Foraminiferal Descendence and its Early Cambrian-Initiated Diversification

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CONTENTS

Plates

PREFACE

This work comes precisely two hundred years after the release of the first classification of foraminifers, which at that time, in 1825, represented a small group of only a few genera included within the cephalopod mollusks. It was the time when organisms were grouped together according to their morphological resemblances, a method that was developed in the early days of science in Antiquity. The classification of the modern and fossilized organisms proved a successful scientific endeavor, and in the specific case of the foraminifers led to the development of about twenty frameworks that accommodated the new data acquired as the scientific advances built up in the study of this group of microorganisms.

A classification framework is a useful tool in practical and fundamental studies. A researcher can figure out the general features of the test architecture simply by knowing the systematic position of the respective organisms and those derived from them, another data set on the distribution in space and geological time, paleobathymetry and paleoecology, etc. A quick look at the classification dynamics shows that the taxonomic principles that form their foundation changed considerably through time, and they became more and more accurate. There is no doubt when studying the different classification frameworks that they are of a scientific nature, and this explains their success over two centuries of massive development. The first of them was produced before we understood the foraminifers are protistans and at the present, more and more scientists speak of foraminiferology as part of micropaleontology. A scientific story of success so to speak. Adding to these developments, a series of studies started implementing the Darwinian principles into the modern classification, which resulted in the grouping of taxa according to inferred ancestor–descendant relationships as recognized in the foraminiferal fossil record. The developments continued in the twentieth century, at a slower pace at first, before accelerating in the last decades of the century. Not only have fundamental advances been made, but the new methodologies also showed their importance in the practical applications of foraminiferology. It was the time when the time-honored grouping based on resemblance started to be replaced by a more refined one, as prefigured in *The Origin of Species*.

A curious turn of events happened in the last decade of the twentieth century, with the onset of a new current of thinking. In general terms, according to it micropaleontology needed to reinvent itself by migrating towards biology, genetics, and geochemistry, without providing a clear argumentation on why such a colossal shift was necessary. Notably, this came in a period of the extensive development of many branches of micropaleontology, foraminiferology among them. I cannot find a rational explanation for the success of this current of thinking, which led to an obvious fragmentation of the publication topics. One of the most affected domains of study in foraminiferology is that of classification development, which became closer to the neontological sciences (biology and genetics). In other words, the principles of classification of the living organisms derived from the small number of taxa were also applied to the fossil record, which is a completely different data set. But the scientific advances of foraminiferology cannot be stopped. The beginnings of the transition from the resemblance-based to evolutionary classification marks in fact the change towards a high-magnitude conceptual leap, namely the first declassification framework, the topic of this work.

The reader will find this work challenging as almost everything is changed when compared with the classical resemblance-only based classifications. So different as it is, it can be the source of ideas for several hundred articles and more. One common feature of the classifications and declassification is the use for now of the Latin names at the genus level and for lineages respectively. I think of it as evidence that two scientific perspectives on the fossil record cannot exclude each other and are compatible at some point. With the mention that one is conceptually stagnant, whereas the other must move forward. This work of declassification is significant, and therefore this book is just the start. It will be followed in time by four companion titles: *Foraminiferal Descendence and its Late Ordovician-Initiated Diversification*; *Foraminiferal Descendence and its Late Silurian-Initiated Diversification*; *Foraminiferal Descendence and its Early Triassic-Initiated Diversification*; and *Foraminiferal Descendence and its Middle Jurassic- and Early Cretaceous-Initiated Diversifications*.

Calgary, July 22, 2025

CHAPTER 1

INTRODUCTORY CONCEPTS

The concept of declassification is new in the study of the foraminifers. It follows a modern history of more than three centuries of classification of the living and fossilized organisms on Earth. The different classification frameworks never eliminated completely from their structure the philosophical and occasionally mystical features of the earliest attempts. Despite these, science advanced and refined continuously in the last three centuries, and considerable changes became apparent with the implementation of the principles from the Darwin's *The Origin of Species*, and with the emergence of evolutionary classification, the path towards declassification was opened.

1.1. Time of classifications

The earliest mention of a foraminifer is from Antiquity. The report is that of Strabo of Amasia from the proximity of the pyramids of Ancient Egypt and the described structures belong probably to one species of the genus *Nummulites*; a detailed account on this report and its interpretation was given in Georgescu (2018a). Other reports began at the end of the Renaissance, when different specimens of the groups were mentioned, briefly described in general and illustrated (Gesner 1565, Hooke 1665, Lang 1708). In addition, there are also some vague mentions of fossilized microfossils that may represent foraminiferal tests (e.g., Ceruto and Chiocco 1622).

The beginnings of classification as scientific methodology date back in the pre-Hellenistic period of Greek Antiquity and are found in the works of Aristotle of Stagira (384–322 BC), who subdivided animals into groups based on their morphology. Almost in parallel, a classification of plants was given by his collaborator, Theophrastus of Eresos (~371– ~287 BC); notably, in his work on plant classification, this scholar noted the fact that classification of one group of organisms is not unique, but multiple. These classifications resulted in the definition of rather informal groups of animals and plants, and for many of them, the chosen name was identical with that used in the everyday language. Another major contribution by Aristotle of Stagira is represented by the definition of the concepts of genus and species. They are widely used today in modified form, and originally were developed as metaphysical concepts, and changed their meaning over time. Practically, long before the birth of modern science, the germs of modern classification were developed. They were used later in the Roman Antiquity, completely abandoned in the Dark Ages and then rediscovered in the late Renaissance.

The development of classifications restarted after the birth of modern science in 1660, with the establishment of the Royal Society of London. The first contributions were those of Charleton (1668) and Ray (1693). They were followed by a classification of the fossilized organisms by Lang (1708), in which we can find different foraminiferal tests grouped together with the corals.

