly included in the class Fusulinata but also represented in the classes Miliolata and Nodosariata. The current classification includes in the Fusulinata: 2 subclasses, 5 orders, 25 superfamilies, 65 families, 51 subfamilies, 572 genera, 14 subgenera, in the Miliolata: 1 order, 2 suborders, 2 superfamilies, 8 families, 9 subfamilies, 89 genera, and in the Nodosariata: 1 order, 2 superfamilies, 10 families, 2 subfamilies, 56 genera. Three other classes remain elusive: Allogromiata, Astrorhizata, and Textulariata. Four new replacement names are introduced: *Leveniranella* pro *Iranella* Leven in Leven and Vaziri Mohaddam, 2004, *Tianshanellites* pro *Triticites* (*Tianshanella*) Da in Da & Sun, 1983, *Gublerites* pro *Gublerina* Minato & Honjo, 1959 and *Qinglongella* pro *Qinglongia* Zhang & Dong in Xiao et al., 1986. The family Globoendothyridae is formally described as new.

Keywords: Foraminifera. Paleozoic. Classification. Taxonomy. Wall microstructures.

INTRODUCTION

The main aim of this study is to concisely propose an exhaustive and updated classification at a genera level of calcareous Paleozoic foraminifera.

Loeblich & Tappan (1987), Vdovenko et al. (1993) and Rauzer-Chernousova et al. (1996) were the main reference publications presenting a classification of Paleozoic foraminifera, which intended to be exhaustive at a genus level. The number of new described genera has been growing constantly since those publications. Particularly there are currently 592 valid genus-group nominal taxa in the class Fusulinata, almost one out of five (~110 new taxa) was described after the last classification (Rauzer-Chernousova et al. 1996), and more than one third if compared with Loeblich & Tappan (1987) (~200 new genera). Moreover, 10 overlooked genera from earlier Chinese publications have also been restudied and added when found valid (*Jilinella*, *Koksarella*, *Kunlunella*, *Nanpanella*, *Quasitriticites*, *Rugosomaklaya*, *Sazhiella*, *Tieliekella*, *Xingshandiscus*, and *Eotriticites* Da in Da & Sun, 1983 (not Wilde, 1984)). To give an order of magnitude, the number of the species in the class Fusulinata is over 10,000.

The current classifications of foraminifera are difficult to reconcile at the genus level as well as at the suprageneric level. Besides, previous classifications, based on the wall structure, have been challenged by the data and suggestions of molecular clocks (see Rigaud et al. 2015, with references therein). In the proposed classification, the wall microstructure remains the preponderant criterion, even if the original microstructures are often difficult to identify because of the usual recrystallization of walls originally composed of aragonite and high-Mg calcite; even the low-Mg calcite transforms itself.

The classification exposed herein differs significantly

from older systematics proposed by Mikhalevich (1980, 2013) and Loeblich & Tappan (1987, 1992). The taxonomical rank of the foraminifera (phylum or subphylum) is still a matter of debate (Adl et al., 2012, 2019) but, herein, the views of Cavalier-Smith (2002, 2003) are adopted. The foraminifera have long been considered as an order or a class in the western European or North American literature (Cushman, 1928; Galloway, 1933; Sigal, 1952; Loeblich & Tappan, 1964, 1987, 1992) and split into orders or superorders. In contrast in Russian literature, it was recognized long ago that similar divisions were mostly subclasses and classes (A. D. Miklukho-Maklay et al., 1958, 1959; Rauzer-Chernousova & Fursenko, 1959; Rozovskaya, 1975; Solovieva, 1978; Mikhalevich, 1980, 2013; Vdovenko et al., 1993; Rauzer-Chernousova et al., 1996).

The proposed suprageneric classification of Paleozoic foraminifera is far more tributary of the works of the "Soviet school of foraminifera" than of the classification of Loeblich & Tappan.

SUPRAGENERIC ADAPTATIONS AND NOMENCLATUREAL QUESTIONS

The present suprageneric classification follows the proposed classification of Vachard (2016, 2018), modified in Vachard & Le Coze (2022; with references therein) for smaller Carboniferous foraminifera, with some main adaptations. Remarks at genus level are found in the Systematics section.

The subclass Afusulinana: suborders are suppressed for being redundant with the superfamilies, lacking a different content.

Similarly, to Vachard & Le Coze (2022), Parathuramminida Mikhalevich, 1980 is not considered as a foraminiferal order, but as a heterogeneous group

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which is part of the Calcitarcha recently created by Versteegh et al. (2009).

The superfamily Mstinoidea Lipina, 1989 is replaced by Haplophragminoidea Reitlinger, 1950 as an earlier overlooked junior synonym. For the same reason, the superfamily Colanielloidea Fursenko in Rauzer-Chernousova & Fursenko, 1959 replaces Robuloidoidea Reiss, 1963 and Geinitzinoidea Bozorgnia, 1973.

In the Miliolata, the classification of the superfamily Calcivertelloidea follows the newly scheme proposed in Vachard & Krainer (2022).

The subfamily Archaediscinae has been suppressed for being redundant with the family Archaediscidae, of which it was the only subfamily.

Biseriamminidae were included in the Globivalvulinoidea in Hance et al. (2011) and in the Mstinoidea = Haplophragminoidea with a question mark in Vachard & Le Coze (2022). Our research efforts have yet to confirm the second set of phylogenies, just like the initial attempts. Therefore, we are reverting back to the hypothesis proposed in Hance et al. (2011) and include back the Biseriamminidae in the Globivalvulinoidea, although it remains somewhat uncertain.

The same process occurred for the family Koktjubinidae. The subfamilies Endospiroplectammininae Loeblich & Tappan, 1986, Endothyriinae Brady, 1884, Omphalotinae Vdovenko in Rauzer-Chernousova et al., 1996, Paraendothyriinae Lipina in Rauzer-Chernousova et al., 1996 and Planoendothyriinae Vachard, Krainer & Schönlaub, 2018 in the family Endothyridae have been set aside. The composition of each family is questionable and the beginning of their lineages in the latest Devonian and Tournaisian need to be reviewed.

The family Cornuspiridae Schultze, 1854 has been divided into two subfamilies Cornuspirinae Schultze, 1854 and Hemigordiinae Reitlinger in Vdovenko et al., 1993 following Vachard & Krainer (2022).

The authorities of a family and a subfamily have been clarified. In Rauzer-Chernousova et al. (1996), the family Triticitidae was given the authority Davydov, 1986 and the subfamily Monodiexodininae was credited to Kanmera, Ishii & Toriyama, 1976. Davydov (1986) refers to the Symposium *Benthos' 86* published in 1988 but Davydov (1988) only included Triticitidae in a figure without description. The first description of Triticitidae is in fact in Rauzer-Chernousova et al. (1996). The case of Monodiexodininae already analysed by Ueno et al. (2011) is identical.

Two exceptions to the principles of coordination and priority have been made.

Biseriamminoidea Chernysheva, 1941 has priority in respect to Globivalvulinoidea Reitlinger, 1950 but as the genus *Biseriammina* and in consequence the exact definition of Biseriamminidae remains problematical. In contrast, Globivalvulinidae is currently well defined. We propose to denominate the Paleozoic foraminifers, with an almost planispirally to partly trochospirally coiled, biserial architecture as Globivalvulinoidea, instead of

Biseriamminoidea. The application of the article 35.5. of the ICZN (after 1999 an older family group name is not to displace a younger name if the latter is in prevailing usage) is under discussion since both Globivalvulinoidea and Biseriamminoidea are currently in usage and no prevailing usage may be determined.

Then, Neoschwagerinoidea Dunbar & Condra, 1927 is a junior synonym of Verbeekinoidea Staff & Wedekind, 1910. The characteristics of the superfamily are the presence of a fine keriothecal wall, the presence of parachomata and the axial and transverse secondary septula. The two first characters are present in three families (Misellinidae, Verbeekinidae and Neoschwagerinidae), but the latter character is only developed in the family Neoschwagerinidae. It is noteworthy that in a classification only based on the internal endoskeleton, Verbeekinidae and Neoschwagerinidae are interpreted as belonging to two different orders/superfamilies. As we considered the family Neoschwagerinidae as the most characteristic of the superfamily, we suggest to denominate the superfamily Neoschwagerinoidea. Neoschwagerinoidea is currently in prevailing usage (see for instance Ueno 2022)) and the article 35.5 of the ICZN may be applied.

NEW TAXA

Four new replacement names have to be introduced. The genus *Iranella* Leven in Leven & Vaziri Mohaddam, 2004 is preoccupied by *Iranella* Uvarov, 1922 a genus of Insecta. The new name *Leveniranella* is proposed. As a consequence, the following new combinations are also introduced *Leveniranella bella* (Leven in Leven & Vaziri Mohaddam, 2004) for the type species, *Leveniranella longa* (Leven in Leven & Vaziri Mohaddam, 2004), *Leveniranella orbiculata* (Leven in Leven & Vaziri Mohaddam, 2004) and *Leveniranella pauca* (Leven in Leven & Vaziri Mohaddam, 2004) for the other species.

The subgenus *Triticites* (*Tianshanella*) Da in Da & Sun, 1983 is a junior homonym of *Tianshanella* Brodsky, 1930 a genus of Insecta. The replacement name *Tianshanellites* is proposed. The genus is masculine. The new combination *Tianshanellites tianshanensis* (Da in Da & Sun, 1983) is consequently introduced for the type species. The genus *Tianshanellites* is monospecific.

The genus *Gublerina* Minato & Honjo, 1959 is a junior homonym of *Gublerina* Kikoine, 1948, another genus of Foraminifera. The replacement name *Gublerites* is proposed. The genus is masculine. The new combination *Gublerites elongatus* (Gübler, 1935) is introduced for the type species. The genus *Gublerites* is monospecific.

The genus *Qinglongia* Zhang & Dong in Xiao et al., 1986 is junior homonym of *Qinglongia* Liao, 1980 (Brachiopoda). The replacement name *Qinglongella* is proposed with the new combination *Qinglongella elliptica* (Zhang & Dong in Xiao et al., 1986) for the type species. The other known species are *Q. qinglongensis* (Zhang & Dong in Xiao et al., 1986) and *Q. lepida*

(Zhou, 1998).

Family group names based upon the type genus *Globoendothyra* have been quoted for around 50 years. A first mention of the family Globoendothyridae was found without mention of any authority in Mamet (1974, p. 470). The first mention with an authority was found in Armstrong & Mamet (1974, pp. 51, 70, 74) as Globoendothyridae Reitlinger, 1959 still without a proper description. The subfamily Globoendothyrinae was later used (e.g., Cózar & Vachard 2001), and was said to be elevated to the family level in Hance et al., 2011. The superfamily Globoendothyroidea has never been described except a quotation in Krainer & Vachard (2015, p. 18).

Those family group names have been erroneously thought to have been described by Reitlinger in Voloshinova & Reitlinger (1959) adding a new layer of complexity to the already complicated taxonomic history of *Globoendothyra* (see Loeblich & Tappan, 1987, p. 240). Reitlinger in Voloshinova & Reitlinger (1959) included *Globoendothyra* in her new subfamily Plectogyrinae, which was later put into synonymy with Endothyrinae (e.g., Loeblich & Tappan, 1987). No mention of family group names based upon the type genus *Globoendothyra* has been found in the Russian literature.

The family Globoendothyridae is now well established even if none of the previous descriptions meet the requirements of the ICZN especially for names published after 1999. Therefore, it is herein formally introduced:

Globoendothyridae new family, type genus *Globoendothyra* Bogush & Yuferev, 1962. Description: Septabrunciinoidea with medium to large sized test. Planispiral to endothyroid. Initially septatourayellid and then endothyroid in coiling and chamber shape. Supplementary deposits generally discrete with hooks and corner fillings. Wall differentiated with often an agglutinated layer and a pseudofibrous layer. Globoendothyridae are differentiated from other Septabrunciinoidea by the complex, multilayered wall, strong deviations of the coiling axis, the terminal spine in the last chamber, from Laxoendothyridae by the thick multilayered wall, more deviations and more chambers by whorl, from Septabrunciinidae by larger size, multilayered wall, and terminal spine. Occurrence. Late Tournaisian–Serpukhovian. Palaeotethyan and Uralian shelves, rarely cosmopolitan.

The genera included in the new family are given in the classification below.

PERSPECTIVES

From an evolutionary point of view, the Paleozoic history of foraminifera can be summarized in three main stages (Vachard et al. 2010):

First, during the Lower Paleozoic–Lower Devonian: “agglutinated” foraminifera are rare, and secreted foraminifera nearly absent; all the typical forms are either unilocular or bilocular.

Then, during the Givetian–Frasnian: plurilocular, secreted foraminifera (*Fusulinata Afusulinana*) became abundant in shallow-water carbonates; many modern architectures of the test are represented: planispiral involute, uniseriate and biseriate. This period is situated between the foraminiferal Givetian revolution (Vachard et al. 2010; i.e., the massive appearance and rapid complexification of the secreted carbonate tests) and the Frasnian/Famennian biotic crisis.

And finally, during the latest Famennian–latest Permian. After a recovery period in the Famennian, as early as latest Famennian, microgranular forms (i.e., the *Fusulinata Fusulinana*) are very numerous in marine shallow waters; from latest Famennian to early Bashkirian, the tests remain small and endothyroid in shape (nautiloid with permanent deviation of the axis of coiling); from the late Bashkirian to middle/late Permian, the coiling becomes planispiral, and the shape fusiform. The oldest larger foraminifera are Middle and Late Pennsylvanian in age.

Personal observations of Paleozoic foraminifera during 55 years, 1969–2024 (Vachard 1974, 2016, 2018; Vachard et al. 2010, 2013a, b, 2015, 2016, 2017; Vachard & Le Coze 2022) allowed to corroborate the status of foraminifera as a phylum and subdivisions in classes, but other results are not consistent with some phylogenetical hypotheses and attempts of dating by using molecular biology (Flakowski et al. 2005; Groussin et al. 2011; Pawlowski et al. 2013), especially concerning the oldest Miliolata and their phylogenic relationships.

Those new molecular phylogenetic studies have had and still have a limited impact on the classification of Paleozoic foraminifera mainly because the class *Fusulinata* is extinct with no equivalent in the present time. The class *Nodosariata* (Rigaud et al. 2015) is kept separated from the three classes defined on a molecular basis (Pawlowski et al. 2013). Tentatively, the Paleozoic class Miliolata could be compared with the order Miliolida included in the Tubothalamea as could Textulariata be compared to the paraphyletic order “Textulariida” included in the Globothalamea by Pawlowski et al. (2013). Another possibility would be to consider the double evolutionary trend: (1) *Fusulinida* and Miliolata; (2) *Earlandiida* and *Nodosariata*, which could be parallelized with the subdivisions Globothalamea and Tubothalamea of Pawlowski et al. (2013) which could correspond, in this case, to two possible foraminiferal subphyla including several of the classes used herein.

The Pseudopalmuloidea present a peculiar acceleration in the evolution of the foraminifera. They were probably photosynthetic symbiont bearers or maybe kleptoplastic foraminifera (Dubicka et al. 2021) and their extinction might have been triggered by the disappearance of those symbionts in a similar way to what is recently observed with various corals. Transition to mutualism (Lutzoni & Pagel 1997) and synergistic coevolution (Preussberg et al. 2021) have been observed as factors of accelerated

evolution (tachytely) in recent organisms but obligate mutualism has a cost and may limit the ability of organisms to adapt evolutionarily to changing environmental conditions (Pauli et al. 2022).

Tubiphytidae recently restudied in Krainer et al. 2019 is another example of possible mutualism. According to numerous authors (Vachard & Krainer 2015 and references therein), it is admitted that the Tubiphytidae are more or less strongly transformed consortial associations of tubular miliolate foraminifers with cyanobacterial algae. Their ecological interaction might have evolved through time from a commensal relationship to a complete mutualism. The symbiosis with a cyanobacterial element was possibly, secondarily integrated at the genetic message level or, in contrast, it remained of lichen-type. In both cases, occurred nevertheless a progressive genetic transformation of the foraminifer to adopt finally a complete cyanobacterial aspect (Vachard et al., 2001a). Even in the most completely transformed consortium foraminifer-cyanobacteria, the ancestral foraminiferal presence may be detected by the arrow-shaped cavities. Without known Recent equivalent, precise hypothesis are difficult to formulate but this consortium is probably very closely associated, may be at the genetic message level, and constitutes probably something unique in paleobiology. The evolving knowledge about Recent foraminifera and their microbiome offers new directions of reflection in palaeontology even if actualism has its limits because of the fossil record preservation.

As mentioned, earlier Parathuramminida Mikhalevich, 1980 have been transferred into the Calcitarcha. The Calcitarcha were initially proposed as a polyphyletic group of calcareous microfossils. They may in some cases represent various life stages of single-celled and higher organisms. Similar to acritarchs, they are considered an informal category and should be classified accurately once their biological affinities are determined. Already some genera and species of microfossils previously classified within the calcispheres have been assigned to the Dinophyceae (calcareous cysts of dinoflagellates) on the basis of definitive morphological criteria. If new discoveries are made or new discriminating criteria are found, part of the Parathuramminida might be regroup into the foraminifera.

In the literature, several Paleozoic taxa are described as organic-cemented siliceous agglutinated. They mainly belong to the classes Allogromiata, Astrorhizata, and Textulariata. Nearly all of them have been described from isolated specimens, which do not allow a thorough investigation of the microstructure of the wall if not also studied in thin section. Such a double study is rarely carried out. Organic-cemented siliceous agglutinated structure remains elusive in specimens only studied from thin sections because they cannot be isolated. Probably many taxa described only on the basis of isolated specimens have an equivalent described only on the basis

of thin sections. There is a methodological bias which requires reviewing all "isolated" taxa. This could partly be solved by the use of micro-CT scans which allow sections to be made without destroying a holotype for example. Though current micro-CT scans may be not sufficient to analyse the wall microstructures, not mentioning again the question of recrystallization. Morphological simplicity may hide significant microstructural differences, which still need to be objectified. A study of the wall composition of agglutinated "isolated" taxa could also help clarify the relevance of using agglutinated genera found in the Recent for Paleozoic taxa, a use which is not constantly supported by a clear evolutionary lineage. It is highly likely that many questions regarding Paleozoic agglutinated foraminifera may remain unanswered. From a taxonomic perspective, the classification of agglutinated foraminifera proposed by Kaminski (2014) remains the most complete to date.