More elaborated classification followed, and probably the most influential were those by Breyn (1732) and Linné (1735). Of them, the latter is by far the better known, for it later developed into the modern Linnean classification. But, at least for the study of the foraminifers, the classification of Breyn (1732) is equally important. This classification was developed for invertebrate organisms, mostly molluscs, which were subdivided into eight classes of which of particular importance is the Class Polythalamium, which includes cephalopod invertebrates; the four cephalopod groups included within this class are the nautiloids, ammonoids, lituitids and orthoceratids. Practically, this class was erected for testate organisms that present a shell consisting of many chambers, hence its name (poly-thalamos in Greek translates as many-chambered). The plates in Breyn leave no doubt on the nature of the organisms included within the newly erected class: they are all cephalopods. Claims by a small number of recent authors that the foraminifers were included in the classification of Breyn (1732) are simply not true. I can only speculate that the confusion was caused by the genus *Ammonia* (Breyn, 1732, pl. II, figs. 8–10), which is the homonym of an accepted and frequently reported foraminiferal genus. The respective plate caption translates from Latin as "*Ammonia* or the horn of Amon"; the "horn of Amon" was a common term for ammonites and occurred frequently in books published till the eighteenth century.

The subsequent reports of foraminifers were influenced by the classification of Breyn (1732). For example, Plancus (1739) assigned the tests of foraminifera to the informal categories of "horn of Amon" and nautili, which evidently indicates that these microorganisms were associated with the cephalopod molluscs. A few years later, Gualtieri (1742) included these microorganisms within the class Polythalamia; the identification was more specific in the case of the tests with rectilinear chamber arrangement, which were assigned to *Orthoceras minimum* (which translates as "the small *Orthoceras*"). This assignment is also apparent in the famous 10th of *Systema Naturae* by Linné (1758) and in the first study that marks the beginning of the systematic study of the foraminifers (Soldani 1780).

The first half of the nineteenth century was the time when the number of genera and species of foraminifers increased significantly, and the earliest classifications of the group were developed. The three classifications included in this category were those given by de Blainville (1825), d'Orbigny (1826) and Crouch (1827). The group was formalized at different taxonomic levels: as class by H.M.D. de Blainville, order by A.D. d'Orbigny and in a group of six families by E.A. Crouch. The order named by d'Orbigny is that of Foraminifères and the classification is the most elaborate, with the addition of numerous new genera and species.

The publication of the *Tableau méthodique de la classe des Céphalopodes* by d'Orbigny (1826) represents a turning point in the study of foraminifera and is often considered the beginning of the modern foraminiferology. The group was named and described as Ordre Foraminifères, the third order of the cephalopod class, and later formalized as order Foraminiferida. It was originally subdivided into five new families, mostly according to the chamber arrangement, but also the general aspect of the test wall: Stichostègues, Enallostègues, Hélicostègues, Agathistègues and Enthomostègues. This classification framework was the subject of two successive improvements by the same author, but these were realized in a completely different context. A major clarification on the systematic position of the foraminifers was the discovery made by Dujardin (1835a, 1835b) that the living representatives have a much simpler structure when compared with that of the cephalopods. It was noted in these studies that the soft body of the foraminifera lacks completely organs for locomotion and respiration and has a rather homogeneous structure. This type of soft body was named "sarcode" by F. Dujardin. Practically, following this discovery, the foraminifers were regarded as a distinct group of single-celled animals, later named protistans.

The subsequent development of the classifications represented a necessity to accommodate our increasing knowledge on the foraminiferal group. On one hand, the number of genera and species increased almost continuously, with rare years in the nineteenth century when no new genera were formalized, and on the other, all these new units required a system of grouping for efficient use in further studies. The development of new classifications became practically a necessity, and following that of d'Orbigny (1826, 1839, 1849), new classification frameworks based on the Aristotelian–Linnean principle of grouping according to similarity were produced: Schultze (1854), Reuss (1862), Carpenter (1862), Griffith and Henfrey (1875), Schwager (1875, 1876), Brady (1884), Neumayr (1887), Rhumbler (1895), Delage and Hérouard (1896), Eimer and Fickert (1899), Lister in Lankester (1903), Schubert (1821), Cushman (1925a, 1927a, 1948), Galloway (1933), Chapman and Parr (1936), Glaessner (1945), Hofker (1951a), Sigal in Pivteau (1952), Pokorný (1958), Reiss (1958, 1963), Rauzer–Chernousova and Fursenko (1959) and Loeblich and Tappan (1964a, 1984a, 1987). Of them, that by Loeblich and Tappan (1987) is widely used today.

One interesting outcome of the development of these classifications was the initiation of a new stream of studies, namely those in which they were evaluated and compared. Besides their role in presenting the historical development of the classification frameworks, such works helped foraminiferologists to permanently adjust the accuracy of the taxonomic principles. These synthesis works are those of Galloway (1928), Loeblich and Tappan (1964a), Solovieva (1981), Haynes (1990), Cifelli (1990) and Richardson (1990). However, it should be mentioned that a complete review of the foraminiferal classifications from de Blainville (1825) to Loeblich and Tappan (1987) was not written.

The beginnings of the evolutionary classification can be found in *The Origin of Species* by Darwin 1859 (pp. 413–414), who noted the morphological resemblance between some organisms is given by the common ancestry. Although succinct, this mention led to the definition of a methodology to infer ancestor–descendant relationships in the decades to come, when different researchers started inferring such relationships between taxa based on a combination of morphological similarities and differences, given by the common ancestry and divergent nature of evolution respectively. The number of such attempts is huge and not all of them are given below, partly because the methodology of how such ancestor–descendant relationships were given.

Following a first attempt to reconstruct the descendence of some benthic taxa by Guppy (1894), a major leap was realized in a pioneering study on the Cenozoic larger foraminifers of Indonesia by Tan Sin Hok (1932). He noted the gradual and discontinuous pattern of different species of one "bioseries" or "line of descent", as well as the linear and branched patterns of such lineages. Moreover, the morphological changes and divergence were analyzed in a strict straigraphical context, resulting in quite accurate results.

Subsequent studies went mainly in two directions: to recognize ancestor–descendant relationships between taxa of the in-use Aristotelian–Linnean classification or to define major trends in the morphology. Some of the most interesting and relevant studies are listed below (Yabe and Hanzawa 1930, Asano 1936, Riccio 1950, Baker and Grimsdale 1936, Brönnimann 1958, Sheng 1963, Lipina 1965, Van Hinte 1965, Liêm 1966, Foury 1968, Hamaoui and Saint–Marc 1970, Cheong 1973, Caudri 1974, Schaub 1981, Frieg and Price 1982, Wannier 1983, Cherchi and others 1984, Garg and Singh 1986, Desai and Banner 1987, Zaninetti and others 1987, Brinkhuis and Zachariasse 1988, Septfontaine 1988, Banner and Highton 1990, Ujiié 1990, Banner and Whittaker 1991, Banner and others 1991, Di Bari and Langhi 1994, Weidich 1995, Matsumaru 1996, Kaiho 1998, Groves and Wahlman 1999, Moullade and others 2002, Wang and Ueno 2009, Altiner and Özkan Altiner 2010, Kulagina 2017, Gedik 2018, etc.).

There were also numerous studies on the Cenozoic planktic foraminifera for distinct streams leading from the Aristotelian–Linnean classification towards an evolutionary one (Parker 1962, 1967, Lipps 1966, Berggren 1968, McGowran 1968, 1971, Frerichs 1971, Steineck 1971, Fleisher 1974, Steineck and Fleisher 1978, etc.). They culminated with the atlases on the Cenozoic planktics (Kenneth and Srinivasan 1983, Olsson and others 1999, Pearson and others 2006, Wade and others 2018). Similarly, evolutionary classification studies were realized in the Cretaceous planktic foraminifera (Georgescu 2007a, b, 2009a, b).

All these studies are relevant for the development of high-resolution studies in which the data on the descendence between different taxa started to be implemented in the in-use Aristotelian–Linnean classification. By using units such as genera and species, these studies document a phase of development of evolutionary classification that is close to its definition according to Simpson (1961, p. 113), namely a more advanced stage of the classical Aristotelian–Linnean classification.

A series of classifications of the foraminiferal group were proposed after 2010. They are based either on data from genetics interpreted through a cladistic approach, biological data from a small number of species and then extrapolated at the scale of the whole group, or a combination of them, with the classification of Loeblich and Tappan (1987), which is the most thorough and accurate, restricted to the lower levels of classification. It is necessary to mention that to provide herein the highest scientific standards and a clean scientific content, all the works of the authors who accepted or developed such questionable classifications were carefully checked for creationism, anti-Darwinism and anti-science.

1.2. Foraminifer declassification

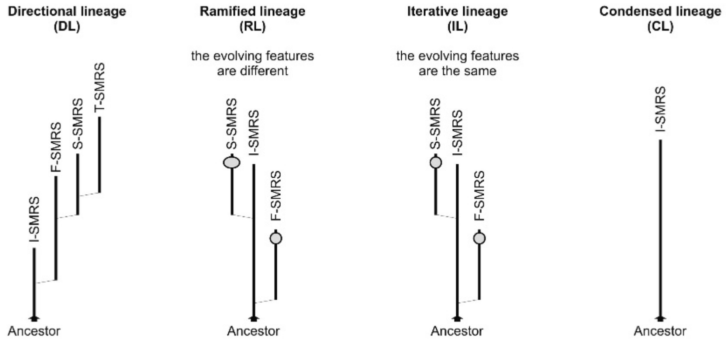
Further developments from the evolutionary classification happened in the Cretaceous planktic foraminifers, when the species started to be grouped according to the ancestor–descendant relationships into lineages rather than genera, emphasizing the dynamic nature of such unit groupings (Georgescu 2009c). Notably, in this pioneering study the level of lineage was conferred a formal status within the Linnaean hierarchy. The new and challenging approach was further developed with the definition of the directional and branched lineages, both with a formal status at the same level (Georgescu 2010a); this new advance effectively detached the new approach from the classical Aristotelian–Linnean one, where one type of unit (i.e., genus) exists at one level of classification. The open system character was further demonstrated afterwards with the development of the iterative lineage and condensed lineage; a review of the four kinds of lineages was given by Georgescu (2014, pp. 160–161). Another advance was represented by the definition of the "stage of morphological relative stability" which largely corresponds with the level of species in the Aristotelian–Linnean classification (Georgescu 2014); in parallel, the first nomenclature system for the stages of morphological relative stability within a lineage was developed. The new approach was further developed for larger groups of foraminifera, both planktics and benthics: rotaliporids (Georgescu 2016), bolivinoidids (Georgescu 2018b) and globotruncanids (Georgescu 2020). Only after a continuous development over more than a decade, did it become evident that with the lineages of different kinds at the same grouping level, the new method represented a declassification. Such scientific advances led to the possibility of applying the new methodology at the scale of the whole foraminiferal group. As an aspect of terminology, the general term chosen of the different recognized entities within the declassification framework is that of unit; the unit has the equivalent of taxon (pl. taxa) in the Aristotelian–Linnean classification.

The declassification framework for the foraminiferal group is realized by grouping the units through a combination of morphological resemblance, which is given by the common ancestry, and differences, which are the result of divergent nature of the descendance process. All the observations that represent the fundament of the declassification are made in stratigraphical order. A description of the units recognized in the fossil record of the foraminiferal group is given below.

The basic unit is that of lineage, which was associated at the time of definition by Georgescu (2014, p. 163) with the evolutionary classification; subsequent observations show that it is equally applicable in declassification. According to the original definition that is followed herein, there are six features that can be used in the description of one lineage: (1) it presents a variable degree of distinctiveness when compared to similar units, (2) is a succession of individuals or groupings of individuals in ancestor–descendant relationships, (3) the similarities between the individuals or groupings of individuals are the result of the common ancestry, (4) the morphological differences individuals or groupings of individuals reflect the descendence or not, (5) consists of one or more stages or morphological relative stability and (6) the descendence history in space and time can be reconstructed from the data from the fossil and rock records, with neontological data available in the cases of the lineages with living representatives. Four kinds of lineages are recognized according to the branching pattern of the component stages of relative morphological stability: directional (DL), ramified (RL), iterative (IL) and condensed (CL) (Georgescu 2014, p. 160) (Fig. 1-1: A). In some cases, the lineage level can be considered equivalent of the genus level in the Aristotelian–Linnean classification; many genera consist of numerous species and are heterogeneous taxa. Such genera are considered groups of lineages (GL) and require further study and splitting in the declassification framework.