The use of genera found in the Recent is not limited to agglutinated taxa, the presence of the genus *Nodosaria* during the Paleozoic could also be more an historical burden than a reality. By a metonymic shift, a part designating the whole, the genus *Nodosaria* has been used to describe a variety of taxa with elongate, multilocular, uniserial and rounded chambers. If the diagnosis of Loeblich & Tappan (1987) was to be strictly applied to those taxa, none could remain included in the genus *Nodosaria*. Additionally, according to those authors, the genus *Nodosaria* appeared during the Jurassic. The genus *Nodosaria* is listed herein for the rare Permian species, which exhibit a radiate aperture (see Vachard & Krainer, 2022) but this remains an open question.

Further information concerning the taxa included in the present classification and also invalid (published synonymies, homonyms) Paleozoic taxa are to be found in the World Foraminifera Database (Hayward et al. 2024) where both authors have been cooperating for several years.

SYSTEMATICS

Phylum **FORAMINIFERA** d'Orbigny, 1826

Class **FUSULINATA** Gaillot & Vachard, 2007

The Fusulinata are foraminifera with a homogeneous, microgranular, and/or pseudofibrous, primary test wall of low-Mg calcite in which crystal units are more or less equidimensional, and only a few microns in size. Rarely, they have an aragonitic wall.

Subclass **AFUSULINANA** Vachard, Pille & Gaillot, 2010

Bilocular Fusulinata generally undivided, except in the three more evolved groups: Tournayellina, Eonodosariina, and Semitextulariida (see Vachard 2016).

Order **ARCHAEDISCIDA** Poyarkov & Skvortsov, 1979

Proloculus followed by an undivided tubular chamber, diversely coiled: streptospiral, oscillating, sigmoidal, retrosigmoidal (i.e., eosigmoilinoïd), planispiral, or helical. Involute or evolute. Only a superfamily, Tournayelloidea, is pseudoseptated. Umbilical pillars exist in helical forms (Lasiodiscina). Wall often bilayered with hyaline pseudofibrous and dark microgranular layers, or unilayered with one of these two layers. Aperture terminal simple; sutural apertures with appendices can exist (Lasiodiscina).

Superfamily **ARCHAEDISCOIDEA** Cushman, 1928 in Piller, 1978

Description. See Fig. 1.

Family **AMMARCHAEDISCIDAE** Conil & Pirlet in Pirlet & Conil, 1974

Archaeodiscoidea with a microgranular dark wall dominant, and a subordinate inner hyaline pseudofibrous and yellow outer layer (Ammarchaediscinae = Planoarchaediscinae), or a remaining important dark layer (Uralodiscinae). Test entirely involute, oscillant, sygmoidal to planispiral. Aperture terminal simple. Early Visean (MFZ10)–Serpukhovian.

Subfamily **AMMARCHAEDISCINAE** Conil & Pirlet in Pirlet & Conil, 1974

Ammarchaediscidae with dark layer predominant, faint clear layer limited to the flanks.

Remark: *Leptarchaediscus* Conil & Pirlet in Conil, 1980, which was included in the Archaeodiscinae in Vachard & Le Coze (2022), has been reassessed as a junior synonym of *Viseidiscus* Mamet, 1975 as already studied in Hance et al. (2011).

Composition: *Ammarchaediscus* Conil & Pirlet in Pirlet & Conil, 1974; *Planoarchaediscus* A. D. Miklukho-Maklay in Kiparisova et al., 1956; *Viseidiscus* Mamet, 1975.

Subfamily **URALODISCINAE** Grozdilova in Vdovenko et al., 1993

Ammarchaediscidae with a developed outer clear layer, but with important subsisting, inner dark layer.

Remark: The genus *Nudarchaediscus* Conil & Pirlet in Pirlet & Conil, 1974 is a possible junior synonym of *Glomodiscus* Malakhova, 1973.

Composition: *Uralodiscus* Malakhova, 1973; *Conilidiscus* Vachard, 1988; *Glomodiscus* Malakhova, 1973; *Nudarchaediscus* Conil & Pirlet in Pirlet & Conil, 1974.

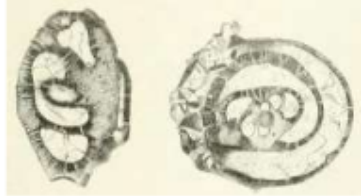



<p>Archaeodiscoidea</p> <p>Discoidal to inflated lenticular Archaeodiscata. Coiling planispiral, oscillating, sigmoidal, or eosigmoilinoïd. Involute, rarely evolute. Lumen of tubular chambers at different evolutionary stages eventually filled with basal nodosities. Wall bilayered dark microgranular and hyaline pseudofibrous, or unilayered hyaline pseudofibrous.</p>	
<p>Lasiodiscoidea</p> <p>This superfamily encompasses three families having in common a tubular chamber, a bilayered wall (microgranular and pseudofibrous), with umbilical pseudofibrous fillings and/or pseudopillars. The chamber remains undivided and the aperture is terminal simple, with possible presence of sutural accessory apertures.</p>	
<p>Pseudoammodiscoidea</p> <p>Free Pseudoammodiscina. Wall microgranular. Spherical proloculus followed by a planispirally or streptospirally coiled, undivided, tubular chamber. Aperture terminal simple, at the extremity of the tubular chamber.</p>	
<p>Tournayelloidea</p> <p>Test planispirally coiled evolute; rarely uncoiled and uniseriate. Septa almost inconspicuous to well developed. Supplementary deposits absent or present as nodes, crusts, and spines. Wall dark microgranular to granular with a calcareous agglutinate. Aperture terminal simple or rarely cribrate.</p>	

Fig. 1. Afusulinana Archaeodiscida. Definitions of the superfamilies. Type figures from top: *Archaediscus karreri* Brady, 1873; *Lasiodiscus granifer* Reichel, 1946; *Ammodiscus priscus* Rauzer-Chernousova, 1948b; *Tournayella discoidea* Dain, 1953.

Family **ARCHAEDISCIDAE** Cushman, 1928

Archaediscoidea with a hyaline wall dominant upon an inner dark layer. Test entirely involute, oscillating, sigmoidal to aligned. Boundaries of the chamber (i.e., sutures and bases of tube) of five types: involutus, concavus, concavo-angulatus, angulatus and tenuis. Nodosities present in several genera. Late early middle Viséan (= late Moliniacian = Arundian = Cf4γ = MFZ11)–earliest Moscovian.

Composition: *Archaediscus* Brady, 1873; *Asteroarchaediscus* A. D. Miklukho-Maklay in Kiparisova et al., 1956; *Hemiarchaediscus* A. D. Miklukho-Maklay, 1957; *Nodasperodiscus* Conil & Pirlet in Pirlet & Conil, 1974; *Nodosarchaediscus* Conil & Pirlet in Pirlet & Conil, 1974; *Paraarchaediscus* Orlova, 1955; *Permodiscus* Dutkevich in Chernysheva, 1948; *Pirletidiscus* Vachard, 1988; *Planospirodiscus* Sosipatrova, 1962; *Tchuisodiscus* Marfenkova, 1991; *Tournarchaediscus* Conil & Pirlet in Pirlet & Conil, 1974.

Family **EOSIGMOILINIDAE** Vachard, 1980

Archaediscoidea with only a hyaline wall. Tests entirely involute, oscillating, sigmoidal, aligned or retrosigmoidal. Boundaries of the chamber (i.e., sutures and bases of tube) of angulatus and tenuis types. Nodosities present in several genera (e.g., *Kasachstanodiscus*, *Brenckleina*) and in two subfamilies: *Kasachstanodiscinae* and *Eosigmoilininae*. Late Serpukhovian–Early Bashkirian.

Subfamily **EOSIGMOILININAE** Vachard, 1980

Eosigmoilinidae involute, retrosigmoidal. Nodosities present in *Brenckleina*.

Composition: *Eosigmoilina* Ganelina in Kiparisova et al., 1956; *Brenckleina* Zaninetti & Altner, 1979; *Quasiarchaediscus* A. D. Miklukho-Maklay, 1960.

Subfamily **KASACHSTANODISCINAE** Marfenkova, 1983

Eosigmoilinidae discoidal, involute to semi-evolute or evolute, oscillating, sigmoidal or aligned. Boundaries of the chamber (i.e., sutures and bases of tube) of angulatus and tenuis types. Nodosities present in *Kasachstanodiscus* and *Neoarchaediscus*.

Remark: *Rugosoarchaediscus* A. D. Miklukho-Maklay, 1957, which was included in the *Archaediscinae* in Vachard & Le Coze (2022), has been recently restudied and found to be a synonym of *Neoarchaediscus* by Vachard & Krainer (2022).

Composition: *Kasachstanodiscus* Marfenkova, 1978; *Betpakodiscus* Marfenkova, 1983; *Brownediscus* Brenckle, Ramsbottom & Marchant, 1987; *Neoarchaediscus* A. D. Miklukho-Maklay in Kiparisova et al., 1956; *Tubispirodiscus* Browne & Pohl, 1973.

Superfamily **LASIODISCOIDEA** Reitlinger, 1956

Description. See Fig. 1.

Family **HOWCHINIIDAE** Martini & Zaninetti, 1988

Tests free, consisting of an undivided tubular chamber, helicoidally coiled in a spire high to low conical. Depressed umbilical region empty (*Vissariotaxis*) or occupied by a hyaline plug, corresponding possibly to anastomosed pseudopillars (*Howchinia* Cushman, 1927; *Monotaxinoides* Brazhnikova & Yartseva, 1956; *Planohowchinia* Cózar & Mamet, 2001). Spiral sutures depressed, without or with small appendices. Aperture terminal simple at the extremity of the tubular chamber; supplementary sutural apertures are present. Middle Viséan (MFZ12)–Moscovian.

Remark: *Vissariotaxis* Mamet, 1970 with its single layered microgranular wall is a transitional form from the *Pseudoammodiscidae* to the *Howchiniidae* and is rattaché to its derived descendant group.

Composition: *Howchinia* Cushman, 1927; *Monotaxinoides* Brazhnikova & Yartseva, 1956; *Planohowchinia* Cózar & Mamet, 2001; *Vissariotaxis* Mamet, 1970.

Family **LASIODISCIDAE** Reitlinger, 1956

Test tubular, undivided, planar or plano-convex. Wall dark microgranular and hyaline, similar to the wall of the *Howchiniidae* Martini & Zaninetti, 1988 (i.e., the hyaline layer is eventually lacking). The hyaline layer is structureless or can display individualized pseudopillars. Aperture terminal simple, frequently, with additional sutural apertures which can be simple or protected by various appendices especially in the Permian genera. Latest Viséan–Late Permian.

Remark: *Postmonotaxinoides* Kulagina & Filimonova, 2020 was published during the process of publication online in 2020 of Vachard & Le Coze (2022) and was therefore not included therein.

Composition: *Lasiotrochus* Reichel, 1946; *Eolasiotrochus* Reitlinger, 1956; *Hemidiscopsis* Cózar in Cózar, Sanz-López & Blanco-Ferrera, 2015; *Hemidiscus* Schellwien, 1898; *Lasiotrochus* Reichel, 1946; *Mesolasiotrochus* Rauzer-Chernousova & Chermnykh, 1990; *Postmonotaxinoides* Kulagina & Filimonova, 2020.

Family **PSEUDOVIDALINIDAE** Altner, 1988

Test small to medium sized, discoidal, inflated or partially inflated, biconvex, or biconcave, bilocular, planispirally coiled, entirely evolute, involute or involute to evolute. Proloculus spherical followed by a second, tubular, undivided chamber. Wall is yellowish, pseudofibrous, bilayered (with a thin, dark, microgranular, inner layer, and an outer, thicker, yellowish, pseudofibrous layer) or pseudofibrous, unilayered. Aperture terminal, simple, at the end of the tubular chamber. ?Late Moscovian. Pennsylvanian–Permian.

Composition: *Pseudovidalina* Sosnina, 1978; *Altneria* Özdikmen, 2009; *Asselodiscus* Mamet & Pinard, 1992; *Falsodiscus* Davydov, 1990; *Xingshandiscus* Zheng, 1986.

Superfamily **PSEUDOAMMODISCOIDEA** Conil & Lys in Conil & Pirllet, 1970
Description. See Fig. 1.

Family **PSEUDOAMMODISCIDAE** Conil & Lys in Conil & Pirllet, 1970

Free Pseudoammodiscoidea. Wall microgranular. Spherical proloculus followed by a planispirally or streptospirally coiled, undivided, tubular chamber. Aperture terminal simple, at the extremity of the tubular chamber. Silurian?–Serpukhovian.

Remark: The genus *Pseudoglomospira* Bykova, 1955 was included in the Pseudoammodiscidae in Vachard & Le Coze (2022). Its type species *P. devonica* described from one poorly oriented Famennian specimen showing very few significant whorls, is rather undiagnostic. Almost exclusively used for Carboniferous and Permian taxa, *Pseudoglomospira* could be a senior synonym of *Eoglomospiroides* (Carboniferous); or a junior synonym of *Glomospirella*; or do not belong to the foraminifera but to the reitlingerellids (incertae sedis). *Pseudoglomospira* is not included in the present classification as being a nomen dubium.

Composition: *Pseudoammodiscus* Conil & Lys in Conil & Pirllet, 1970; *Brunsia* Mikhailov, 1935; *Cepekia* Vašíček & Růžicka, 1957; *Lapparentidiscus* Vachard, 1980.

Superfamily **TOURNAYELLOIDEA** Dain, 1953
Description. See Fig. 1.

Family **TOURNAYELLIDAE** Dain, 1953

Test planispirally coiled evolute; rarely uncoiled and uniseriate (*Rectoseptatourayella*, *Forschiella*). Septa almost inconspicuous (*Eotourayella*) to well developed (*Septatourayella*, *Septaforschia*). Supplementary deposits absent or present as nodes, crusts, and spines. Wall dark microgranular (*Tourayella*) to granular with a calcareous agglutinate (*Forschia*). Aperture terminal simple or rarely cribrate (*Forschia*, *Forschiella*). Frasnian–late Serpukhovian.

Subfamily **FORSCHIINAE** Dain, 1953

Tests planispiral, evolute, of relatively great size, and with a thick wall, brownish, differentiated with agglutinated calcareous particles. They are undivided or pseudoseptated, and sometimes uncoiled. Supplementary deposits are faint or absent. Aperture terminal simple to cribrate.

Composition: *Forschia* Mikhailov, 1935; *Eoforschia* Mamet, 1970; *Forschiella* Mikhailov, 1939; *Septaforschia* Conil & Lys, 1977; *Uviella* Ganelina, 1966; *Viseina* Conil & Lys, 1977.

Subfamily **TOURNAYELLINAE** Dain, 1953

Tournayellidae planispiral evolute, biumbilicate, with rare to common pseudosepta and rare supplementary deposits. Wall undifferentiated, dark. Aperture terminal,

simple, basal.

Composition: *Tourayella* Dain, 1953; *Carbonella* Dain, 1953; *Chernyshinellina* Reitlinger, 1959; *Costayella* Conil & Lys, 1977; *Eotourayella* Lipina & Pronina, 1964; *Pohlia* Conil & Lys, 1977; *Septatourayella* Lipina, 1955; *Septatourayella* (*Eoseptatourayella*) Lipina in Poyarkov, 1963; *Septatourayella* (*Neoseptatourayella*) Bogush, 1980; *Spinotourayella* Mamet, 1970; *Uvatourayella* Ganelina, 1966.

Order **EARLANDIIDA** Loeblich & Tappan, 1982

Test cylindrical to tapering, rectilinear to oscillating, undivided to divided, and uniseriate. Wall dark microgranular, rarely bilayered with a pseudofibrous layer. Aperture terminal simple.

Superfamily **CALIGELLOIDEA** Reitlinger in Rauzer-Chernousova & Fursenko, 1959
Description. See Fig. 2.

Family **BAITUGANELLIDAE** Özkan & Vachard, 2015
Tests irregular, elongate or polygonal, generally lacking of the symmetries of the other foraminiferal groups. Proloculus inconspicuous or eventually absent, followed by irregular pseudochambers (without the architectural regularity of the modern foraminifera), separated by wall constrictions and pseudosepta randomly arranged. Wall brownish, microgranular to granular, thick to very thick, including (agglutinating?) clearer calcitic particles, unilayered, rarely bilayered, with an inner pseudofibrous, clearer layer. Apertures poorly characterized, generally difficult to distinguish of broken or dissolved parts of the wall. Eifelian–Serpukhovian.

Remark: *Vulgarella* Mikhno in Mikhno & Balakin, 1975 was originally described in the Parathuramminidae. It has never been re-described and is here tentatively included in the Baituganellidae because of its irregular and asymmetrical test, without openings or well-expressed septa, but it could also be a more or less atypical bisphaerid.

Composition: *Baituganella* Lipina, 1955; *Ademassa* Vachard in Vachard et al., 1993; *Halevikia* Özkan & Vachard, 2015; *Paracaligelloides* Reitlinger in Chuvashov, 1965; *Petchorina* Reitlinger, 1962; *Vulgarella* Mikhno in Mikhno & Balakin, 1975.

Family **CALIGELLIDAE** Reitlinger in Rauzer-Chernousova & Fursenko, 1959

Earlandioidea deformed by a particular endobenthic way of life. Wall dark, thin microgranular. Late Silurian (Ludlow)–Early Pennsylvanian.

Composition: *Caligella* Antropov, 1950; *Eocaligella* Pronina, 1980; *Eotikhinella* Pronina, 1980; *Glubokoevella* Pronina, 1970; *Halenopora* Hance, 1983; *Paracaligella* Lipina, 1955.

Family **INSOLENTITHECIDAE** Loeblich & Tappan, 1986

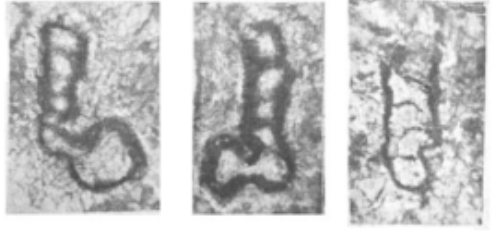
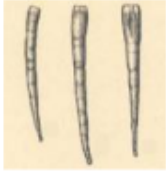

<p>Caligelloidea</p> <p>Irregular tests or permanent cysts of naked foraminifera surrounding their cytoplasm. Wall thin to thick, eventually with bricks composed of agglutinated or linked together tests of smaller foraminifera. Proloculus and apertures inconspicuous or questionable. Wall dark microgranular, often with a calcareous agglutinate and bilayered, dark microgranular and hyaline pseudofibrous.</p>	
<p>Earlandioidea</p> <p>Test cylindrical to tapering, rectilinear to oscillating, undivided to divided, and uniserial. Wall dark microgranular, rarely bilayered with a pseudofibrous layer. Aperture terminal simple.</p>	
<p>Eonodosarioidea</p> <p>Test uniserial, tapering. Chambers hemispherical to arcuate, undivided or with radiate septula. Wall bilayered, microgranular, and pseudofibrous, rarely only dark microgranular. Aperture simple, terminal, central.</p>	

Fig. 2. Afusulinana Earlandiida. Definitions of the superfamilies. Type figures from top: *Caligella borovkensis* Antropov, 1950; *Earlandia perparva* Plummer, 1930; *Eonodosaria evlavensis* Lipina, 1950.

Test elongate, irregular in form, without septa; wall calcareous, microgranular, homogeneous, with numerous small endothyroid and fusulinid foraminifera attached as agglutinated inclusions in wall; no recognizable aperture (Loeblich & Tappan 1986). Rare in late Viséan. Early Serpukhovian–early middle Permian. Rare and questionable in late Permian.

Composition: *Insolentitheca* Vachard in Bensaid et al., 1979; *Floritheca* Gaillot & Vachard, 2007; *Protoinsolentitheca* Vachard & Cózar, 2004.

Family **TOURNAYELLINIDAE** Reitlinger in Rauzer-Chernousova et al., 1996

Test irregularly nautiloid, planispiral involute, with only one or two spires and only 3 to 5 pseudochambers. A second terminal stage, uniserial exist in several genera. Latest Devonian–late Tournaisian.

Composition: *Tournayellina* Lipina, 1955; *Rectochernella* Vachard, 1980; *Rectotournayellina* Lipina, 1965.

Superfamily **EARLANDIOIDEA** Cummings, 1955
Description. See Fig. 2.

Family **EARLANDIIDAE** Cummings, 1955

Shell long, cylindrical, tubular, rectilinear or slightly tapering, and undivided. Proloculus spherical more or less prominent, commonly broken. Aperture simple, terminal, as wide as the tubular chamber. Wall dark microgranular,

more or less differentiated. Shell long, cylindrical, tubular, rectilinear or slightly tapering, and undivided. Proloculus spherical more or less prominent, commonly broken. Aperture simple, terminal, as wide as the tubular chamber. Wall dark microgranular, more or less differentiated. Silurian-Cretaceous.

Composition: *Earlandia* Plummer, 1930; *Chitralina* Angiolini & Rettori, 1994; *Earlandinita* Cummings, 1955; *Elevenella* Vachard, 1994; *Lobatiquinella* Vachard, 1994; *Lugtonia* Cummings, 1955; *Magnitella* Malakhova, 1975; *Oldella* Pronina, 1968; *Paratikhinella* Reitlinger, 1954; *Rectoformata* Okuyucu, 2007; *Reitlingerlandia* Vachard, 1994.

Superfamily **EONODOSARIOIDEA** Rauzer-Chernousova in Vdovenko et al., 1993
Description. See Fig. 2.

Family **EONODOSARIIDAE** Rauzer-Chernousova in Vdovenko et al., 1993

Test multilocular, rectilinear, sometimes with secondary radially located septa; Wall bilayered, with external pseudo-fibrous, hyaline, yellowish layer and internally microgranular, forming secondary septa; the aperture is simple. Middle and Upper Devonian.

Composition: *Eonodosaria* Lipina, 1950; *Eogeinitzina* Lipina, 1950; *Fronnilina* Bykova, 1952; *Juferevella* Zadorozhnyy, 1987; *Multiseptida* Bykova, 1952; *Tikhinella* Bykova, 1952.

Order **PSEUDOPALMULIDA** Mikhalevich, 1993

Superfamily **PSEUDOPALMULOIDEA** Bykova in
Rauzer-Chernousova & Fursenko, 1959
Description. See Fig. 3.

foramina.

Order **ENDOTHYRIDA** Fursenko, 1958

Tests nautiloid, lenticular, discoid. Proloculus small and spherical. Endothyroidally or planispirally coiled tests, rarely uncoiled. Chambers globular and not numerous.

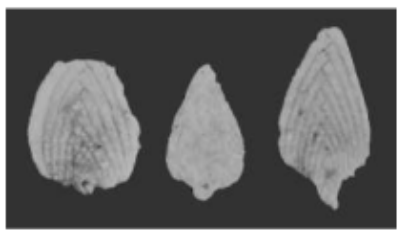
<p>Pseudopalmuloidea</p>	
<p>Tests planispirally coiled, biseriate, biseriate to uniseriate, or uniseriate. Chambers undivided or rarely with pillars, tapering compressed to palmate. Aperture basal, or terminal; simple or rarely multiple.</p>	

Fig. 3. Afusulinana Pseudopalmulida. Definition of the superfamily. Type figure: *Pseudopalmula palmuloides* Cushman & Stainbrook, 1943.

Family **NANICELLIDAE** Fursenko, 1959

Tests planispirally coiled, uniseriate, involute to evolute. Chambers undivided. Aperture simple, basal. Rare in Emsian; relatively common to common from Eifelian to Frasnian.

Composition: *Nanicella* Henbest, 1935.

Family **PSEUDOPALMULIDAE** Bykova in Rauzer-Chernousova & Fursenko, 1959

Tests biseriate. Chambers undivided, tapering compressed to palmate. Aperture terminal simple, occasionally with a neck. Eifelian-Frasnian.

Composition: *Pseudopalmula* Cushman & Stainbrook, 1943; *Paratextularia* Pokorný, 1951.

Family **SEMITEXTULARIIDAE** Pokorný, 1956

Tests planispirally coiled, biseriate to uniseriate. Chambers with pillars, compressed, palmate. Aperture terminal, multiple. Eifelian-Frasnian.

Composition: *Semitextularia* Miller & Carmer, 1933.

Subclass **FUSULINANA** Maslakova, 1990

Tests nautiloid, lenticular, discoid, subquadratic, inflated fusiform, elongate fusiform, subrhombic, subcylindrical. Proloculus spherical, small to large, and reniform or rectangular. Juvenaria often present. Endothyroidally or planispirally coiled tests, rarely uncoiled. Chambers globular and not numerous (endothyrids), to quadratic to fusiform and numerous (fusulinids). Septa planar to moderately folded to strongly folded. Endoskeleton always developed (crusts, hooks, pseudochomata, chomata). Wall dark microgranular occasionally bilayered to multilayered (globoendothyrids, ozawainelloids) often with a dark-microgranular thin tectum, and a differentiated inner layer (schubertelloids with primatheca; fusulinoids with diaphanotheca; schwagerinoids with keriotheca; neoschwagerinoids with "fine keriotheca"). Aperture terminal simple, basal, rarely cribrate, occasionally reduced to septal pores, cuniculi or

Septa planar. Endoskeleton generally developed (crusts, hooks, pseudochomata). Wall dark microgranular, occasionally bilayered to multilayered. Aperture terminal simple, basal, rarely cribrate or central.

Superfamily **BRADYINOIDEA** Reitlinger, 1950

Description. See Fig. 4.

Family **BRADYINIDAE** Reitlinger, 1950

Bradyinoidea nautiloid, planispirally coiled and involute. Whorls and chambers are not numerous. Septa are short with additional pre- and post-septal lamellae. Alveolar wall overlain by a continuous tectum. Simple aperture becoming cribrate at the last chamber. Additional sutural pores present. Late Asbian (middle part of MFZ14)-late Early Permian.

Composition: *Bradyina* Möller, 1878; *Bradyinelloides* Mamet & Pinard, 1992; *Glyphostomella* Cushman & Waters, 1928; *Parabradyina* Mamet & Pinard, 1992; *Postendothyra* Lin, 1984; *Pseudobradyina* Reitlinger, 1950; *Pseudojanischewskina* Mamet & Pinard, 1992.

Family **ENDOTHYRANOPSIDAE** Reitlinger, 1958

Bradyinoids small to medium in size having in common the test planispiral involute generally nautiloid. Moderate number of whorls and chambers. Septa truncated at the base. Supplementary deposits absent or represented by a terminal hook. Wall dark simple, to calcareously agglutinated. A pseudokeriotheca exists in the most advanced *Endothyranopsis*. Aperture terminal, simple, basal. Early Ivorian (MFZ 5)-Changhsingian.

Subfamily **ENDOTHYRANOPSINAE** Reitlinger, 1958

Bradyinoids small to medium in size, planispiral involute and generally nautiloid. Moderate number of whorls and chambers. Septa truncated at the base. Supplementary deposits absent or represented by a terminal hook and some pseudochomata. Wall dark simple, relatively thick and generally calcareously agglutinated. A fine


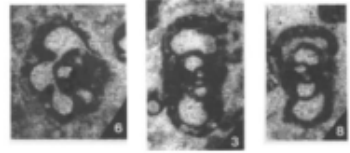
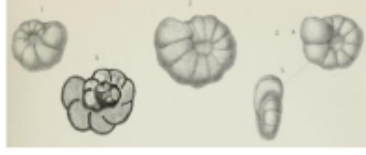


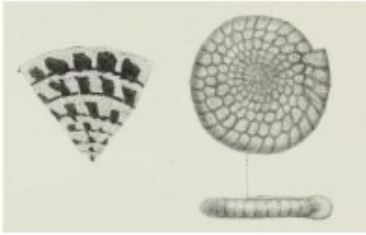
<p>Bradyinoidea</p> <p>Test planispirally coiled, involute, discoid to nautiloid. No supplementary deposits or isolated spines. Wall coarsely granular to calcareously agglutinated. Septa often truncated at the base, chamber quadrate to hemispherical. Sutures generally few marked. Aperture simple to cribrate. Sutural supplementary pores in most advanced forms.</p>	
<p>Endoteboidea</p> <p>Planispirally to endothyroidally coiled Palaeotextulariina with a biseriata terminal part or only endothyroidally coiled.</p>	
<p>Endothyroidea</p> <p>Endothyroid coiling at least in the initial stage, rarely becoming uniseriata or biseriata. Supplementary deposits well developed. Wall dark microgranular or with tectum and a differentiated inner layer. Aperture simple basal, rarely central, rarely cribrate.</p>	
<p>Globivalvulinoidea</p> <p>Test free, biserially coiled to biseriata. Few whorls, few chambers increasing rapidly in height. An oral valvula near the aperture. Supplementary deposits absent or very rare. Supplementary chamberlets occasionally present. Wall unilayered dark microgranular or granular with calcareous agglutinate, or bilayered with an inner pseudofibrous layer. Aperture simple basal.</p>	
<p>Lituotubelloidea</p> <p>Free to attached (pseudolituotubids) Lituotubellina streptospirally coiled; rarely or with uncoiled terminal part. Wall dark microgranular to granular with calcareous agglutinates. Aperture terminal, simple, and basal; rarely cribrate.</p>	
<p>Loeblichioidea</p> <p>Test endothyrid with more numerous chambers than the typical endothyroid forms of this group, and becoming strongly deviated to aligned and even planispiral and evolute. Numerous quadratic chambers without sutures. Spines in the primitive forms pseudo-chomata in the typical forms. Wall simple dark, or bilayered with tectum and grey inner layer or more rarely calcareously agglutinated. Aperture terminal, basal simple.</p>	

Fig. 4. Fusulinana Endothyrida. Definitions of the superfamilies: Bradyinoidea, Endoteboidea, Endothyroidea, Globivalvulinoidea, Lituotubelloidea, Loeblichioidea. Type figures from top: *Bradyina nautiliformis* Möller, 1878; *Endoteba controversa* Vachard & Razgallah, 1988; *Endothyra bowmani* Phillips, 1846 sensu Brady, 1876; *Valvulina bulloides* Brady, 1876; *Lituotubella glomospiroides* Rauzer-Chernousova, 1948a; *Endothyra ammonoides* Brady, 1876.

pseudokeriotheca exists in the most advanced *Endothyranopsis*. Wall terminal, simple, basal.

Remark: This subfamily has been partially restudied by Vachard & Cózar in Liu et al. (2023): *Bibradya* Strank, 1983 was transferred in the family Janischewskinae with its subjective junior synonym *Groessensella* Strank in Somerville & Strank, 1984. *Rectocribranopsis* Kobayashi & Vachard, 2022 is a recent addition published after Vachard & Le Coze (2022). *Spinothyra* is transferred herein in the Endothyridae. Its microgranular wall structure makes it closer to this latter family.

Composition: *Cribranopsis* Conil & Longersstaey, 1980; *Endothyranopsis* Cummings, 1955; *Granuliferella* Zeller, 1957; *Latiendothyranopsis* Lipina, 1977; *Plectogyranopsis* Vachard, 1977; *Rectocribranopsis* Kobayashi & Vachard, 2022.

Subfamily **NEOENDOTHYRINAE** Reitlinger in Rauzer-Chernousova et al., 1996

Test from discoid to pseudolenticular and subrhombic, involute or less often partially pseudoevolute, umbilici wide or narrow, periphery narrowly rounded in the first whorl, in the latter, rounded-angular or pointed, planispiral coiling, less often endothyroid in the first stage, the spiral is free, more compact in the first whorl, often rapidly increasing in the last whorl, septa are usually straight, slightly inclined forward, wall thick or moderate, inconstant microstructure, heterogeneous or homogeneous, dark or light gray in cross-section, poorly differentiated; secondary deposit lining or filling the lateral parts of the chamber, often massive, represented by chomata or pseudo-chomata; the aperture is simple.

Composition: *Linendothyra* Mamet & Pinard, 1992; *Neoendothyra* Reitlinger, 1965; *Neoendothyranella* Nestell & Nestell, 2006.

Family **EOENDOTHYRANOPSIDAE** Reitlinger in Rauzer-Chernousova et al., 1996

Test involute, almost planispiral, with numerous quadratic chambers, truncated septa, no sutures, and a carinate to rounded periphery. Pseudo-chomata, often associated with a terminal hook. Wall brownish with calcareous agglutinate. Early–late Viséan.

Remark: The wall microstructure of *Ninella* is unfortunately poorly known; either microgranular or granular. Consequently and hypothetically, we reattached *Ninella* to the Eoendothyranopsidae. *Ninella staffelliformis* (Chernysheva, 1948) is relatively similar to *Eoendothyranopsis*, whereas *Ninella asiatica* is more comparable, morphologically, to a big dainellid; furthermore, *N. extremus* Ponomaryova, 2009 is most probably a dainellid *Vissarionovella* rather than a true *Ninella*. The emended description of *Ninella* by Reitlinger in Rauzer-Chernousova et al. (1996) is here followed.

Composition: *Eoendothyranopsis* Reitlinger & Rostovzeva, 1966; *Ninella* Malakhova, 1975; *Skippella* Mamet, 1974.

Family **JANISCHEWSKINIDAE** Reitlinger in Rauzer-Chernousova et al., 1996

Test free, nautiloid to compressed laterally, with a juvenarium endothyroid passing to a planispiral final coiling. Coiling follows a progressive increase of the spire with a common rapid increase of the final whorl, in species trending to the uncoiling. Secondary deposits absent. The most common septa are simple, curved backward, but also furrowed, blunt, swollen, and bifurcated. Cribrate aperture in the final whorl, rarely present in the penultimate chambers. Wall microgranular to granular with some agglutinated grains in the more ancestral forms, or with a porous tectum. Late Viséan–early Bashkirian.

Remark: The composition of the family Janischewskinae Reitlinger in Rauzer-Chernousova et al., 1996 has been reviewed by Vachard & Cózar in Liu et al. (2023). The genera *Rhodesinella* and *Groessensella* have been considered to be synonyms of *Criboospira* and *Bibradya*, respectively.

Composition: *Janischewskina* Mikhailov, 1939; *Bibradya* Strank, 1983; *Criboospira* Möller, 1878; *Parajanischewskina* Cózar & Somerville, 2006.

Superfamily **ENDOTEBOIDEA** Vachard, Martini, Rettori & Zaninetti, 1994
Description. See Fig. 4.

Family **ENDOTEBIDAE** Vachard, Martini, Rettori & Zaninetti, 1994

Test free, planispirally coiled with small initial deviations; sometimes lately uncoiled. Profile of coiled part nautiloid and compressed, with chambers chernyshinellid to endothyroid. Wall granular with carbonate or rarely siliceous agglutinate. Aperture simple basal in the coiled part, to areal to cribrate in the uncoiled part. Rare in the Artinskian–Kungurian. Present from Middle Permian to Late Triassic.

Composition: *Endoteba* Vachard & Razgallah, 1988; *Rectoendoteba* Vachard in Krainer, Vachard & Schaffhauser, 2019; *Vachardella* Nestell & Nestell, 2006.

Family **SPIREITLINIDAE** Vachard, Krainer & Lucas, 2013

Endoteboidea with a coiled, nearly planispiral, endothyroid (and/or multiseriate) initial stage, more or less developed, followed by a biseriate terminal stage always relatively large. Late Mississippian (early Serpukhovian)–Middle Permian (Capitanian).

Composition: *Spireitlina* Vachard in Vachard & Beckary, 1991; *Globispiropectamina* Vachard, 1977.

Superfamily **ENDOTHYROIDEA** Brady, 1884
Description. See Fig. 4.

Family **ENDOTHYRIDAE** Brady, 1884

All the representatives display the endothyroid coiling at least at the initial stage (eventually becoming uniseriate

or biseriata) with supplementary deposits generally well developed. Wall dark simple, or with calcareous particles agglutinated (Paraendothyridae) or microperforated with tectum (Omphalotidae). Aperture simple basal rarely areal or cribrate. Late Tournaisian to middle (late?) Permian.

Composition: *Endothyra* Phillips, 1846; *Birectoendothyra* Lipina, 1970; *Endospiroplectamina* Lipina, 1970; *Endothyranella* Galloway & Harlton in Galloway & Ryniker, 1930; *Globoomphalotis* Bogush, 1987; *Iriclinella* Malakhova, 1980; *Mediendothyra* Brazhnikova & Vdovenko in Vdovenko, 1972; *Mediopsis* Bogush in Bushmina et al., 1984; *Melatolla* Strank, 1983; *Mikhailovella* Ganelina, 1956; *Omphalotis* Shlykova, 1969; *Paraendothyra* Chernysheva, 1940; *Paraplectogyra* Okimura, 1958; *Planoendothyra* Reitlinger, 1959; *Rectoendothyra* Brazhnikova, 1983; *Semiendothyra* Reitlinger, 1980; *Spinothyra* Mamet, 1976; *Timanella* Reitlinger, 1981; *Tuberendothyra* Skipp, 1969; *Ugurus* Özdikmen, 2009; *Vachardites* Cózar, Somerville, Sanz-López & Blanco-Ferrera, 2016.

Superfamily **GLOBIVALVULOIDEA** Reitlinger, 1950

Description. See Fig. 4.

Family **BISERIAMMINIDAE** Chernysheva, 1941

Test free, biserially coiled to biseriata, with a few whorls and a few chambers increasing rapidly in height. An oral valvula near the aperture. Supplementary deposits absent or very rare. Supplementary chamberlets occasionally present. Wall unilayered dark microgranular or granular with calcareous agglutinate, or bilayered with an inner pseudofibrous layer. Aperture simple basal. Tournaisian–Visean.