Some of the lineages can be grouped and form more complex units termed branches. One branch can consist of two or more lineages, but in general the number of component lineages is small. The branches recognized in this work are directional (DB), ramified (RB) and complexly ramified (CRB) (Fig. 1-1: B).

A: kinds of lineages



B: kinds of branches

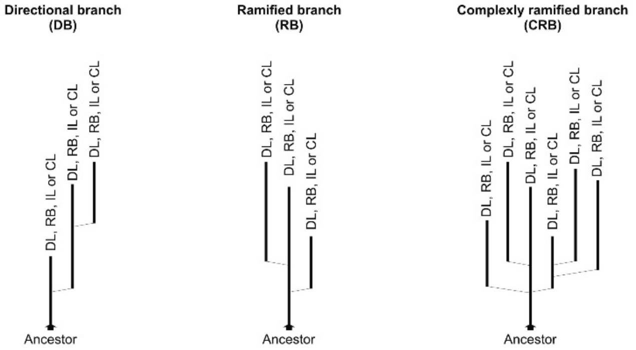


Fig. 1-1. Idealized representation of the kinds of lineages and branches and their terminology used in the foraminiferal declassification framework. Abbreviation: SMRS-stage of morphological relative stability.

The lineages and branches are grouped into a larger entity, herein termed nexus (pl. nexuses); the whole foraminiferal group consists of 203 nexuses. One nexus consists of two to around one hundred lineages and therefore, the branching and diversity varies considerably between the nexuses; in general, one stalk is represented by a group of lineages. The structure of one nexus shows that one lineage emerges from the ancestral unit and in general is a longer ranging one. The stalk can be simple or multiple and in the latter case the component lineages are labelled Stalk 1, Stalk 2 or Stalk 3; maximum three stalk components are recognized in this work (Fig. 1-2). The lineages and branches that derive from the stalk units are considered independent originations from the stalk (IOS) and labelled in stratigraphical order from IOS-1.

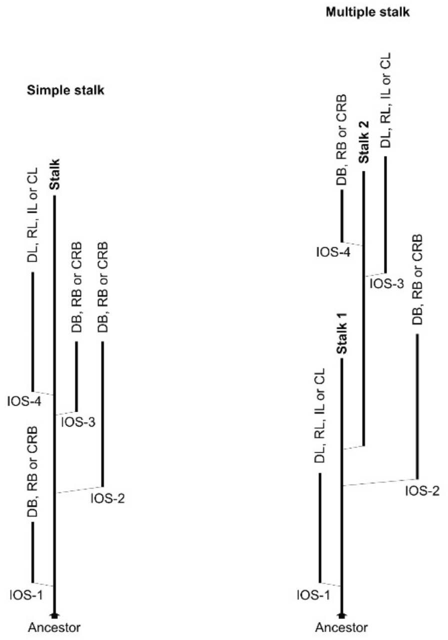


Fig. 1-2. Idealized representation of the two kinds of stalk in foraminiferal declassification. Abbreviations: IOS- independent origination from the stalk, and all the others as in Fig. 1-1.

The names of the nexuses and branches are formed from the generic name of the stalk unit in the Aristotelian–Linnean classification, which is informalized and in plural form (Fig. 1-3). In the case of the stalk units, lineages or groups of lineages, the temporary names are those of the original generic units.

1.3. Unit presentation format and data significance

Five sets of data are presented for each of the units in the descriptive part: the system of reference, synonyms, test morphology, stratigraphical and geographical distribution, and ancestry. Additional data occur in the case of the units that were already revised in an evolutionary classification framework.

In the classical Aristotelian–Linnean classification, each taxon of a certain level requires the naming of a type from the included taxa of the immediate lower level. The wide acceptation of the designation of types in the modern Aristotelian–Linnean classification led to its renaming as typological classification.

The units described as new in the earlier pioneering works on foraminifers did not have designated types (e.g., Soldani 1780, 1789, 1791, 1795, Walker and Boys 1784, de Bruguière 1792, Fichtel and Moll 1798, Adams 1800, Lamarck 1801, 1804a, b, c, Montagu 1803, 1808, etc.). The word “type” occurs in the sense of “kind” in the Latin text of only one work (Soldani 1789, p. 21). The type-based system was started practically by de Montfort (1808), who designated a type species for the genera of the foraminifers he described. This system was widely accepted in France in the 1820s and will be further developed in the typological system.

The modern typological foraminiferal nomenclature is regulated by the International Code of Zoological Nomenclature. The rules of this convention are often rigid, resulting in situations where the so-important authorship is changed. For example, and in direct connection with the assigned types, a new genus is not considered valid without the designation of a type species; consequently, such a genus must be renamed and a type species assigned to it to be validated, one act that leads to the change of the respective genus’s authorship. Another example of a rule that led to nomenclatural instability is that which states that a name of a foraminifer is unique and no other animal or taxon previously considered an animal should bear it; a necessary mention is that foraminifers are protistans, but in the past were often considered unicellular animals. This rule led to the change of name of many foraminifer names, to avoid the confusion with other protistans, invertebrates or vertebrates; notably, such name changes led to the challenge of authorship. The practice and the administrative system that governs such a convention for the nomenclature of Aristotelian–Linnean classification added further to problems with a reduced chance of being corrected, which are not presented in this work.