Composition: *Biseriammina* Chernysheva, 1941; *Dariopsis* Malakhova, 1975; *Globochernella* Hance, 1983; *Lipinella* Malakhova, 1975.

Family **GLOBIVALVULINIDAE** Reitlinger, 1950

Test biserial, entirely planispiral or initially trochospiral, or entirely uncoiled, or trochospiral, becoming planispiral. Wall thin, dark, microgranular, eventually granular with inclusions of clearer carbonate particles, or differentiated into two, three or four layers; nevertheless, this differentiation does not affect all the chambers and/or corresponds to fossil diagenetic features, and is not admitted here as a generic criterion. Endoskeletal folds or partitions lead to the formation of chamberlets. Oral tongue often present, occasionally passing to a siphon. Aperture terminal simple. Mississippian (latest Tournaisian)–Permian (latest Changhsingian). ?Earliest Triassic.

Subfamily **DAGMARITINAE** Bozorgnia, 1973

Uncoiled biserial Globivalvulinidae (or exceptionally biserially coiled: *Crescentia*). Undivided chambers (or divided on chamberlets: *Louissetita*), often with thornlike

lateral projections. Aperture terminal, basal simple with a valvula.

Composition: *Dagmarita* Reitlinger, 1965; *Bidagmarita* Gaillot & Vachard in Gaillot et al., 2009; *Crescentia* Ciarapica, Cirilli, Martini & Zaninetti, 1986; *Danielita* Altner & Özkan-Altner, 2010; *Labiogdagmarita* Gaillot & Vachard, 2007; *Louissetita* Altner & Brönnimann, 1980; Sengoerina Altner, 1999.

Subfamily **GLOBIVALVULININAE** Reitlinger, 1950

Test biserially coiled, hemispherical. Oral tongue generally well developed. Wall dark simple to calcareously agglutinated; rarely bilayered with a pseudofibrous inner layer.

Composition: *Globivalvulina* Schubert, 1921; *Admiranda* Marfenkova, 1991; *Biseriella* Mamet in Armstrong & Mamet, 1974; *Charliella* Altner & Özkan-Altner, 2001; *Dzhamansorina* Marfenkova, 1991; *Globigaetania* Gennari & Rettori, 2019; *Labioglobivalvulina* Gaillot & Vachard, 2007; *Lateenoglobivalvulina* Filimonova, 2016; *Parabiseriella* Cózar & Somerville, 2012; *Retroseptellina* Gaillot & Vachard, 2007; *Tenebrosella* Villa & Sánchez de Posada, 1986; *Verispira* Palmieri, 1988.

Subfamily **PARADAGMARITINAE** Gaillot & Vachard, 2007

A subfamily of Globivalvulinidae (i.e., with a biserially coiled growth and a microgranular wall, occasionally differentiated) characterized by an uncoiling more or less developed after an initial coiling generally slightly trochospiral.

Composition: *Paradagmarita* Lys, 1978; *Paradagmacrusta* Gaillot & Vachard, 2007; *Paradagmaritella* Gaillot & Vachard, 2007; *Paradagmaritopsis* Gaillot & Vachard, 2009; *Paremiratella* Gaillot & Vachard, 2007; *Paynita* Altner, Özkan-Altner, Atasoy & Şahm, 2021.

Subfamily **PARAGLOBIVALVULININAE** Gaillot & Vachard, 2007

Globivalvulinidae with entirely or almost entirely enveloping last chamber, i.e., tending to a spherical shape of the test, and some endoskeletal supplementary formations (for example, septal chamberlets and interseptal stolons). Wall microgranular single layered occasionally differentiated with an *Omphalotis*-type.

Composition: *Paraglobivalvulina* Reitlinger, 1965; *Paraglobivalvulinoides* Zaninetti & Jenny-Deshusses, 1985; *Septoglobivalvulina* Lin, 1978; *Urushtenella* Pronina-Nestell in Pronina-Nestell & Nestell, 2001.

Family **KOKTJUBINIDAE** Marfenkova, 1991

Test biserially coiled. Initially, the first three chambers might be multiserial and constitute a juvenarium followed by a rapidly expanding stage of one or two whorls. Because of the complex type of coiling, chamber shape is very variable in sections. Sutures indistinct or faint. No

supplementary deposits. Oral valvula absent or faint. Wall thin, unilayered, microgranular in the juvenarium. In the adult whorls, the wall is differentiated with a tectum and an inner coarse layer with calcareous agglutinated particles, fine to medium-sized. Aperture on last chamber, basal, simple). Tournaisian–Serpukhonian.

Composition: *Koktjubina* Marfenkova, 1991; *Praekoktjubina* Vachard, Haig & Mory, 2014; *Ulanbella* Marfenkova, 1991.

Superfamily **LITUOTUBELLOIDEA** A. D. Miklukho-Maklay, 1963

Description. See Fig. 4.

Family **CHERNYSHINELLIDAE** Reitlinger, 1958

Endothyroidally coiled to uncoiled, uniseriate or biseriata. Complete septa in all whorls. Chambers characteristically teardrop-shaped. Rare supplementary deposits. Wall dark and simple, with rare agglutinated calcareous particles in some representatives. Aperture terminal simple. Tournaisian–Visean (MFZ3–MFZ12).

Remark: *Neochernyshinella* Brenckle, 2005 was included in the valid genera of the family Chernyshinellidae in Vachard & Le Coze (2022). Its type species *Endothyra oldae* Grozdilova & Lebedeva, 1954 has been included in the genus *Prochernyshinella* by various authors like Vdovenko & Zhulitova in Makhlina et al. (1993), Reitlinger in Rauzer-Chernousova et al. (1996) and Kulagina (2013). We agree that *Neochernyshinella* Brenckle, 2005 is a junior subjective synonym of *Prochernyshinella* Reitlinger in Rauzer-Chernousova et al., 1996.

Composition: *Chernyshinella* Lipina, 1955; *Chernyshinella* (*Endochernyshinella*) Durkina, 1997; *Endochernella* Conil & Lys in Conil et al., 1980; *Nodochernyshinella* Conil & Lys, 1977; *Prochernyshinella* Reitlinger in Rauzer-Chernousova et al., 1996; *Spinochernella* Conil & Lys, 1977; *Spinotournayellina* Wu in Wu & Liao, 2001.

Family **LITUOTUBELLIDAE** A. D. Miklukho-Maklay, 1963

Tests streptospirally coiled becoming uncoiled. Complete septa in all whorls. Chambers characteristically teardrop-shaped. Rare supplementary deposits. Wall dark and simple, with rare agglutinated calcareous particles in some representatives. Aperture terminal simple. Late Tournaisian–late Serpukhonian.

Remark: Compared with Vachard & Le Coze (2022) a more concise composition of the family Lituotubellidae is followed similarly to the one in Hance et al. (2011). *Bogushella* Conil & Lys, 1977, *Criboaperturata* Lipina, 1990 (probable juvenile of *Lituotubella*), *Eocribrella* Lipina, 1989 are synonymized with *Lituotubella*, whereas *Mstiniella* Conil & Lys, 1977 is synonymized with *Pseudolituotubella*.

Composition: *Lituotubella* Rauzer-Chernousova, 1948; *Alticonilites* Hance, Hou & Vachard, 2011;

Pseudolituotubella Vdovenko, 1967.

Family **PALAEOSPIROPLECTAMMINIDAE** Loeblich & Tappan, 1984

Test streptospirally coiled in the initial part, later planispiral and finally biserial; wall microgranular calcareous, undifferentiated, and may have some agglutinated particles; aperture at the base of the final chamber (Loeblich & Tappan 1987). Tournaisian-Late Visean.

Composition: *Palaeospiroplectamina* Lipina, 1965; *Plectinopsis* Vachard, Haig & Mory, 2014; *Rectochernyshinella* Lipina, 1960; *Rectogranuliferella* Conil & Lys in Mansy et al., 1989.

Family **PSEUDOLITUOTUBIDAE** Conil & Longerstaey in Conil et al., 1980

Attached Lituotubelloidea, streptospiral to uncoiled, with a thick brownish wall with numerous clearer calcitic particles. ?Late Famennian. Late Tournaisian-early Serpukhonian.

Composition: *Pseudolituotuba* Vdovenko, 1971; *Scalebrina* Conil & Longerstaey, 1980.

Superfamily **LOEBLICHIOIDEA** Cummings, 1955

Description. See Fig. 4.

Family **DAINELLIDAE** Cózar & Vachard, 2001

Tests medium-sized to large, nautiloid, with permanent strong deviations of axis, involute to rarely evolute. Chambers numerous, subquadratic, and not sutured. Wall simple dark, bilayered with tectum or coarsely granular. Pseudochomata, chomata or arches as secondary deposits. Aperture terminal, simple and basal. Late early Tournaisian-late Serpukhonian.

Composition: *Dainella* Brazhnikova, 1962; *Bessiella* Conil & Hance in Groessens et al., 1982; *Lysella* Bozorgnia, 1973; *Paralysella* Cózar & Vachard, 2001; *Praedainella* Hance, Hou & Vachard, 2011; *Pseudodainella* Wu in Wu & Liao, 2001; *Vissarionovella* Cózar & Vachard, 2001.

Family **EOPARASTAFFELLIDAE** Vachard & Arefifard, 2015

This family encompasses the most advanced Loeblichioidea, which give rise to the primitive Fusulinida; i.e., those with dainellid first whorls followed by a few whorls more or less planispiral. Chambers subquadratic, not sutured. Periphery rounded to carinate. Chomata variously developed. Wall microgranular with a luminotheca. Aperture terminal, basal, and simple. Late early Tournaisian–late Serpukhonian.

Composition: *Eoparastaffella* Vdovenko, 1954; *Bozorgnites* Cózar, Vachard & Le Coze, 2019; *Eoparastaffellina* Vdovenko, 1971; *Klubonibelia* Conil, 1980; *Neoparadainella* Vdovenko in Brazhnikova & Vdovenko, 1973; *Paradainella* Brazhnikova, 1971; *Pojarkovella* Simonova & Zub, 1975.

Family **LOEBLICHIIDAE** Cummings, 1955

Advanced loeblichoids with marked quasiendothyroid trends: numerous chambers, absence of sutures, evolute whorls and pseudochomata. Various types of wall, from microgranular to granular. Early Visean–late Serpukhovian.

Subfamily **BANFELLINAE** Vachard & Le Coze, 2022

Test discoid to nautiloid. Primitive loeblichoids with marked endothyroid trends: numerous chambers, absence of sutures, initial juvenarium followed by semi-evolute to evolute whorls and pseudochomata or arches or spines. Microgranular wall.

Composition: *Banffella* Mamet, 1970; *Brenckleites* Hance, Hou & Vachard, 2011; *Florennella* Conil in Groessens et al., 1982; *Spinobrunsiina* Conil & Longerstae, 1980.

Subfamily **ENDOSTAFFELLINAE** Loeblich & Tappan, 1984

Tests small, nautiloid, lenticular or discoid strongly quasiendothyroid (i.e., with numerous chambers), often umbilicate or biumbilicate. Strong deviations of axis; rarely planispiral. Sutures faint to absent. Pseudochomata generally present. No case of uncoiling. Wall dark simple, microgranular, stable (*Endostaffella* Rozovskaya, 1961) to recrystallized (*Euxinita* Conil & Dil in Conil, Longerstae & Ramsbottom, 1980). Aperture terminal, simple.

Remark: *Zellerinella* Mamet, 1981 was included as valid in the subfamily Endostaffellinae in Vachard & Le Coze (2022). It was confirmed as a junior subjective of *Endostaffella* Rozovskaya, 1961 in Kobayashi & Vachard (2022). The same opinion was shared earlier by many authors (Kobayashi & Vachard (2022) with references therein).

Composition: *Endostaffella* Rozovskaya, 1961; *Euxinita* Conil & Dil, 1980; *Praeastaffellina* Cózar, Somerville & Burgess, 2008; *Praeplectostaffella* Cózar, Somerville & Burgess, 2008.

Subfamily **LOEBLICHINIINAE** Cummings, 1955

Test discoid to flat. Planispiral, evolute coiling, numerous chambers, absence of sutures, pseudochomata or chomata. Microgranular wall.

Composition: *Loeblichia* Cummings, 1955; *Endostaffellopsis* Cózar, Somerville, Sanz-López & Blanco-Ferrera, 2016.

Subfamily **MEDIOCRINAE** Hance, Hou & Vachard, 2011

Test discoidal with rounded periphery, planispiral to irregularly coiled involute. Numerous chambers, eostaffelloid in shape. Axial filling well developed covering all the lateral parts. Pseudochomata rare. Wall microgranular. Simple terminal aperture.

Composition: *Mediocris* Rozovskaya, 1961; *Chomatemediocris* Vdovenko, 1973; *Plectomediocris*

Brazhnikova & Vdovenko, 1983.

Subfamily **SPINOENDOTHYRINAE** Cózar & Vachard, 2001

Advanced Endothyroidea that, despite a great number of chambers, remain markedly endothyroid in coiling and shape of chambers (i.e., relatively less numerous and more inflated than in the Loeblichioidea; see later); supplementary formations in spines or crustae but without pseudochomata. Wall dark or faintly differentiated.

Composition: *Spinoendothyra* Lipina, 1963; *Elergella* Conil, 1984; *Inflatoendothyra* Brazhnikova & Vdovenko, 1972; *Palaeospinoendothyra* Wu in Wu & Liao, 2001; *Pseudochernyshinella* Brazhnikova, 1974; *Pseudoinflatoendothyra* Wu in Wu & Liao, 2001.

Superfamily **HAPLOPHRAGMINOIDEA** Reitlinger, 1950

Description. See Fig. 5.

Family **HAPLOPHRAGMINIDAE** Reitlinger, 1950

Haplophragminoidea with strong pseudosepta, especially in the uncoiled terminal/uniseriate part. Aperture terminal cribrate or simple. Visean–Moscovian.

Composition: *Haplophragmina* Reitlinger, 1950; *Darjella* Malakhova, 1964; *Haplophragmella* Rauzer-Chernousova & Reitlinger in Rauzer-Chernousova et al., 1936.

Family **MSTINIIDAE** Lipina, 1989

Tests free, entirely coiled or with an initial coiling followed by a secondary erected tubular part. Early stage planispiral, involute, with chernyshinellid chambers, adult stage uncoiled uniseriate, rarely biseriate. Pseudosepta to well-developed septa. Aperture simple basal followed by a cribrate aperture in the last coiled chambers. Wall brownish, granular, including a calcareous agglutinate. ?Early Tournaisian. Late Tournaisian–late Serpukhovian.

Composition: *Mstinia* Dain, 1953; *Condruustella* Conil & Longerstae in Conil & Lys, 1977; *Eotextularia* Mamet, 1970; *Granuliferelloides* McKay & Green, 1963; *Halenia* Conil, 1980; *Holkeria* Strank, 1982; *Rectopravina* Vachard, Haig & Mory, 2014.

Superfamily **PALAEOTEXTULARIOIDEA** Galloway, 1933

Description. See Fig. 5.

Family **KOSKINOTEXTULARIIDAE** Loeblich & Tappan, 1984

Palaeotextularioidea with unilayered walls. Early Visean (upper MFZ11, Cf4δ)–late Serpukhovian.

Composition: *Koskinotextularia* Eickhoff, 1968; *Consobrinellopsis* Krainer & Vachard, 2015; *Koskinobigenarina* Eickhoff, 1968.




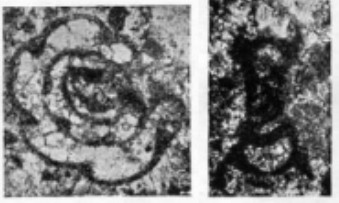

<p>Haplophragminoidea</p> <p>Lituotubellina morphologically diversified (planispirally coiled, uniseriate, biseriata, or biserially coiled), having in common the thick walls, chernyshinellid chambers, and well-developed calcareous agglutinates.</p>	
<p>Palaeotextularioidea</p> <p>Entirely biseriata Palaeotextulariina.</p>	
<p>Quasiendothyroidea</p> <p>Endothyroid to planispiral coiling, involute to seminvolute. Chambers numerous, quadratic, without sutures. Secondary deposits strong: crusts, pseudo-chomata, chomata. Aperture simple, terminal, basal.</p>	
<p>Septabrunsiinoidea</p> <p>Test discoid to subnautiloid, biumbilicate or with prominent flanks. Pseudoseptate to septate from early to last whorls, or rarely completely septate. Supplementary deposits often absent, or represented by corner fillings, or rarely by curved spines in the last chambers. Wall dark microgranular forming tectum, or differentiated with clearer particles, or rarely multilayered.</p>	
<p>Tetrataxoidea</p> <p>Test conical, trochospiral, with a planar to slightly depressed face. Umbilical face depressed to planar or forming more or less developed umbilical pivots. Mode of life attached to vagile, epiphytic on algae or corals. Four or five chambers in each whorl. Undivided chambers, or with secondary partitions. Aperture in the umbilicus, occasionally protected by a micro-aquarium. Wall thin dark microgranular, thick with the hyaline microgranular always as the outer layer and only located in the umbilicus, and not on the flanks.</p>	

Fig. 5. Fusulinana Endothyrida. Definitions of the superfamilies (continuation of Fig. 4): Haplophragminoidea, Palaeotextularioidea, Quasiendothyroidea, Tetrataxoidea. Type figures from top: *Haplophragmina kashirica* Reitlinger, 1950; *Textularia texulariformis* of Schellwien (1898); *Endothyra kobeitusana* Rauzer-Chernousova, 1948c; *Endothyra krainica* Lipina, 1948; *Tetrataxis conica* Ehrenberg, 1854.

Family **PALAEOTEXTULARIIDAE** Galloway, 1933
Bilayered Palaeotextularioidea. Early late Viséan (MFZ13)–latest Permian.

Composition: *Palaeotextularia* Schubert, 1921; *Climacammina* Brady in Etheridge, 1873; *Cribrogenerina* Schubert, 1908; *Cribrostomum* Möller, 1879; *Deckerella* Cushman & Waters, 1928; *Deckerellina* Reitlinger, 1950; *Palaeobigenerina* Galloway, 1933.

Superfamily **QUASIENDOTHYROIDEA** Reitlinger, 1961

Description. See Fig. 5.

Family **QUASIENDOTHYRIDAE** Reitlinger, 1961
Endothyroid to planispiral coiling, involute to seminvolute. Chambers numerous, quadratic, without sutures. Secondary deposits strong: crusts, pseudo-chomata, chomata. Aperture simple, terminal, basal. Late early Famennian (DFZ3) to latest Famennian (DFZ8). Rare in earliest Tournaisian and Uralian.

Composition: *Quasiendothyra* Rauzer-Chernousova, 1948; *Baelenia* Conil & Lys, 1977; *Eoendothyra* A. D. Miklukho-Maklay, 1960; *Eoquasiendothyra* Durkina, 1963; *Klubovella* Lebedeva, 1956.

Superfamily **SEPTABRUNSIINOIDEA** Conil & Lys, 1977
Description. See Fig. 5.

Family **GLOBOENDOTHYRIDAE** familia nova
Description: see introduction.

Composition: *Globoendothyra* Bogush & Yuferev, 1962; *Carbotarima* Brenckle, 2004; *Eblanaia* Conil & Marchant, 1977; *Eogloboendothyra* Vdovenko, 1972; *Planogloboendothyra* Hance, Hou & Vachard, 2011; *Plectogyrina* Reitlinger, 1959.

Family **LAXOENDOTHYRIDAE** Hance, Hou & Vachard, 2011

Incomplete septation in the inner whorls, followed by adult whorls with a complete septation. Adult chamber endothyrid; i.e., inflated, hemispherical with sutures generally deep. Supplementary deposits absent in many genera or represented by discontinuous tubercles or a terminal spine. Wall simple, dark. Aperture generally simple. Late Devonian–late Brigantian.

Composition: *Laxoendothyra* Brazhnikova & Vdovenko, 1972; *Andrejella* Malakhova, 1975; *Avesnella* Conil & Lys, 1970; *Crassiseptella* Brenckle & Hance, 2005; *Endolaxina* Hance, Hou & Vachard, 2011; *Laxoseptabrunsiina* Vachard, 1977; *Rectoavesnella* Conil & Lys, 1977; *Spinolaxina* Conil & Naum, 1977.

Family **SEPTABRUNSIINIDAE** Conil & Lys, 1977
Test small, involute, inflated to discoid, streptospirally to planispirally coiled. Rarely undivided, often with faint pseudosepta. Rare supplementary deposits. Wall dark to brownish. Aperture terminal simple. Questionable in the Middle Devonian; from Late Devonian to middle late Viséan (late Asbian).

Subfamily **SEPTABRUNSIININAE** Conil & Lys, 1977
Coiling streptospiral to planispiral or endothyroid. Pseudosepta or complete septa in the last whorls. Supplementary deposits in the advanced forms. Wall dark and simple, with agglutinated calcareous particles in some representatives. Aperture terminal simple.

Composition: *Septabrunsiina* Lipina, 1955; *Brunsiina* Lipina in Dain & Grozdilova, 1953; *Neobrunsiina* Lipina, 1965; *Pseudoplanoendothyra* Brazhnikova & Vdovenko, 1982; *Rectoseptabrunsiina* Lipina, 1965.

Subfamily **SEPTAGLOMOSPIRANELLINAE**
Reitlinger in Rauzer-Chernousova et al., 1996

Test streptospirally coiled with faint to developed pseudosepta. Terminal stage of growth occasionally uncoiled. Wall dark, simple, microgranular. Aperture terminal simple.

Composition: *Septaglomospiranella* Lipina, 1955; *Glomospiranella* Lipina, 1951; *Neoseptaglomospiranella* Lipina, 1963; *Rectoseptaglomospiranella* Reitlinger, 1961.

Superfamily **TETRATAXOIDEA** Galloway, 1933
Description. See Fig. 5.

Family **TETRATAXIDAE** Galloway, 1933

Test conical, trochospiral, with a planar to slightly depressed face. Umbilical face depressed to planar or forming more or less developed umbilical pivots (*Globotetrataxis*, some *Tetrataxis*). Mode of life attached to vagile, epiphytic on algae or corals. Four or five chambers in each whorl. Undivided chambers, or with secondary partitions (*Valvulinella*, *Abadehella*). Aperture in the umbilicus, occasionally protected by a micro-aquarium. Wall thin dark microgranular, thick with the hyaline microgranular always as the outer layer and only located in the umbilicus, and not on the flanks. Late Tournaisian (MFZ6)–Changhsingian.

Remark: *Globotetrataxis* Brazhnikova, 1983 is a reproductive stage of *Tetrataxis* and a junior synonym of the latter.

Composition: *Tetrataxis* Ehrenberg, 1854; *Abadehella* Okimura & Ishii, 1975; *Abadehellosis* Vachard in Krainer, Vachard & Schaffhauser, 2019; *Endotaxis* Bogush & Brazhnikova, 1983; *Polytaxis* Cushman & Waters, 1928; *Pseudoendotaxis* Vachard, Krainer & Schönlaub, 2018; *Pseudotaxis* Mamet, 1974; *Valvulinella* Schubert, 1908.

Order **FUSULINIDA** Fursenko, 1958

Test lenticular, subglobular or fusiform, generally planispirally coiled. Coiling uniform or presence of juvenaria. Terminal uncoilings are rare. Aperture generally basal, central, simple, occasionally replaced by foramina or cuniculi. No cribrate or complex apertures. Endoskeletal secondary deposits represented by pseudochomata, chomata and parachomata; septula of first and second order, axial fillings, and phrenothecae. Proloculi spherical and small to reniform and larger. Septal folding planar to strongly folded in the whole chamber. Microstructures and microtextures of wall are considered here as a suborder and superfamily criterion: Wall simple under the form of a dark tectum (*Ozawainelloidea*) or a neospartitized tectum (*Staffelloidea*; bilayered with tectum and protheca (*Schubertelloidea*), multilayered with tectum, tectoria and diaphanotheca (*Fusulinoidea*); coarsely keriothecal (*Schwagerinoidea*); or finely keriothecal (*Neoschwagerinoidea*). Aperture terminal, simple, basal, rarely areal or reduced to cuniculi and/or septal pores.

Remark. Some evolutionary trends are shared by these superfamilies: (1) they are successively: planispiral lenticular, spherical, inflated fusiform, elongate fusiform or cigar-shaped, rarely uncoiled (two genera of *Schwagerinoidea* and two genera of *Schubertelloidea*); (2) *Staffelloidea*, *Ozawainelloidea*, and *Schubertelloidea* are small to medium-sized; *Fusulinoidea* are large; *Schwagerinoidea* and *Neoschwagerinoidea* are large to giant. (3) The gigantic taxa adopt two types of mechanical re-inforcements of the tests: either a very


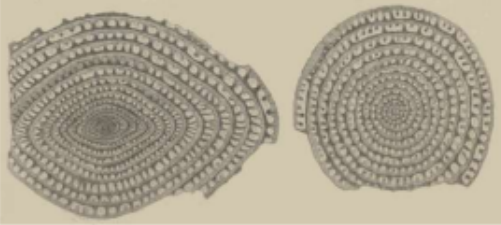

<p>Fusulinoidea</p> <p>Globular, subquadratic, and fusiform Fusulinida with a wall including a diaphanotheca; the primitive forms having still a dark microgranular of their ozawainelloid ancestors. Very finely porous walls rarely present. Septa planar to partly folded and finally, entirely folded. Chomata always present, but diversely developed.</p>	
<p>Neoschwagerinoidea</p> <p>Test large-inflated fusiform to spherical, planispirally coiled and involute. Supplementary deposits as parachomata often present. Numerous genera display chambers divided into chamberlets by transverse septula of first order (which connect with the parachomata in neoschwagerinids; and shorter transverse septula of second order, as well as axial septula. Wall microgranular and finely keriothecal or re-becoming apparently dark microgranular (sumatrinins). Poorly developed apertures as small foramina between the parachomata and the chamberlets.</p>	
<p>Ozawainelloidea</p> <p>Test free, planispirally coiled, nautiloid to subspherical, lenticular to rhombic to discoid, entirely involute or becoming evolute, and vice versa, subcarinate to carinate. Some deviations of coiling present in rare tests. Proloculus, small, spherical. Juvenarium rarely developed. Pseudochomata developing to chomata, weak to strong. Septa planar, perpendicular to the wall or falciform. Chambers quadratic, relatively numerous. No sutures. Wall thin dark microgranular or layered with tectum and inner less dark layer. Regular tunnel up to a basal, simple, terminal aperture.</p>	

Fig. 6. Fusulinana Fusulinida. Definitions of the superfamilies: Fusulinoidea, Neoschwagerinoidea, Ozawainelloidea. Type figures from top: *Fusulina cylindrica* Fischer de Waldheim, 1830; *Schwagerina craticulifera* Schwager, 1883; *Fusulinella angulata* Colani, 1924.

strong septal folding (advanced Fusulinoidea and Schwagerinoidea), or a more developed endoskeleton with septula and parachomata whereas the septa remain plane (Neoschwagerinoidea).

Superfamily **FUSULINOIDEA** Möller, 1878
Description. See Fig. 6.

Family **ALJUTOVELLIDAE** Solovieva in Rauzer-Chernousova et al., 1996

Test subrhomboidal with pointed axial ends, or fusiform, or less often ovoid; initial part usually nautiloid; rarely the first whorls endothyroid; wall trilayered, less often bilayered, the outer tectorium is absent, sometimes a rudimentary diaphanotheca (from gray to light) is developed under the tectum; septa are flat in the median

part of external whorls and wavy on the sides of the test near the axial ends or folded with the formation of arches near the axial ends; the number of septa is small; chomata are usually quite strongly developed, often subquadratic, rounded, rarely ribbon-shaped in internal whorls; additional deposits usually absent, the aperture is narrow to moderate. Upper Bashkirian-lower Moscovian.

Composition: *Aljutovella* Rauzer-Chernousova in Rauzer-Chernousova et al., 1951; *Priscoidella* Solovieva in Rauzer-Chernousova et al., 1996; *Skelnevatella* Solovieva in Rauzer-Chernousova et al., 1996; *Tikhonovichiella* Solovieva in Rauzer-Chernousova et al., 1996.

Family **FUSULINELLIDAE** Staff & Wedekind, 1910
Tests inflated fusiform (Fusulinellinae, Pulchrellinae) to

ovoid or elongate fusiform (Wedekindellinae). Septa planar in the center of the chambers; only folded at the poles. Chomata developed in Fusulinellinae and Pulchrellinae. Axial filling developed in Wedekindellinae. Wall diaphanothecal, rarely porous: *Pulchrella* Solovieva; *Anulofusulinella* Wilde; *Praeobsoletes* Remizova. Aperture simple. Moscovian-Early Permian.

Subfamily **FUSULINELLINAE** Staff & Wedekind, 1910

A fusulinellid subfamily characterized by inflated fusiform tests with narrow to moderately broad tunnel and moderate to strong chomata of various forms. Wall diaphanothecal, rarely porous.

Composition: *Fusulinella* Möller, 1877; *Anulofusulinella* Wilde, 2006; *Hidaella* Fujimoto & Igo, 1955; *Nipperella* Solovieva, 1984; *Obsoletes* Kireeva, 1950; *Plectofusulina* Stewart, 1958; *Praefusulinella* Akbaş in Akbaş & Okuyucu, 2022; *Praeobsoletes* Remizova, 1992; *Protriticitis* Putrya, 1948; *Uralofusulinella* Chuvashov, 1980; *Zellerella* Wilde, 2006.

Subfamily **PULCHRELLINAE** Solovieva, 1983

Test medium-sized, rhomboidal, inflated fusiform, with gradually enlarging whorls. Septa similar to *Fusulinella*. Wall with four layers. Chomata relatively high and asymmetrical. Aperture terminal simple.

Composition: *Pulchrella* Solovieva, 1983; *Dagmarella* Solovieva, 1955; *Eowaeringella* Skinner & Wilde, 1967; *Kammeraia* T. Ozawa, 1967; *Parafusulinella* Stewart, 1970; *Pseudofusulinella* Thompson, 1951; *Usvaella* Remizova, 1992; *Waeringella* Thompson, 1942.

Subfamily **WEDEKINDELLININAE** Kahler & Kahler, 1966

Test ovoid to subcylindrical, involute, symmetrical, with no ancestral stages in ontogenesis; coiling is compact; wall four-layered with diaphanotheca, sometimes two-layered (tectum and primatheca); septa straight, short, slightly folded on the sides and in the axial region; chomatas are small, subtriangular in cross-section, turning into thick axial fillings.

Composition: *Wedekindellina* Dunbar & Henbest in Cushman, 1933; *Eowedekindellina* Ektova, 1977; *Fru mentella* Stewart, 1958; *Parawedekindellina* Safonova, 1951; *Thompsonella* Skinner & Wilde, 1965.

Family **FUSULINIDAE** Möller, 1878

Tests inflated fusiform (Beedeininae) to elongate fusiform (Fusulininae, Eofusulininae, Quasifusulininae). Septal folding developed in the entire chambers. Chomata developed in Beedeininae. Axial filling developed in Eofusulininae and Quasifusulininae. Wall diaphanothecal. Aperture simple. Latest Bashkirian. Acme during the Moscovian. Late Pennsylvanian. Rare in early Permian (up to the Artinskian).

Subfamily **BEEDEININAE** Solovieva in Rauzer-Chernousova et al., 1996

Test medium-sized, less often small or large, subrhomboidal with rounded or angular middle region or fusiform; in early ontogenesis, the test is subrhomboidal, less often rounded-subrhomboidal, coiling is tight to moderate; wall four-layered, porous, rarely two-layered with dichotomous pores. Moderate to strong folding of septa. Chomata and pseudo-chomata are expressed to varying degrees; the aperture has a constant position in the whorls, and is from narrow to moderate in shape.

Composition: *Beedeina* Galloway, 1933; *Citronites* Solovieva in Rauzer-Chernousova et al., 1996; *Parabeedeina* Solovieva in Rauzer-Chernousova et al., 1996; *Putrella* Rauzer-Chernousova in Rauzer-Chernousova et al., 1951.

Subfamily **EOFUSULININAE** Rauzer-Chernousova & Rozovskaya, 1959

Test elongate fusiform, subcylindrical, subtriangular with pointed or blunted axes and ends; coiling is tight with an axis shift in the first whorl; wall in internal whorls three-layered with a non-permanent outer tectorium, in the outer whorl wall thin, poorly differentiated into tectum and homogeneous primatheca with inconsistent and weakly defined outer tectorium, sometimes wall with a translucent rudimentary diaphanotheca in the upper part of the primatheca, in the outer whorl. sometimes fine pores; septa in the beginning whorls from flat to wavy and slightly folded in the axes, in parts of the test, in subsequent whorls. The folding of the septa intensifies along the entire length; tall, narrow or rounded angular arches; chomata are absent or weakly expressed; axial, thickenings are constant, from moderate to highly developed; the aperture is usually narrow, sometimes poorly distinguishable, less often moderate; sometimes there are cuniculi in the outer whorls.

Composition: *Eofusulina* Rauzer-Chernousova in Rauzer-Chernousova et al., 1951; *Akiyoshiella* Toriyama, 1953; *Neofusiella* Ektova, 1989; *Neofusulina* A. D. Miklukho-Maklay, 1963; *Paraeofusulina* Putrya, 1956; *Postverella* Ivanova, 2008; *Siliculites* Fang, 1988; *Verella* Dalmatskaya, 1951.

Subfamily **FUSULININAE** Möller, 1878

Test medium to large, fusiform to subcylindrical, less often elongate-ovoid, in early stage fusiform or short-ovoid; coiling from tight to fairly loose; wall usually four-layered with a clear diaphanotheca, sometimes the tectoria are poorly expressed, porous septa usually strongly folded; chomata, constant in early stage, in external whorls often replaced by pseudo-chomata, sometimes absent; secondary deposits in the form of axial fillings; aperture often narrow, less often moderate, usually with a constant position.

Composition: *Fusulina* Fischer de Waldheim, 1829; *Bartramella* Verville, Thompson & Lokke, 1956; *Hemifusulina* Möller, 1877; *Hemifusulinella*

Rumyantseva, 1962; *Kamaina* Solovieva in Rauzer-Chernousova et al., 1996; *Pseudotriticites* Putrya, 1940; *Undatafusulina* Leven, 1998.

Subfamily **QUASIFUSULININAE** Putrya, 1956

Test large, subcylindrical; whorls planispiral, loosely coiled. Septa intensively folded. Rare cuniculi are present in the more advanced species. Axial fillings heavy. Wall of Fusulinoidea. Tunnel straight, narrow, poorly developed. Aperture terminal simple.

Composition: *Quasifusulina* Chen, 1934; *Quasifusulinoides* Rauzer-Chernousova & Rozovskaya, 1959.

Family **PROFUSULINELLIDAE** Solovieva in Rauzer-Chernousova et al., 1996

Test usually small, subspherical to moderately elongated and ovoid, fusiform and subrhomboid, in the first whorls usually narrow-nautiloid or subspherical; in the first whorls sometimes endothyroid; wall three-layered (tectum, primatheca and external tectorium), less often two-layered without external tectorium or with a clear layer in the upper part of the primatheca (type of rudimentary diaphanotheca); septa weakly to moderately curled at axial ends. Chomata are clear, less often weak, round in cross-section, symmetrical or asymmetrical, flattening towards the poles, subquadratic or ribbon-shaped; additional deposits are sometimes present in the form of a thickening of the outer tectorium; significant deposits are possible in the axial region; the aperture is usually narrow to moderate. Late Bashkirian-Moscovian.

Composition: *Profusulinella* Rauzer-Chernousova & Belyaev in Rauzer-Chernousova et al., 1936; *Depratina* Solovieva in Rauzer-Chernousova et al., 1996; *Moellerites* Solovieva, 1986; *Shachella* Zhu, 1995; *Solovievaia* Vachard & Le Coze, 2018; *Staffellaeformes* Solovieva, 1986; *Taitzhoella* Sheng, 1951.

Family **PSEUDOSTAFFELLIDAE** Putrya, 1956

Tests medium to large in size, subspherical, subquadratic and subglobular, sometimes compressed along the coiling axis, somewhat elongate, with a straight, slightly concave or rounded umbilical regions and the same peripheral edge; involute, less often evolute in the outer whorl; coiling is often symmetrical, less often with oscillation of the axis in the early stage of growth; septa numerous, straight, short; wall three-four layered with diaphanotheca; Chomata from short weak and moderate in the beginning to powerful and ribbon-like in outer whorls. The aperture is simple, basal. Pennsylvanian (Bashkirian-Kasimovian).

Remark: *Hanostaffella* Cheong, 1984 is thought to be a deformation stage of *Neostaffella* A. D. Miklukho-Maklay, 1959 and therefore a synonym of this latter genus as already analysed by Villa et al. (2022).