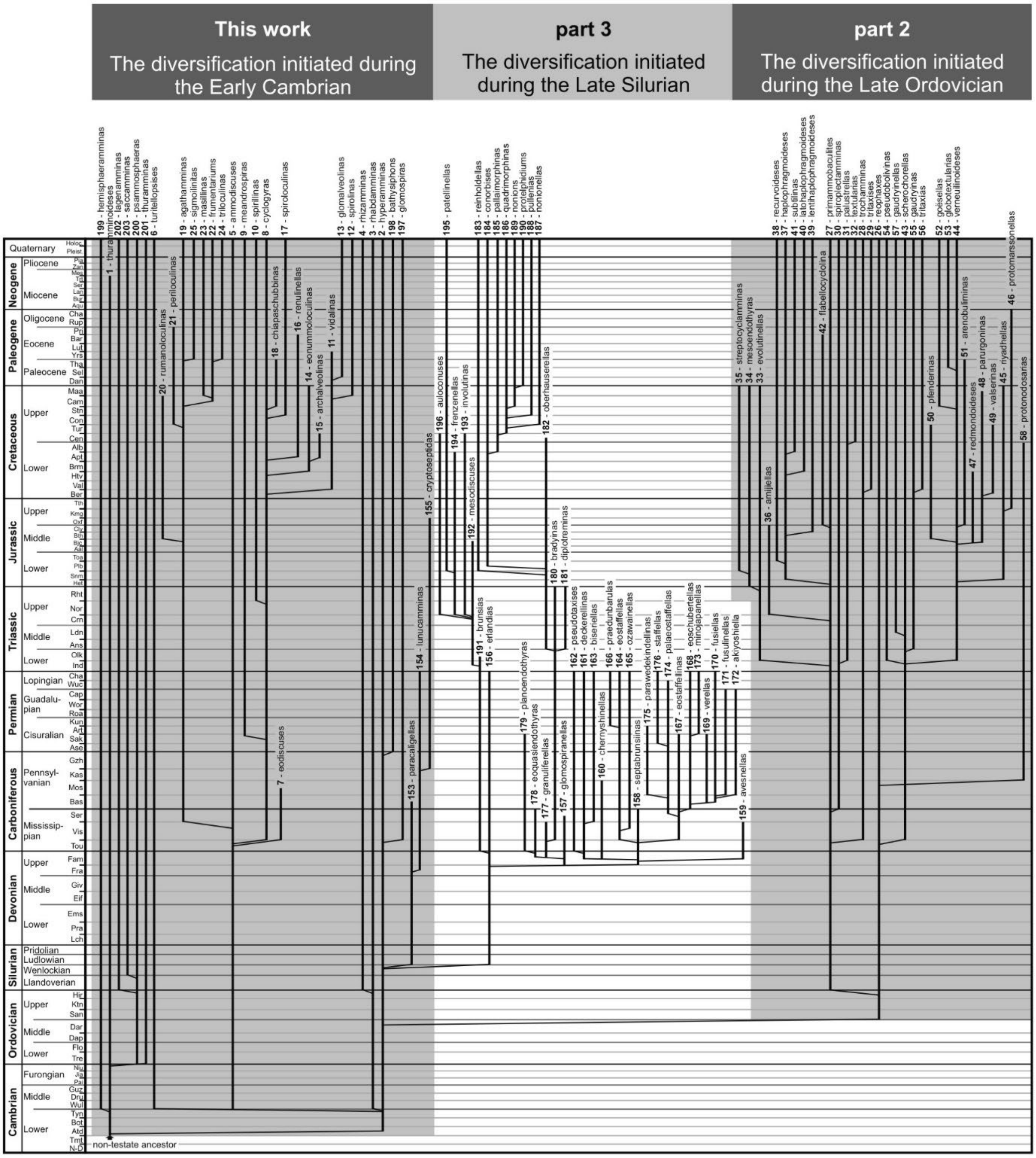


Fig. 1-3. Descendence and stratigraphical distribution of the foraminiferal nexuses recognized in this work. Each of the nexuses is numbered according to the descendence order.