Composition: *Pseudostaffella* Thompson, 1942; *Hubeiella* Lin, 1977; *Neostaffella* A. D. Miklukho-Maklay, 1959; *Quasistaffella* Solovieva, 1986;

Quydatella Liêm, 1966; *Semistaffella* Reitlinger, 1971; *Semistaffella* (*Praesemistaffella*) Orlova, 1997; *Topilinia* Ivanova, 2008; *Xenostaffella* Cheong, 1973.

Superfamily **NEOSCHWAGERINOIDEA** Dunbar & Condra, 1927

Description. See Fig. 6.

Family **MISELLINIDAE** A. D. Miklukho-Maklay, 1958
Test small to medium in size, from subspherical, slightly compressed along the coiling axis, to ellipsoidal; number of whorls 6-14; wall with tectum, finely porous keriotheca and thin dark inner layer; septa flat, septula absent; the apertures are numerous, separated by well-defined parachomata. Lower Permian (Bolorian) - Upper Permian (Kubergandian, Murghabian and lower Midian zone).

Composition: *Misellina* Schenck & Thompson, 1940; *Brevaxina* Schenck & Thompson, 1940; *Metadololina* Ishii & Nogami, 1961; *Neomisellina* Sheng in Sheng & Wang, 1962; *Pamirina* Leven, 1970; *Pamirina* (*Levenella*) Ueno, 1994; *Zarodella* Sosnina, 1981.

Family **NEOSCHWAGERINIDAE** Dunbar & Condra, 1927

Test fusiform to subcylindrical; transverse septula always present, axial septula may occur, as secondary transverse or axial septula or both; wall with tectum and finely alveolar keriotheca or a single dense layer; foramina throughout length of test, parachomata prominent (modified from Loeblich & Tappan 1987). Middle Permian (Kubergandian/Rodian to Midian/Capitanian).

Subfamily **NEOSCHWAGERININAE** Dunbar & Condra, 1927

Test large, fusiform to nearly spherical; wall with tectum and fine keriotheca and may have inner tectorium; development of spiral and axial septula variable; parachomata well developed but may be reduced in advanced forms; numerous foramina at base of septa (Loeblich & Tappan 1987).

Composition: *Neoschwagerina* Yabe, 1903; *Cancellina* Hayden, 1909; *Colania* Lee, 1934; *Gifuella* Honjo, 1959; *Gifuelloides* Kobayashi, Ross & Ross, 2010; *Gublerites* nomen novum; *Lepidolina* Lee, 1934; *Maklaya* Kanmera & Toriyama, 1968; *Rugosomaklaya* Nie & Song, 1983; *Shengella* Yang, 1985; *Yabeina* Deprat, 1914.

Subfamily **SUMATRININAE** Silvestri, 1933

Test of medium to large size, ellipsoid to fusiform or subcylindrical; pendant secondary spiral and axial septula of uniform length, with up to four secondary septula between two primary ones; wall thin, compact, with poorly differentiated structure; thin long parachomata present, axial fillings in all but last part of final whorl (Loeblich & Tappan 1987).

Composition: *Sumatrina* Volz, 1904; *Afghanella* Thompson, 1946; *Neosumatrina* Chediya in Kotlyar et

al., 1989; *Presumatrina* Tumanskaya, 1950.

Family **VERBEEKINIDAE** Staff & Wedekind, 1910

Test large, subspherical to cylindrical; planispiral, completely involute; wall of tectum and finely alveolar keriotheca and may have secondary layers; multiple tunnels present, foramina numerous and parachomata may occur (modified from Loeblich & Tappan 1987). Middle Permian (Kubergandian- Midian).

Subfamily **KAHLERININAE** Leven, 1963

Test nautiloid, highly compressed along the axis, to subspherical, in the inner whorls sometimes with a weak sharpening of the periphery and with an unstable position of the coiling axis; septal sutures poorly marked; number of whorls up to 5-7; septa thick, flat or slightly convex, thickened at ends; number of septa up to 8-11 in the last whorls; wall thick, two-layered, with simple fine porosity, inconsistently expressed; the aperture is single, sometimes foramina are present at the base of the septa in the outer whorls; chomata are weakly expressed; parachomata in external whorls small and inconstant.

Remark: Recently published *Kahlerinella* Okuyucu, 2022 is considered herein as a subjective junior synonym of *Kahlerina* Kochansky-Devidé & Ramovš, 1955. We cannot see neither morphological nor microstructural differences with *Kahlerina*.

Composition: *Kahlerina* Kochansky-Devidé & Ramovš, 1955.

Subfamily **PSEUDODOLIOLININAE** Leven, 1963

Test small to large, ellipsoidal, subcylindrical with widely rounded ends, rarely subspherical; coiling is uniform; wall dense with an indistinguishable microstructure, in more highly developed representatives with a fine keriotheca; parachomata are well developed.

Composition: *Pseudodoliolina* Yabe & Hanzawa, 1932.

Subfamily **VERBEEKININAE** Staff & Wedekind, 1910
Test globose, wall of tectum and thicker light-colored alveolar layer and may have thin lower dense layer, chomata may occur in early whorls and parachomata in outer ones; numerous apertures (Loeblich & Tappan 1987).

Composition: *Verbeekina* Staff, 1909; *Armenina* A. D. Miklukho-Maklay, 1955; *Paraverbeekina* A. D. Miklukho-Maklay, 1955; *Quasiverbeekina* Wang, Sheng & Zhang, 1981.

Superfamily **OZAWAINELLOIDEA** Thompson & Foster, 1937
Description. See Fig. 6.

Family **EOSTAFFELLIDAE** Mamet in Mamet et al., 1970

Staffelloidea discoidal or lenticular. Pseudochomata relatively poorly developed. Rare axial filling. Wall simple, trilayered or with a faint luminotheca. Early Viséan-late Moscovian.

Remark: *Paramillerella* Thompson, 1951 is morphologically similar to *Eostaffella* as indicated by numerous authors. *Ikensieformis* Orlova, 1997, has only morphological differences with *Eostaffella*, which are pertinent at a specific level (i.e, Maslo & Vachard 1997). We support the synonymy between *Eostaffella*, *Paramillerella* and *Ikensieformis*.

Composition: *Eostaffella* Rauzer-Chernousova, 1948; *Eostaffellina* Reitlinger, 1963; *Neomillerella* Gaillot & Vachard, 2007; *Plectostaffella* Reitlinger, 1971; *Varistaffella* Kulagina & Sinitsyna, 2003; *Varvariella* Orlova, 1997.

Family **OZAWAINELLIDAE** Thompson & Foster, 1937

Ozawainelloidea discoid, lenticular or rhomboidal, involute to evolute. Septa not folded, but curved and falciform. Pseudochomata diversely developed (poorly in Millerellinae; strongly, in Ozawainellinae). Rare axial filling. Wall simple, unilayered to eodiagenetically? trilayered. Early Viséan-late Moscovian.

Subfamily **MILLERELLINAE** Vachard, Krainer & Lucas, 2013

Ozawainellidae with a diversely developed evolute stage (i.e., short or long, terminal or initial, broad or narrow). Pseudochomata always poorly marked. Wall simple unilayered.

Composition: *Millerella* Thompson, 1942; *Novella* Grozdilova & Lebedeva, 1950; *Plectomillerella* Brazhnikova & Vdovenko, 1983; *Pseudoacutella* Vachard, Krainer & Lucas, 2013; *Pseudonovella* Kireeva, 1949; *Rectomillerella* Liêm, 1974; *Seminovella* Rauzer-Chernousova in Rauzer-Chernousova et al., 1951.

Subfamily **OZAWAINELLINAE** Thompson & Foster, 1937

Test small, lenticular, involute or rarely evolute, early coiling may be streptospiral; wall simple, microgranular, single layered or with weakly developed diaphanotheca; secondary deposits in the form of chomata and pseudochomata.

Composition: *Ozawainella* Thompson, 1935

Superfamily **SCHUBERTELLOIDEA** Skinner, 1931
Description. See Fig. 7.

Family **BOULTONIIDAE** Skinner & Wilde, 1954

Schubertelloidea fusiform to elongate fusiform, with a juvenarium, lenticular or discoidal, generally deviated at 90° in relation with the adult whorls. Septa moderately to intensively fluted. Septal pores common; chomata present on each side on a central tunnel. Artinskian-Capitanian.

Composition: *Boultonia* Lee, 1927; *Codonofusiella* Dunbar & Skinner, 1937; *Dilatofusulina* Wang & Ueno, 2009; *Gallowayinella* Chen, 1937; *Lantschichites* Tumanskaya, 1953; *Minojapanella* Fujimoto & Kanuma, 1953; *Minojapanella* (*Neimonggolina*) Xia, 1983;


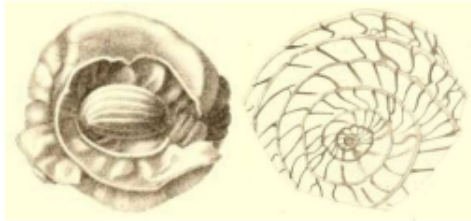

<p>Schubertelloidea</p> <p>Test of medium size, short fusiform, inflated fusiform to elongated fusiform. Proloculus spherical. Juvenarium generally lenticular deviated at 90 degrees with the adult whorls. Wall unilayered in the ancestral genera, or more frequently, bilayered with an outer, dark microgranular tectum and an inner, thicker, yellowish, microgranular layer, called the protheca; very finely porous wall rarely present. Septa faintly to moderately folded at the poles, planar in the central parts of the chambers. Tunnel obvious. Chomata small to moderate. Rare genera display cuniculi.</p>	
<p>Schwagerinoidea</p> <p>Elongate fusiform to inflated fusiform fusulinids with keriothecal wall. Chomata developed or absent. Axial fillings developed or absent. Septal folding present in the entire chambers or only at the pole. Aperture median simple with tunnel or absent. Supplementary small apertures as septal pores or cuniculi.</p>	
<p>Staffelloidea</p> <p>Tests planispiral, involute, lenticular or spherical, very rarely subfusiform or uncoiled. The septa remain planar during all the history of the suborder (in contrast to the other suborder, Fusulinina). Chomata are often present but poorly developed. Some structures confused with parachomata are occasionally described. Wall calcareous secreted, probably initially dark aragonitic (probably fibrous and finely perforated), then neomicrosparitized from aragonite. Aperture simple terminal basal.</p>	

Fig. 7. Fusulinana Fusulinida. Definitions of the superfamilies (continuation of Fig. 6): Schubertelloidea, Schwagerinoidea, Staffelloidea. Type figures from top: *Schubertella transitoria* Staff & Wedekind, 1910; *Schwagerina princeps* (Ehrenberg, 1842) sensu Möller, 1878; *Staffella sphaerica* (Abich, 1859) from Baulina (1963).

Novonanlingella Özdikmen, 2009; *Ogbinella* Chediya in Kotlyar, Zakharov, Kropacheva, Pronina, Chediya & Burago, 1989; *Palaeofusulina* Deprat, 1912; *Paradoxiella* Skinner & Wilde, 1955; *Parananlingella* Rui & Sheng, 1981; *Pseudodunbarula* Chediya in Kotlyar et al., 1984; *Russiella* A. D. Miklukho-Maklay, 1957; *Tewoella* Sun, 1979; *Wutuella* J. C. Sheng, 1963; *Ziguiella* Lin, 1980.

Family **DUNBARULIDAE** Vachard in Vachard et al., 1993

Schubertelloidea with a lenticular juvenarium followed by a more or less fusiform or irregular stage. Wordian to Changhsingian.

Composition: *Dunbarula* Ciry, 1948; *Paradunbarula* Skinner, 1969; *Paradunbarula* (*Shindella*) Chediya in Kotlyar, 1984; *Praedunbarula* Vachard in Kolodka et

al., 2012; *Rauserella* Dunbar, 1944.

Family **REICHELINIDAE** A. D. Miklukho-Maklay, 1959

Tests small, lenticular at least in the juvenile stage, sometimes fusiform or irregular in the adult stage. Septa flat or folded in the adult stage. Chomata weak to absent. Middle-Upper Permian, Kubergandian (=Roadian)-Changhsingian.

Composition: *Reichelina* Erk, 1942; *Baudiella* Altner & Özkan-Altner, 1998; *Chenella* A. D. Miklukho-Maklay, 1959; *Eostaffelloides* A. D. Miklukho-Maklay, 1959; *Jilinella* Han, 1980; *Parareichelina* A. D. Miklukho-Maklay, 1959; *Primoriina* Sosnina, 1981; *Pseudokahlerina* Sosnina, 1968; *Sichotenella* Tumanskaya, 1953.

Family **SCHUBERTELLIDAE** Skinner, 1931

Test shortly fusiform to fusiform, often asymmetrical. Early stage discoidal, deviated in comparison with the later stage more or less fusiform, with acute poles. Septa numerous, unfluted in the center of the chambers but slightly fluted at the poles, especially in the outer whorls. Chomata low, asymmetrical and bordering a broad and low tunnel; occasional strong and ribbon-shaped. Wall bilayered with an outer tectum and a protheca. Primitive forms (*Schubertina* or *Eoschubertella* of the authors) exhibit only the dark tectum; advanced forms (*Dutkevitchites*, *Oketaella* and *Biwaella*) exhibit, in the wall, the tectum and an inner porous layer. Aperture terminal simple. Bashkirian to latest Permian.

Subfamily **BIWAELLINAE** Davydov, 1984

Test shortly fusiform, often asymmetrical. Early stage discoidal; later stage more or less fusiform with acute poles. Septa numerous, unfluted in the center but slightly fluted at the poles, especially in the outer whorls. Chomata low, asymmetrical and bordering a broad and low tunnel. Wall bilayered with a tectum and an inner porous layer. Aperture terminal simple.

Composition: *Biwaella* Morikawa & Isomi, 1960; *Douglasites* Read & Nestell, 2018; *Dutkevitchites* Davydov, 1984; *Oketaella* Thompson, 1951.

Subfamily **SCHUBERTELLINAE** Skinner, 1931

Test with plane of coiling changing during early whorls; septa flat to axially undulating; weakly differentiated wall structure; chomata present (Loeblich & Tappan 1987).

Remark: *Eoschubertella* Thompson, 1937 was considered a valid genus in Loeblich and Tappan (1987) and Rauzer-Chernousova et al. (1996). It is herein put in synonymy with *Schubertella* Staff & Wedekind, 1910. The type species of *Eoschubertella*, *Schubertella lata* Lee & Chen, 1930 is understood as a true *Schubertella*. Species of «*Eoschubertella*», especially in North America, corresponds to another genus, the wall of which is microgranular.

Composition: *Schubertella* Staff & Wedekind, 1910; *Depratella* Ozawa, 1928; *Fusiella* Lee & Chen, 1930; *Grovesella* Davydov & Arefifard, 2007; *Mesoschubertella* Kanuma & Sakagami, 1957; *Multiavoella* Li, 1986; *Neofusulinella* Deprat, 1912; *Neoschubertella* Saurin, 1962; *Paramisellina* Zhang & Dong in Xiao et al., 1986; *Schubertina* Marshall, 1969; *Toriyamaia* Kanmera, 1956.

Family **YANGCHIENIIDAE** Leven, 1987

Test small, fusiform or ellipsoidal; juvenarium small; in the first internal whorls winding at an angle to subsequent ones; wall with diaphanotheca; septa are straight; massive, ribbon-shaped chomata; the aperture is distinct. The evolution of the family proceeded by increasing the number of whorls and, accordingly, the size of the tests. It differs from other families in its wide ribbon-like chomata combined with straight septa and wall with

diaphanotheca. Permian: Artinskian-Capitanian.

Composition: *Yangchienia* Lee, 1934

Superfamily **SCHWAGERINOIDEA** Dunbar &

Henbest, 1930

Description. See Fig. 7.

Family **POLYDIEXODINIDAE** A. D. Miklukho-Maklay, 1953

Medium sized to large to giant Schwagerinoidea, with very strong septal folding, small secondary apertures opened at the points of septal loops; with cuniculi and concomitant disappearance of the central aperture and even of the septal pores; generally fusiform, elongate fusiform to subcylindrical; without chomata or very residual; with axial fillings poor or absent. Artinskian–Capitanian.

Subfamily **PARAFUSULININAE** Bensch in Rauzer-Chernousova et al., 1996

Test large, elongated in the inside whorls, in the outer whorls strongly elongated fusiform or subcylindrical, sometimes short fusiform with steep sides and a flattened middle region, moderate spiral, uniformly expanding; Wall thin, usually with thin alveolar keriotheca; the septa are thin, their folding is strong and regular; Cuniculi from low in the outer whorls. to high, continuous in almost all whorls. There are no chomata; axial fillings and single aperture.

Composition: *Parafusulina* Dunbar & Skinner, 1931; *Laosella* Leven, 1997; *Paraskinnerella* Bensch in Rauzer-Chernousova et al., 1996; *Praeskinnerella* Bensch, 1991; *Skinnerella* Coogan, 1960.

Subfamily **POLYDIEXODININAE** A. D. Miklukho-Maklay, 1953

Test large, from fusiform to highly elongated, elongated-fusiform or subcylindrical; numerous whorls; tightly coiled, evenly expanding; wall thin alveolar; septa are thin, strongly and regularly folded with frequent high and uniform arches; cuniculi are high, continuous at all stages of growth; constant axial thickenings of various shapes and intensity, no chomata; from two to several apertures.

Composition: *Polydiexodina* Dunbar & Skinner, 1931; *Bidiexodina* Leven, 1986; *Eopolydiexodina* Wilde, 1975; *Koksarella* Da in Da & Sun, 1983; *Skinnerina* Ross, 1964.

Family **PSEUDOFUSULINIDAE** Dutkevich, 1934

Schwagerinoidea elongate fusiform to subcylindrical, with strongly folded septa, an absence of central aperture with tunnel, common septal pores, rugose wall, axial filling diversely developed, chomata limited to the proloculus and/or first whorls, rare phrenothecae, no cuniculi. Late Pennsylvanian–late Middle Permian.

Composition: *Pseudofusulina* Dunbar & Skinner, 1931 *Crenulosepta* Stevens & Stone, 2009; *Inyoschwagerina* Stevens & Stone, 2009; *Kunlunella* Da in Da & Sun,

1983; *Kutkanella* Bensch, 1987; *Lapigerella* Vilesov, 2002; *Nigribaccinus* Stevens & Stone, 2009; *Retijugulites* Vilesov, 2002; *Ruzhenzevites* Davydov in Chuvashov et al., 1986; *Sakmarella* Bensch & Kireeva in Bensch, 1987; *Schagonella* Davydov, 1980; *Stewartina* Wilde, 1971; *Tastubella* Bensch & Kireeva in Bensch, 1987.

Family **SCHWAGERINIDAE** Dunbar & Henbest, 1930
Schwagerinoidea rhombic to fusiform, rarely globular, with very folded septa, an absence of central aperture with tunnel, wall smooth, axial filling diversely developed, chomata limited to the proloculus and/or first whorls, rare phrenothecae, cuniculi only present in some advanced forms. Gzhelian to Capitanian.

Subfamily **CHUSENELLINAE** Kahler & Kahler, 1966
Test small to large, pseudo- to elongated fusiform, often with a flattened median region; juvenarium usually small; relatively numerous whorls; wall in early stage very thin, sometimes wavy, in the outer parts even, from thin to moderate, two-layered, sometimes with an inconsistent outer tectorium; the spiral expands with a slight jump after the tightly coiled internal whorls; septa thin, in early stage unfolded or slightly folded along the axis, in the outer whorls quite strongly folded along the entire length of the test, folding from irregular and low to regular, frequent, narrow and deep; secondary deposits in the form of thickenings in septa in the middle part of the test or on its sides weak chomata in early stage; aperture narrow to quite wide.

Remark: The recently proposed subfamily Kwantoellinae Okuyucu, 2022 is either a junior synonym of Schubertellinae or of Chusenellinae depending on the understanding of the wall composition/structure. Furthermore, the genus *Postkwantoella* Okuyucu, 2022 is also a taxon inquirendum. Its type species is probably a primitive *Chusenella*.

Ueno (2022) redescribed the genus *Kwantoella*. We agree that *Kwantoella* has more affinity with the schwagerinids than with the schubertellids where it was earlier classified (Ueno, 2022). *Kwantoella* is included in the Chusenellinae in the present classification rather than in the Triticitinae because of the absence of strong chomata, the moderate axial fillings limited to the median part of the test and the absence of strong septal folding.

Composition: *Chusenella* Hsu, 1942; *Chusenella* (*Sosioella*) Skinner & Wilde, 1966; *Dunbarinella* Thompson, 1942; *Eochusenella* Huang in Huang & Zeng, 1984; *Kwantoella* Sakagami & Omata, 1957; *Orientoschwagerina* A. D. Miklukho-Maklay, 1955; *Pseudochusenella* Bensch, 1987; *Rugosochusenella* Skinner & Wilde, 1965; *Rugosochwagerina* A. D. Miklukho-Maklay, 1959; *Xiaoxinzhaiella* Shi, Yang & Jin, 2005.

Subfamily **MONODIEXODININAE** Rauzer-Chernousova et al., 1996

Test involute ovoid, fusiform to strongly elongated,

fusiform and subcylindrical, rarely unfolded in the last whorl; the spiral is uniformly expanding, sometimes free from the first whorl; wall moderate to thick with fine or coarse alveolar keriotheca; intense folding, spreading along the entire length of the test, the depth of folding varies from limited to the lower edge of the septum to widespread throughout the entire septum, in some genera it is irregular, in most it is quite regular, especially in the middle part of the test, where the arches are uniform in shape and height; the cuniculi are low and narrow, only in one to three external whorls; phrenothecae variable; secondary deposits in the form of unstable axial fillings; weak chomata often replaced by pseudochomata in the external whorl.

Composition: *Monodiexodina* Sosnina in Kiparisova et al., 1956; *Alaskanella* Skinner & Wilde, 1966; *Eoparafusulina* Coogan, 1960; *Mccloudia* Ross, 1967; *Pseudofusulinoides* Bensch, 1972; *Qinglongella* nomen novum; *Timanites* Davydov & Arefifard, 2007.

Subfamily **RUGOSOFUSULININAE** Davydov, 1980
Pseudofusulinidae with strongly rugose wall, strong to very strong axial folding, rare septal pores, axial filling generally weak to absent (except for *Benshiella*), and phrenothecae absent.

Composition: *Rugosofusulina* Rauzer-Chernousova, 1937; *Benshella* Vilesov, 1997; *Benshiella* Leven in Leven & Gorgij, 2009; *Darvasella* Leven, 1992; *Dutkevitchia* Leven & Shcherbovich, 1978; *Kahlerella* Bensch, 1996; *Laxifusulina* Xia, 1983; *Rugosofusulinoides* Bensch in Rauzer-Chernousova et al., 1996.

Subfamily **SCHWAGERININAE** Dunbar & Henbest, 1930

Schwagerinidae with very folded septa, an absence of central aperture with tunnel, no rugose wall, chomata limited to the proloculus and/or first whorls, no cuniculi, and rare phrenothecae.

Composition: *Schwagerina* Möller, 1877; *Advenella* Wilde, 2006; *Anderssonites* Syomina, Solovieva & Bensch, 1987; *Chalaroschwagerina* Skinner & Wilde, 1965; *Changmeia* Zhou & Luo Hui, 1998; *Codonoschwagerina* Viën, 1959; *Concavutella* Bensch, 1987; *Cuniculinella* Skinner & Wilde, 1965; *Daixina* Rozovskaya, 1949; *Daixina* (*Bosbytauella*) Isakova, 1982; *Grozdilovia* Bensch, 1987; *Juresanella* Bensch, 1987; *Leeina* Galloway, 1933; *Leveniranella* nomen novum; *Linxinella* Zhuang, 1989; *Nagatodarvasiella* Wilde, 2006; *Neodutkevitchia* Davydov & Arefifard, 2007; *Paraleeina* Leven, 2004; *Perigondwania* Davydov & Arefifard, 2007; *Praeparafusulina* Tumanskaya, 1962; *Praepseudofusulina* Ketat & Zolotukhina, 1984; *Pravitoschwagerina* Toriyama, 1982; *Pseudodaixinoides* Getman & Dzhenchuraeva, 2007; *Shichanella* Bensch & Kireeva in Bensch, 1987; *Taiyuanella* Zhuang, 1989; *Thompsonites* Bensch, 1987; *Uraloverneuilites* Isakova, 2023.

Family **TRITICITIDAE** Davydov in Rauzer-Chernousova et al., 1996
Schwagerinoidea with chomata, and, commonly incompletely strong septal folding. Aperture central with a median tunnel. Late Pennsylvanian–Middle Permian.

Subfamily **DARVASITINAE** Leven, 1992

Test small to medium in size, from oval to subcylindrical, less often pseudofusiform, usually with smoothly rounded ends. The shape of the test is established in the early whorls and remains almost unchanged; the test only slightly lengthens as it grows. The spiral is wound closely and evenly with a very smooth and slow increase in the height of volutions. The initial chamber is small and medium in size. The wall has a distinct keriotheca, moderate, gradually increasing thickness. The septa are folded along their entire length. The folding covers only their lower edge, so the arches are usually flat and low. Cuniculi are observed in the outer whorls. The aperture occupies a stable position gradually and rapidly expanding. The septa along the edges of the aperture are thickened by secondary deposits, which can also accumulate in the axial part of the test.

Composition: *Darvasites* A. D. Miklukho-Maklay, 1959; *Darvasites* (*Alpites*) Davydov, Krainer & Chernykh, 2013; *Nagatoella* Thompson, 1936; *Tieliekella* Da in Da & Sun, 1983.

Subfamily **PARASCHWAGERININAE** Bensch in Rauzer-Chernousova et al., 1996

Test small to large, short pseudofusiform and elongated fusiform, often very elongated and flattened; the spiral is tight in the juvenarium, loose in the outer whorls with a jump in expansion at the beginning of the adult stage. Wall thin, weakly and gradually thickening; septa thin, weakly to strongly folded in the juvenile stage, strong but irregularly folded in the adult stage, in sections with wide and narrow, low and high, often loop-shaped multi-tiered arches, sometimes randomly placed; Phrenothecae are represented; secondary deposits in the form of unstable and intermittent axial fillings, and weak chomata in the juvenarium or only in the first chambers; the aperture is indistinct.

Composition: *Paraschwagerina* Dunbar & Skinner, 1936; *Acervoschwagerina* Hanzawa, 1949; *Klamathina* Skinner & Wilde, 1965.

Subfamily **PSEUDOSCHWAGERININAE** Chang, 1963

Test large, inflated fusiform to subspherical, Poles rounded to slightly umbilicated. Proloculus spherical small to moderately large. Juvenarium often developed under the form of triticitids, generally with developed chomata (absent in the adult stage). Adult septa unfolded to faintly folded, sometimes with numerous septal pores, thinner than the wall. Wall finely to moderately keriothecal. Aperture terminal, basal, simple.

Composition: *Pseudoschwagerina* Dunbar & Skinner,

1936; *Alpinoschwagerina* Bensch, 1972; *Eozellia* Rozovskaya, 1975; *Kubergandella* Leven, 1992; *Occidentoschwagerina* A. D. Miklukho-Maklay, 1959; *Robustoschwagerina* A. D. Miklukho-Maklay, 1959; *Sphaeroschwagerina* A. D. Miklukho-Maklay, 1959; *Zellia* Kahler & Kahler, 1937.

Subfamily **TRITICITINAE** Davydov in Rauzer-Chernousova et al., 1996

Triticitidae, subcylindrical to inflated fusiform with strong, relatively strong or moderate chomata, and incompletely strong septal folding in the polar extremities. Aperture central with a median tunnel.

Remark: *Ruzhentsevella* Solovieva & Bensch in Rauzer-Chernousova et al., 1996 is an invalid genus, its type species is a nomen nudum and the genus is not monospecific (Ueno et al. 2009). “*Likharevites*” a still unavailable name is included herein because of its taxonomical importance. It should be formally described in a near future (Davydov, written communication, 2023).

Composition: *Triticites* Girty, 1904; *Carbonoschwagerina* T. Ozawa, Watanabe & Kobayashi, 1992; *Darvasoschwagerina* Leven & Davydov, 2001; *Eotriticites* Da in Da & Sun, 1983; *Iowanella* Thompson, 1957; *Jigulites* Rozovskaya, 1948; *Kansanella* Thompson, 1957; *Kushanella* Leven & Davydov, 2001; *Leptotriticites* Skinner & Wilde, 1965; “*Likharevites*” unavailable, awaiting publication; *Montiparus* Rozovskaya, 1948; *Nipponitella* Hanzawa, 1938; *Paratriticites* Kochansky-Devidé, 1969; *Quasitriticites* Zhuang, 1984; *Rauserites* Rozovskaya, 1950; *Reticulosepta* Maggini, Stevens & Stone, 1988; *Schwageriniformis* Bensch in Rauzer-Chernousova et al., 1996; *Schwageriniformis* (*Tumefactus*) Leven & Davydov, 2001; *Tianshanellites* nomen novum; *Tumulotriticites* Wilde, 2006.

Superfamily **STAFFELLOIDEA** A. D. Miklukho-Maklay, 1949

Description. See Fig. 7.

Family **NANKINELLIDAE** A. D. Miklukho-Maklay, 1963

Staffelloids with rounded carinate to carinate periphery, medium to large-sized. Chomata weak. Wall microsparitized. Aperture terminal simple. Middle Bashkirian–late Changhsingian.

Remark: As already suggested by Ueno (2001), *Guangxiella* Li, 1987 is considered as a subjective junior synonym of *Sazhiella* Dong, 1984. Both genera had been overlooked in Loeblich and Tappan (1987) and Rauzer-Chernousova et al. (1996).

Composition: *Nankinella* Lee, 1934; *Eoverbeekina* Lee, 1934; *Hayasakaina* Fujimoto & Kawada, 1953; *Nanpanella* Huang in Huang & Zheng, 1984; *Pseudoreichelina* Leven, 1970; *Quasireichelina* Ueno, 1992; *Reitlingerina* Rauzer-Chernousova, 1985; *Sazhiella* Dong, 1984.

Family **PSEUDOENDOTHYRIDAE** Mamet in Mamet et al., 1970

Tests lenticular or nautiloid, planispirally coiled with deviations in the primitive genera. Chomata weak to moderate, generally in monticules. Wall differentiated with calcitic grains (luminotheca), false diaphanotheca or transformed in neosparite. Aperture terminal simple. Middle Viséan-Early Permian.

Composition: *Pseudoendothyra* Mikhailov, 1939

Family **STAFFELLIDAE** A. D. Miklukho-Maklay, 1949

Tests planispiral, involute, lenticular or spherical, very rarely subfusiform, small to medium-sized. The septa remain planar during all the history of the group (in contrast to the other order, Fusulinida). Chomata are often present but poorly developed. Some structures confused with parachomata are occasionally described. Wall calcareous secreted, initially aragonitic (probably fibrous and finely perforated?), then neomicrosparitized from aragonite. Aperture always simple, terminal and basal. Bashkirian (Early Pennsylvanian) to Changhsingian (latest Permian).

Composition: *Staffella* Ozawa, 1925; *Caspiella* Gibshman & Sipko, 1985; *Haoella* Gung, 1966; *Jinzhangia* Ueno, 2001; *Leella* Dunbar & Skinner, 1937; *Mufushanella* Chen, 1964; *Necdetina* Altner, Groves, Özkan-Altner, Yılmaz & Atakul, 2007; *Palaeoreichelina* Liêm, 1974; *Palaeostaffella* Liêm, 1966; *Parastaffelloides* Reitlinger, 1963; *Pisolina* Lee, 1934; *Praemisellina* Kalmykova, 1972; *Sphaerulina* Lee, 1934; *Staffelloides* Liêm, 1976; *Tsukumiella* Kobayashi, 2013; *Turgutia* Özdikmen, 2009; *Volgella* Reitlinger, 1977.

Class **MILIOLATA** Saidova, 1981

Test of porcelaneous high magnesium calcite, of fine randomly oriented rodlike crystals, 1.5 µm to 2.0 µm in length and 0.24 µm in diameter, seen only with the electron microscope, the random crystal orientation refracting light in all directions to result in the milky opacity or porcelaneous appearance in reflected light, wall appears brown and glassy in transmitted light, may have surface layer of variously arranged tabular rhombohedral crystals, commonly with organic lining and may have added adventitious material; true pores may occur in protoconch of some, generally imperforate in post embryonic stage, but may have pseudopores; may have flexostyle or spiral passage between proloculus and later chambers; sexual reproduction in some known to involve many inequally biflagellate gametes with characteristically long blepharoplast and axostyle that are freed in the water column. Carboniferous to Holocene (Loeblich and Tappan, 1987).

Order **CORNUSPIRIDA** Mikhalevich, 1980

All late Paleozoic miliolates, which have only one undivided, tubular, and no septated chamber, belong to the order Cornuspirida

Suborder **NUBECULARIINA** Jones in Griffith & Henfrey, 1875

Attached Cornuspirida.

Superfamily **CALCIVERTELLOIDEA** Reitlinger in Vdovenko et al., 1993

Family **CALCIVERTELLIDAE** Loeblich & Tappan, 1964

Description. See Fig. 8.

Remark: *Palaeonubecularia* was included in the Tubiphytidae in Vachard and Le Coze (2022). The familiar assignment to the Calcivertellidae of this well-defined genus is here preferred. *Rectoglomus* is potentially a senior synonym of *Eoglomospiroides* or a junior synonym of *Pseudoglomospira* (nomen dubium herein). *Warnantella* was included in the Glomospiroididae with a question mark in Vachard and Le Coze (2022), it is here transferred to the Calcivertellidae also with a question mark.

Composition: *Calcivertella* Cushman & Waters, 1928; *Apterrinella* Cushman & Waters, 1928; *Calcitornella* Cushman & Waters, 1928; *Orthovertella* Cushman & Waters, 1928; *Orthovertellopsis* Vachard, Krainer & Lucas, 2015; *Palaeonubecularia* Reitlinger, 1950; *Rectoglomus* Malakhova, 1980; *Tansillites* Nestell & Nestell, 2006; *Trepeilopsis* Cushman & Waters, 1928; *Warnantella* Conil & Lys in Conil et al., 1977.

Family **ELLESMERELLIDAE** Vachard in Krainer, Vachard & Schaffhauser, 2019

Description. See Fig. 8.

Composition: *Ellesmerella* Mamet & Roux in Mamet et al., 1987; *Paraellesmerella* Vachard in Krainer, Vachard & Schaffhauser, 2019.

Family **GLOMOSPIROIDIDAE** Reitlinger in Vdovenko et al., 1993

Description. See Fig. 8.

Remark: *Quasilituotuba* has been included in the family Glomospiroididae in Vachard & Krainer (2022).

Composition: *Glomospiroides* Reitlinger, 1950; *Baryshnikovia* Reitlinger in Vdovenko et al., 1993; *Glomospirita* Reitlinger in Vdovenko et al., 1993; *Plummerinella* Cushman & Waters, 1928; *Pseudospira* Reitlinger in Vdovenko et al., 1993; *Quasilituotuba* Brazhnikova in Aizenverg et al., 1983.

Family **PSEUDOVERMIPORELLIDAE** Vachard in Krainer, Vachard & Schaffhauser, 2019

Description. See Fig. 8.

Composition: *Pseudovermiporella* Elliott, 1958; *Hedraites* Henbest, 1963; *Henbestites* Vachard in Krainer, Vachard & Schaffhauser, 2019.




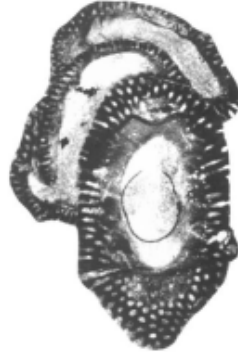
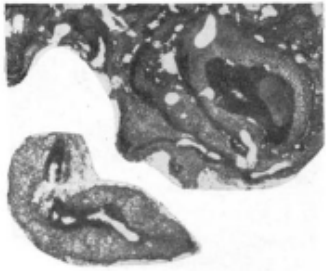
<p>Glomospiroididae</p> <p>Test attached or semi-attached, generally initially streptospirally coiled and then uncoiled. Proloculus spherical followed by a tubular undivided chamber. Pseudosepta can exist in advanced forms. Wall microgranular to granular, brownish, with a carbonate agglutinate of clear calcitic particles, eventually passing to porcelaneous walls. Earliest Serpukhovian–latest Permian.</p>	
<p>Calcivertellidae</p> <p>Attached, undivided tubes, with initial coiling and terminal uncoiling more or less zigzagging. Wall porcelaneous, simple or relatively complex (with pits). Late Mississippian (early Serpukhovian)–latest Permian.</p>	
<p>Ellesmerellidae</p> <p>Encrusting groups of tubular chambers forming flat nodules or oncoids. The elongate cylindrical undivided chambers are arranged parallel to each other in subhorizontal or roughly concentric layers. Their measurements may be distorted by the presence of pseudoconstrictions. The basal part of the tubular chambers is flatter than the upper part, which is more rounded. Early Cisuralian.</p>	
<p>Pseudovermiporellidae</p> <p>Test attached. Proloculus spherical to reniform and juvenarium glomospiroid, both rarely preserved. Adult stage, most commonly preserved under the form of a cylindrical, undivided chamber with thick wall, perforated by pits, perpendicular to oblique to the periphery, shallow or deep; perhaps without connections with the cytoplasm of the chambers. Wall porcelaneous generally dark; rarely well-preserved with amber-color, commonly also neomicrosparitized and whitish, and giving in this case the “vermiporellacean” aspect. Aperture at the extremity of the tubular chamber. ?Asselian–Sakmarian. Latest Sakmarian–late Changhsingian.</p>	
<p>Tubiphytidae</p> <p>More or less strongly transformed consortial associations of tubular miliolate foraminifers with cyanobacterial algae. Poorly transformed tubular miliolates still exhibit sagittiform cavities evoking uniseriate series of chambers. Strongly transformed tubiphytid consortia appear as masses of a rounded, thick-walled skeletons pierced by a small rounded cavity, central or excentred. Late Moscovian–Early Cretaceous.</p>	

Fig. 8. Paleozoic Cornuspirida. Definitions of the families: Glomospiroididae, Calcivertellidae, Ellesmerellidae, Pseudovermiporellidae, Tubiphytidae. Type figures from top: *Glomospiroides fursenkoi* Reitlinger, 1950; *Calcivertella adherens* Cushman & Waters, 1928, left, Smithsonian USNM CC 7689 pic of the holotype; *Ellesmerella permica* (Steinmann in Pia, 1937) from Mamet et al. (1987); *Pseudovermiporella sodalica* Elliott, 1958; *Tubiphytes obscurus* Maslov, 1956.