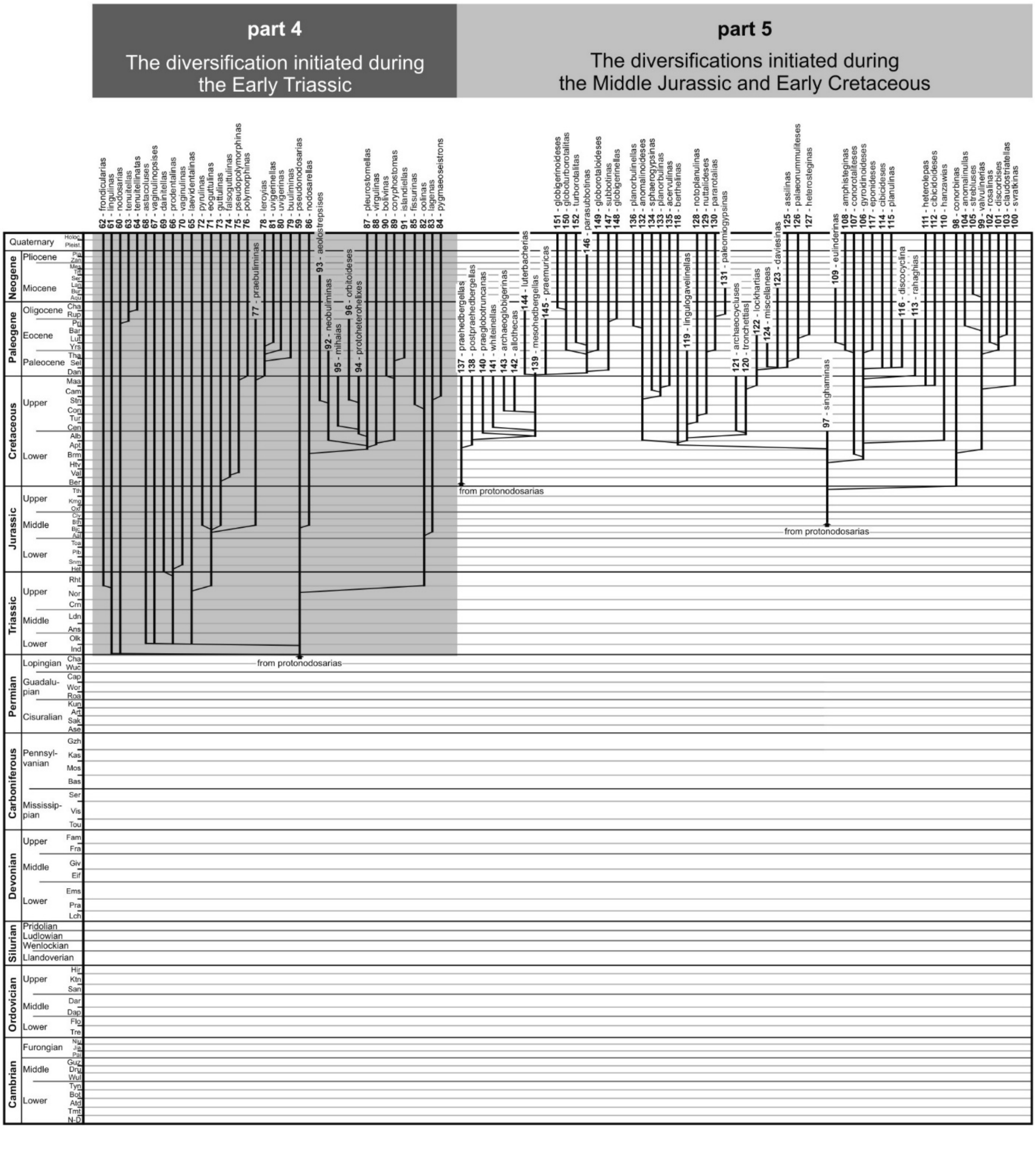


Fig. 1-3. Descendence and stratigraphical distribution of the foraminiferal nexuses recognized in this work. Each of the nexuses is numbered according to the descendence order (continued).

A new system of reference is proposed herein to be used in the declassified framework of the foraminiferal units. The unit of reference is one and any stage of relative morphological stability of a lineage; it is defined through the original description and/or figuration, which is termed as first reference. The original material can be further analyzed through subsequent studies, which could result in a dynamic database. This approach started with the definition of the concept of “hypodigm” by Simpson (1940, pp. 417–420) as part of the Aristotelian–Linnean classification, but the separation from the classical typological methodology is evident and most likely prevented its use at a wider scale in the following decades. The system of reference overcomes a major deficiency of the typological classification and nomenclature, namely that the “types” do not exist in nature and they are rather creations of the human minds. This practice had a detrimental effect in the past, which materialized especially in a tendency of many authors to illustrate specimens closer to the holotype, which resulted in a rather artificial impression of a low morphological stability of the genera and species of the Aristotelian–Linnean classification; this is mostly apparent in the opinion that a species is centered around the holotype.

Some of the units presented in this work present synonyms, which are separated into scientific and nomenclatural, according to their nature. Most of the scientific synonyms are objective synonyms, i.e. names applied to the same unit. A part of them are the result of attempts by some authors to find units within one unit that present a wide range of morphological stability. In other cases, the units considered synonyms are based on discrete test morphological features, which are considered trivial. Notably, the possibility that further descendence based studies to validate these units cannot be ruled out, but probably this will happen at a higher level of detail. A third category of synonyms is generated by errors in the evaluation of the effects of the fossilization process.

The nomenclatural synonyms are those generated by the provisions of the nomenclatural conventions. These are evaluated on a case-by-case basis, and in most cases rejected. A relatively small number of changes are accepted to avoid possible confusions with other foraminiferal units with resembling morphology.

Our data on the foraminiferal tests indicate that they are mineralized (e.g., agglutinated, calcitic, or aragonitic) in most cases and the units with an organic test (proteinaceous, chitinous, pseudochitinous) represent a minority. The foraminiferal tests, fossilized or of living units, provide the most data in the development of the group's declassification framework.

Traditionally, the description of one taxon in the Aristotelian–Linnean classification is the presentation of the morphological data of the test as a sum of features collected from throughout the known stratigraphical range of the respective taxon. The transition to units of significance in the declassified framework shows that the changes of the test morphological features must be followed, resulting in a dynamic morphology (e.g., Georgescu 2013a, 2013b, 2014, 2016, 2018b, 2021). Despite these recent advances, most of the data are those from the Aristotelian–Linnean classification, and they require further refinement as the original material is revisited and new material acquired. The dynamic morphology in this work is consistently but briefly apparent in the description of the branches and nexuses.

Every unit or group of units has a definite distribution range in space and time. The concept of stratigraphical range encompasses the known data of such a distribution in the case of every unit. At the fundamental level, the definition of the stratigraphical range as a unifying concept in describing the distribution of one unit in the fossil record, which is used in this work, is that given by Georgescu (2021). The two components of the stratigraphical range are given separately as "stratigraphical interval" and "geographical distribution", following the format used in the past by other authors, such as Loeblich and Tappan (1987).

The stratigraphical interval of the units presented in this work are defined between the best-known evolutionary occurrence (BKEO) event and best-known extinction (BKE) event, as defined by Georgescu (2017). It represents the interval corresponding to the global stratigraphical range of the respective units. The use of a terminology that includes the words 'appearance' and "datum" was avoided for reasons that do not need to be further elaborated upon. The stratigraphical units are primarily those of the Geological Time Scale 2004 by Gradstein et al. (2004) for the reasons already given by Georgescu (2021). Similarly, the geographical distribution is intended to represent the maximum known extension of the respective unit throughout its history.

Inferring the ancestor–descendant relationship between two units is the basic procedure in the development of the foraminiferal declassification framework. This involves the morphological study of the two taxa and the overlapping of their stratigraphical ranges. The result is the identification of the morphological features that do not present changes or show low magnitude modifications, with the potential of demonstrating the ancestry between the two units on one hand, and on the other, those features with conspicuous modifications, which document the divergence between the units.

Due to the large amounts of space required by the presentation of these data for each of the inferred ancestor–descendant relationships, together with the large number of units included in this work, the ancestry is presented in a somewhat shortened form. The presented morphological features are those that show considerable changes in the descendence from the ancestral unit. Notably, this system was developed by Kaiho (1998), one work that makes the transition from the Aristotelian–Linnean to the evolutionary classification.

The stratigraphical ranges of the ancestral and descendant units overlap in most cases. A gap spanning between less than one to maximum two stages was identified only in a small number of inferred ancestor–descendant relationships; such gaps are also mentioned.

One special case is that of the units that do not yet have a stratigraphical record, and therefore, are known only through living representatives or restricted to the Holocene. The methodology applied in such cases is to evaluate the morphology and recognize the development of certain features and the stability of others, consider for comparison the changes occurring in other lineages of the respective nexus and the to infer the ancestor–descendent relationship. Practically, this is a situation where additional technological advances are needed for a large-scale investigation of the units with younger stratigraphical ranges.

Most of the illustrations of the specimens presented in the plates come from a variety of works. The largest proportion is represented by specimens illustrated in the original reports, but a considerable number include those illustrated in subsequent reports. The name of the author, year of publication and position within the respective work is given for each of these specimens. The plate captions include a full acknowledgment of the work of the respective authors. They are used herein in a fair way and for the creation of a new work of science. Special thanks are for the permission to use photographs from the collections of the United States National Museum, Smithsonian Institution, Washington, D.C. and The American Museum of Natural History, New York (Dr. B.M. Hussaini). Additional thanks are for the permissions to use illustrated specimens from the Journal for Foraminiferal Research and Micropaleontology and their other publications. Special thanks are for Dr. K. Dewing (Paleontographica Canadiana), Dr. P. Esquier (TOTAL S.A.), Dr. Kroh (NHM Vienna Publishing House) for the permission to use foraminifer illustrations from their publications. I am grateful for the photographs provided by Drs. A. Almogi–Labin, B. Hayward, M. Hesemann, S. Lipson–Benitah, S. Rigaud, F. Schlagintweit, F. Siemensma and M. Septfontaine. I greatly appreciate the help of Dr.

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CHAPTER 2

SYSTEMATIC DESCRIPTIONS AND DESCENDENCE

This chapter contains systematic descriptions and the inferred descendence of the nexuses, branches and lineages in the foraminiferal declassification framework.

2.1. Nexus thuramminoideses

(Fig. 2.1)

Description. This nexus is the oldest in the history of the foraminifers and the beginning of its evolutionary history is marked by the development of an agglutinated test; notably, nothing is known about its non-testate ancestor. Most of the representatives are unilocular, with a laterally compressed test that is convex–concave to biconvex in edge view; the chambers present a circular outline, but they can be slightly elongated in the direction of growth in some multilocular tests. Multilocular tests occur later in the group history. The aperture consists of small interparticle openings within the wall and single and larger apertures are later developments. Most of the representatives have a free test and an attached mode of life is less frequent and was adopted later.
Stratigraphical interval: Lower Cambrian–Upper Miocene (Atdabanian–Tortonian).

Stalk: group of lineages *Thuramminoides* (Plate 1, Figure 1)

First reference: Plummer 1945, p. 218. Unit of reference: *Thuramminoides sphaeroidalis* Plummer 1945, p. 218, pl. 15, figs. 4–10.
Scientific synonym : *Luekatiella*-Mens and Zhigulina in Zhigulina 1999, p. 499.
Morphology. Test is free and unilocular, with a circular to subpentagonal–rounded outline. It is laterally compressed resulting in an ovate outline or with parallel sides in edge view, and less frequently convex–concave. Wall is relatively thick and consists of fine to moderately coarse agglutinated particles in an organic, clayey or siliceous matrix. The test interior communicates with the exterior through small pores that have an irregular outline and are situated between the agglutinated particles. Specimens with a small aperture situated on one side of the compressed test are also known but are rare.
Stratigraphical interval: Lower Cambrian–Upper Cretaceous (Atdabanian–lower Campanian). Geographical distribution: cosmopolitan.
Ancestry. *Thuramminoides* descended from an unknown unit, which is presumed to have been non-testate.

IOS-1: ramified lineage *Metamorphina* (Plate 1, Figure 2)

First reference: Browne in Browne and Schott 1963, p. 223. Unit of reference: *Webbinella tholus* Moreman 1933, p. 395, pl. 47, figs. 8, 10.
Test morphology. Test is attached, unilocular to multilocular, consisting of up to 13 hemispherical chambers; each chamber presents a convex–concave shape in edge view. In general, chambers do not present a distinct growth in size through ontogenetic development. One weak flange occurs around the attachment surface of each chamber. There is no apparent aperture. Test wall is agglutinated, consisting of fine to moderately coarse particles bounded by cement.
Stratigraphical interval: Ordovician–Lower Mississippian (Tremadocian–Tournaisian). Geographical distribution: USA (Indiana, Oklahoma), EU (Germany), Australia.
Ancestry. *Metamorphina* descended from *Thuramminoides* by adopting an attached mode of life and through the development of multilocular tests.

IOS-2: condensed lineage *Patellammina* (Plate 1, Figure 3)

First reference: Bell 1996, p. 97. Unit of reference: *Patellammina prona* Bell 1996, p. 97, fig. 8: L–M.
Test morphology. Test is free and multilocular, consisting of a short row of up to three chambers; each chamber presents a convex–concave shape in edge view. One small-sized aperture occurs on the concave side of each chamber. The wall is agglutinated, consisting of well-sorted and small-sized particles bounded by cement.
Stratigraphical interval: Lower Devonian (Emsian). Geographical distribution: Australia.
Ancestry. *Patellammina* descended from *Thuramminoides* through the development of multilocular tests and with an aperture on the concave face of each chamber.