Family **TUBIPHYTIDAE** Vachard, Krainer & Lucas, 2012

Description. See Fig. 8.

Composition: *Tubiphytes* Maslov, 1956; *Latitubiphytes* Vachard, Krainer & Lucas, 2012; *Ramovsia* Kochansky-Devidé, 1973.

Suborder **CORNUSPIRINA** Jirovec, 1953
Free Cornuspirida.

Superfamily **CORNUSPIROIDEA** Schultze, 1854

Family **CORNUSPIRIDAE** Schultze, 1854

Description. See Fig. 9.

Subfamily **CORNUSPIRINAE** Schultze, 1854

Test small, discoid to inflated, and small- to moderate-sized. Undivided deuterolocus showing generally two types of coiling with one at least which is planispiral, streptospiral or agathamminoid and involute often becoming evolute in the last whorls. Initial coiling glomospiral/streptospiral, sometimes agathamminoid or quinqueloculine. Lumen of chamber reniform or semicircular. Pseudosepta absent or rarely present in a few taxa. Wall porcelaneous, unilamellar. Aperture terminal, simple, at the extremity of the deuterolocus.

Composition: *Cornuspira* Schultze, 1854; *Eoglomospiroides* Reitlinger in Vdovenko et al., 1993; *Eoturrispiroides* Kobayashi & Vachard, 2022; *Glomomidiella* Vachard, Rettori, Angiolini & Checconi, 2008; *Hemigordiellina* Marie in Deleau & Marie, 1961; *Kozhimia* Igonin, 1998; *Megacrassispirella* Zhang in Zhang et al., 2016; *Olgaorlovella* Vachard, Krainer & Lucas, 2015; *Postcladella* Krainer & Vachard, 2011; *Pseudoagathammina* Lin, Li & Sun, 1990; *Rectocornuspira* Warthin, 1930; *Turrispiroides* Reitlinger in Rauzer-Chernousova & Fursenko, 1959.

Subfamily **HEMIGORDIINAE** Reitlinger in Vdovenko et al., 1993

Test small, discoid to inflated, and small- to moderate-sized. Undivided, tubular chamber showing generally two or three successive types of coiling with one at least which is planispiral and involute often becoming evolute in the last whorls. Initial coiling glomospiral/streptospiral, sometimes agathamminoid or subquineloculine. Lumen of chamber reniform or semicircular. Pseudosepta present in a few taxa (e.g., *Hemigordius irregulariformis* Zaninetti, Altner & Çatal, 1981 and *Septigordius* Gaillot & Vachard, 2007). Wall porcelaneous, unilamellar at the periphery, but with several lamellae covering the flanks. Aperture terminal, simple, at the extremity of the tubular chamber.

Composition: *Hemigordius* Schubert, 1908; *Brunsiella* Reitlinger, 1950; *Okimuraites* Reitlinger in Vdovenko et al., 1993; *Praeodiscus* Vachard, Krainer & Lucas, 2015; *Pseudohemigordius* Nestell & Nestell, 2006; *Rectogordius* Alipour & Vachard in Alipour, Hosseini-

Nezhad, Vachard & Rashidi, 2012; *Septigordius* Gaillot & Vachard, 2007.

Family **NEODISCIDAE** Lin, 1984

Description. See Fig. 9.

Subfamily **BAISALININAE** Loeblich & Tappan, 1986
Baisalinidae with developed pseudosepta.

Composition: *Baisalina* Reitlinger, 1965; *Aulalina* Nie & Song, 1985; *Pseudobaisalina* Sosnina, 1983.

Subfamily **MULTIDISCINAE** Vachard & Krainer, 2022

Large Miliolida tests composed of a spherical proloculus followed by an undivided tubular chamber, diversely coiled: entirely glomospiral, initially glomospiral and then planispiral (or aligned) involute, glomospiral becoming planispiral evolute or semi-involute, planispirally involute compressed or inflated agathamminoid, i.e., subquineloculine. The chamber is semicircular in section (some flosculinisations are present). Aperture terminal simple.

Composition: *Multidiscus* A. D. Miklukho-Maklay, 1953; *Multidiscella* Vachard & Krainer, 2022; *Nikitinella* Sosnina, 1983.

Subfamily **NEODISCINAE** Lin, 1984

Neodiscidae medium - to large-sized, undivided or with weak pseudosepta, involute or with a short evolute terminal stage of coiling, and devoid of flosculinisation.

Composition: *Neodiscus* A. D. Miklukho-Maklay, 1953; *Crassiglomella* Gaillot & Vachard, 2007; *Crassispirellina* Gaillot, Vachard & Le Coze in Vachard et al., 2019; *Graecodiscus* Vachard in Vachard et al., 1993; *Midiella* Pronina, 1988; *Neodiscopsis* Gaillot & Vachard, 2007; *Neohemigordius* Wang & Sun, 1973; *Pseudomidiella* Pronina-Nestell in Pronina-Nestell & Nestell, 2001; *Uralogordiopsis* Vachard in Krainer et al., 2019; *Uralogordius* Gaillot & Vachard, 2007.

Subfamily **SEPTAGATHAMMININAE** Mikhalevich, 1988

Test entirely streptospiral, elongated, chambers with incomplete septa formed by internal thickenings of the wall.

Composition: *Septagathammina* Lin, 1984

Family **HEMIGORDIOPSIDAE** Nikitina, 1969

Description. See Fig. 9.

Subfamily **HEMIGORDIOPSINAE** Nikitina, 1969

Test subspherical, ovoid, occasionally nautiloid, involute, rarely evolute at the end of growth; the coiling in the juvenarium is ball-shaped, in the following whorls planispiral; the second chamber is very low and wide along the entire width of the test, undivided or with inconsistent and rare pseudosepta; wall very thick, quickly thickens after juvenarium; secondary deposits absent or weakly expressed.



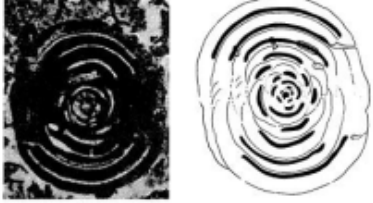
<p>Cornuspiridae</p> <p>Small porcelaneous undivided tubes with streptospiral, or planispiral evolute coiling, or a succession of both types. Late Serpukhovian–Holocene.</p>	
<p>Neodiscidae</p> <p>Large Miliolida composed of a spherical proloculus followed by an undivided tubular chamber, with a thick wall, diversely coiled: entirely glomospiral; initially glomospiral and then planispiral (or aligned) involute; glomospiral becoming planispiral evolute or seminvolute; planispirally involute compressed or inflated. The chamber is semicircular in section (some flosculinisations are observable in advanced forms). The thick wall is reinforced by buttresses at the contact with the preceding whorl. Aperture terminal simple. ?Sakmarian, ?Artinskian-Lopingian with a late Changhsingian acme.</p>	
<p>Hemigordiopsidae</p> <p>Test large, entirely streptospiral or initially streptospiral with a planispiral coiling in the terminal stage, involute. Undivided tube, or presence of pseudosepta or true pillars. Diagenetic features of the wall were interpreted as perforations but would correspond more to a comb teeth structure. Midian-Changhsingian, ?Early Triassic.</p>	

Fig. 9. Paleozoic Cornuspirida. Definitions of the families (continuation of Fig. 8): Cornuspiridae, Neodiscidae, Hemigordiopsidae. Type figures from top: *Cornuspira (Turrispiroides) multivoluta* (Reitlinger, 1949) from Krainer et al. (2005); *Neodiscus milliloides* Miklukho-Maklay, 1953; *Hemigordiopsis renzi* Reichel, 1945.

Composition: *Hemigordiopsis* Reichel, 1945; *Agathammina* Neumayr, 1887; *Globidiscus* Okuyucu, 2021; *Glomomidiellopsis* Gaillot & Vachard, 2007; *Lysites* Reitlinger in Vdovenko et al., 1993.

Subfamily **KAMURANINAE** Trifonova, 1984

Composition: *Kamurana* Altiner & Zaninetti, 1977

Subfamily **SHANITINAE** Loeblich & Tappan, 1986

Similar to Hemigordiopsinae but chamber interior with vertical pillars.

Composition: *Shanita* Brönnimann, Whittaker & Zaninetti, 1978

Class **NODOSARIATA** Mikhalevich, 1993

Test rectilinear, lenticular to elongate, ovoid to subglobular, or lanceolate; formed by a bulbous to globular, well-distinct proloculus open either on an undivided to pseudoseptate, non-enrolled, slightly increasing tubular chamber or on a series of more brevithalamous ever-increasing chambers set, at least in the juvenile part, in a rectilinear, planispiral, polymorphine-like, or biserial to trochospiral arrangement (plurilocular test). Wall calcareous, microgranular with crystals either randomly distributed or arranged in inverted paraboloids and/or hyaline with

crystals' c-axes perpendicular to the test surface; perforate or imperforate, with an inner organic lining. Aperture terminal, in the test elongation axis, foraminal distance maximized (Rigaud et al. 2015).

Order **NODOSARIIDA** Calkins, 1926

Foraminifers with a monolamellar wall of radiate calcite, with crystal c-axis perpendicular to the surface and without secondary lamination (Loeblich & Tappan 1987).

Superfamily **COLANIELLOIDEA** Fursenko in Rauzer-Chernousova & Fursenko, 1959

Family **SYZRANIIDAE** Vachard in Vachard & Montenat, 1981

Description. See Fig. 10.

Composition: *Syzrania* Reitlinger, 1950; *Amphoratheca* Mamet & Pinard, 1992; *Rectostipulina* Jenny-Deshusses, 1985; *Syzranella* Mamet & Pinard, 1992; *Tezaquina* Vachard, 1980.

Family **PROTONODOSARIIDAE** Mamet & Pinard, 1992

Description. See Fig. 10.


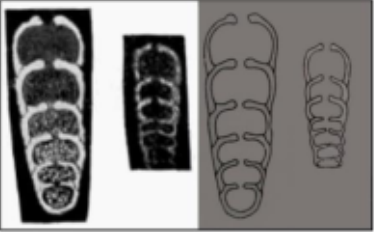

<p>Syzraniidae</p> <p>Very primitive, tubular Nodosariata without septation or with faint pseudosepta. Wall bilayered: ancestral dark microgranular inner layer, outer evolved hyaline fibrous. Aperture simple at the end of tubular chamber. Late early Moscovian to late Changhsingian.</p>	
<p>Protonodosariidae</p> <p>Colanielloidea rectilinear to curved, tapering to cylindrical; i.e., with sagittal axial and frontal axial sections similar. Apertures simple, round. Wall single or two layered. Late Pennsylvanian–Late Triassic.</p>	
<p>Geinitzinidae</p> <p>Colanielloidea with different sagittal axial and frontal axial sections. Sagittal axial sections exhibiting geinitzinoid chambers; i.e., low, medially arched, and non-enveloping. Frontal axial sections are nodosarioid in shape. Aperture terminal, simple. Latest Pennsylvanian to Triassic.</p>	

Fig. 10. Paleozoic Colanielloidea Nodosariida. Definitions of the families: Syzraniidae, Protonodosariidae, Geinitzinidae. Type figures from top: *Syzrania bella* Reitlinger, 1950; *Protonodosaria praecursor* (Rauzer-Chernousova, 1949) from Gerke (1959); *Textularia jonesi* Brady, 1876.

Subfamily **LANGELLINAE** Gaillot & Vachard, 2007

Large uniserial tests, slightly tapering and then cylindrical. Wall thick to thin. Aperture simple or absent. Chambers globose few enveloping.

Composition: *Langella* Sellier de Civrieux & Dessauvage, 1965; *Pseudolangella* Sellier de Civrieux & Dessauvage, 1965.

Subfamily **PROTONODOSARIINAE** Mamet & Pinard, 1992

Uniseriate Nodosariata with hemispherical chambers, complete septa, and a cylindrical, terminal aperture.

Composition: *Protonodosaria* Gerke, 1959; *Echinonodosaria* Xia & Zhang, 1984; *Nestellorella* Gaillot & Vachard, 2007; *Nodosinelloides* Mamet & Pinard, 1992; *Paravervilleina* Vachard in Krainer et al., 2019; *Polarisella* Mamet & Pinard, 1992; *Tauridia* Sellier de Civrieux & Dessauvage, 1965; *Tauridiopsis* Vachard in Krainer et al., 2019; *Vervilleina* Groves in Groves & Boardman, 1999.

Family **GEINITZINIDAE** Bozorgnia, 1973

Description. See Fig. 10.

Composition: *Geinitzina* Spandel, 1901;

Frondinodosaria Sellier de Civrieux & Dessauvage, 1965; *Howchinella* Palmieri, 1985; *Lunucamma* Spandel, 1898; *Omoloniella* Karavaeva & Nestell, 2007; *Praerectoglandulina* Vachard in Krainer et al., 2019; *Reitlingeria* Pronina in Kotlyar et al., 1989; *Spandelinoides* Cushman & Waters, 1928.

Family **ROBULOIDIDAE** Reiss, 1963

Description. See Fig. 11.

Composition: *Robuloides* Reichel, 1946; *Calvezina* Sellier de Civrieux & Dessauvage, 1965; *Cryptomorphina* Sellier de Civrieux & Dessauvage, 1965; *Eocristellaria* A. D. Miklukho-Maklay, 1954; *Eomarginulinella* Sosnina, 1969; *Gourisina* Reichel, 1946; *Hubeirobuloides* Lin, Li & Zheng in Lin et al., 1990; *Pararobuloides* K.V. Miklukho-Maklay, 1954.

Family **PARTISANIDAE** Loeblich & Tappan, 1984

Description. See Fig. 11.

Composition: *Partisania* Sosnina, 1978; *Xintania* Lin, 1984.

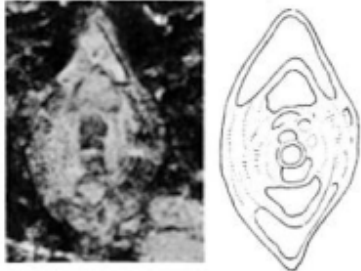



<p>Robuloididae</p> <p>Planispirally coiled Colanielloidea, sometimes secondarily uncoiled. Earliest to latest Permian.</p>	
<p>Partisaniidae</p> <p>Test biseriolate, later becoming uniseriate. Early chambers spiralling about a long axis and/or arranged biserially but with successive chambers added slightly less than 180° apart, resulting in a more or less sigmoid arrangement seen in transverse section. Aperture terminal. Wordian, Kazanian, Capitanian, Tatarian and Lopingian.</p>	
<p>Fronidinidae</p> <p>A family of Colanielloidea relatively common during the Midian/Capitanian and the Late Permian. This family is characterized by its dark (microgranular?) wall and the embracing shape of the chambers. Aperture are smooth or accompanied by an internal neck. Capitanian-Changhsingian, ?lowermost Triassic.</p>	
<p>Colaniellidae</p> <p>Test uniseriate, chambers strongly overlapping, internally subdivided by vertical radial partitions; wall with outer vitreous layer and finely granular inner layer; aperture rounded to radiate. U. Permian.</p>	

Fig. 11. Paleozoic Colanielloidea Nodosariida. Definitions of the families (continuation of Fig. 10): Robuloididae, Partisaniidae, Fronidinidae, Colaniellidae. Type figures from top: *Robuloides lens* Reichel, 1946; *Partisania typica* Sosnina, 1978; *Fronдина permica* Sellier de Civrieux & Dessauvagie, 1965; *Pyramis parva* Colani, 1924 from Reichel (1946).

Family **FRONIDINIDAE** Gaillot & Vachard, 2007
Description. See Fig. 11.

Composition: *Fronдина* Sellier de Civrieux & Dessauvagie, 1965; *Ichthyofronдина* Vachard, 1991.

Family **COLANIELLIDAE** Fursenko in Rauzer-Chernousova & Fursenko, 1959
Description. See Fig. 11.

Composition: *Colaniella* Likharev, 1939; *Cylindrocolaniella* Loeblich & Tappan, 1985; *Pseudowanganella* Sosnina, 1983.

Superfamily **NODOSARIOIDEA** Ehrenberg, 1839

Family **NODOSARIIDAE** Ehrenberg, 1839

Remark: The relevance of the use of the genus *Nodosaria* is discussed above.

Composition: *Nodosaria* Lamarck, 1816; *Dalongella* Gu, Feng & He, 2007.

Family **PACHYPHLOIDAE** Loeblich & Tappan, 1984

Composition: *Pachyphloia* Lange, 1925; *Aulacophloia* Gaillot & Vachard, 2007; *Maichelina* Sosnina, 1977; *Robustopachyphloia* Lin, 1980.

Family **ICHTHYOLARIIDAE** Loeblich & Tappan, 1986

Composition: *Ichthyolaria* Wedekind, 1937; *Cryptoseptida* Sellier de Civrieux & Dessauvagine, 1965; *Geinitzinita* Sellier de Civrieux & Dessauvagine, 1965; *Gerkeina* Grozdilova & Lebedeva in Sosipatrova, 1969; *Involuntaria* Gerke, 1957; *Nodoinvoluntaria* Lin, 1978; *Pachyphloides* Sellier de Civrieux & Dessauvagine, 1965; *Pseudotristix* K. V. Miklukho-Maklay, 1960.

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