IOS-3: condensed lineage *Teichertina* (Plate 1, Figure 4)

First reference: Palmieri 1994, p. 8. Unit of reference: *Crithionina teicherti* Parr 1942a, p. 107, pl. 1, figs. 9–10. Nomenclatural synonym: *Palmierina*-Özdikmen 2009, p. 244; it is not accepted herein because this foraminifer cannot be reasonably confused with the homonym brachiopod.

Morphology. The test is free and unilocular, spherical to laterally compressed. The wall consists of fine to moderately coarse agglutinated particles. There is no main aperture, and the test interior communicates with the exterior through large pores that do not present a preferential distribution pattern.

Stratigraphical interval: Lower Permian (Sakmarian–Kungurian). Geographical distribution: Australia.

Ancestry. *Teichertina* descended from *Thuramminoides* through the development of thicker tests that can present a spherical shape and larger pores.

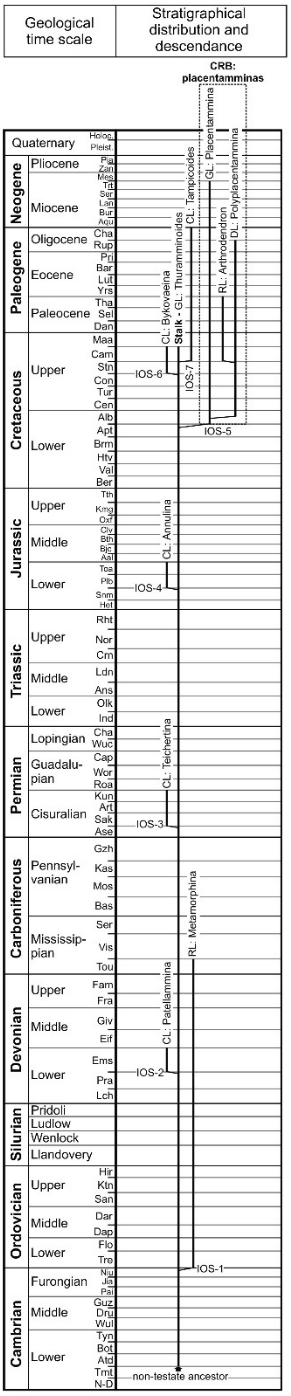

Fig. 2-1. Stratigraphical distribution and descendence of the representatives of the nexus thuramminoideses.

IOS-4: condensed lineage *Annulina* (Plate 1, Figure 5)

First reference: Terquem 1862, p. 432. Unit of reference: *Annulina metensis* Terquem 1862, p. 433, pl. 5, fig. 6.
Morphology. Test is free and unilocular, with a circular, rarely slightly elliptical outline. It is laterally compressed and has a convex–concave outline. Test periphery is broadly rounded in edge view. The wall consists of fine to moderately coarse particles in a siliceous matrix. There is no main aperture, but the test presents randomly distributed pores, which in general have a circular outline.
Stratigraphical interval: Lower Jurassic (Pliensbachian–Toarcian). Geographical distribution: EU (France, Germany).
Ancestry. *Annulina* descended from *Thuramminoides* through the evolution of larger pores over the lateral sides and a convex–concave shape in edge view.

IOS-5: complexly ramified branch-placentamminas

Description. This CRB was initiated with the evolution of unilocular tests with one small aperture produced mostly on a short neck, which is situated on the test's lateral sides in eccentric positions or at the periphery. The diversification continued with the development of multilocularity along one simple or ramified growth axis. The chambers can be slightly elongated in the direction of growth. The tests are mostly free, but units that are attached to the substrate occur later in the group history.
Stratigraphical interval: Cretaceous–Upper Miocene (Albian–Tortonian).

Group of lineages *Placentammina* (Plate 1, Figure 6)

First reference: Majzon 1943, p. 62, 151. Unit of reference: *Reophax placenta* Grzybowski 1898, p. 276, pl. 10, figs. 9–10.
Scientific synonyms: *Silicammina*-Vialov 1966a, p. 9; *Bogdanovicziella*-Myatlyuk 1970, p. 51.
Morphology. The test is free and unilocular, with a circular to slightly elliptical outline. It is laterally compressed resulting in parallel sides or less frequently convex–concave in edge view. Aperture is small and produced on a short conical or cylindrical neck; it can be situated on the test's lateral sides in eccentric positions or at the periphery. The wall consists of fine to moderately coarse agglutinated particles in an organic, clayey or siliceous matrix; it presents pores with an irregular shape in the spaces between the agglutinated particles.
Stratigraphical interval: Lower Cretaceous–Upper Miocene (Albian–Tortonian). Geographical distribution: EU (Austria, Hungary, Poland, Romania, Slovakia), Morocco, Ukraine.
Ancestry. *Placentammina* descended from *Thuramminoides* through the development of tests with a small aperture on the lateral sides.

Directional lineage *Polyplacentammina* (Plate 1, Figure 7)

First reference: this work; the name translates as "the multiple *Placentammina*". Unit of reference: *Reophax guttifera scalaria* Grzybowski 1896, p. 277, pl. 8, fig. 26.
Morphology. Test is multilocular and free, consisting of a series of successively added chambers along a slightly twisted growth axis. Chambers increased slowly in size as added, are laterally compressed, and each presents parallel sides or a convex–concave shape in edge view. In the early portion of the test, the chambers are attached on the lateral side and towards the periphery, whereas those of the adult portion present the attachment in peripheral position along the growth axis. The main aperture is single and situated at the anterior end of the last-formed chamber; the main aperture shape is variable circular to elliptical. Wall consists of fine, less frequently moderately coarse agglutinated particles and in general presents a smooth aspect.
Stratigraphical interval: Lower Cretaceous–Lower Oligocene (upper Albian–Rupelian). Geographical distribution: EU (Austria, Italy, Poland, Romania, Slovakia, Spain), Morocco, Ukraine, Caribbean region (Trinidad), North Atlantic Ocean.
Ancestry. *Polyplacentammina* descended from *Placentammina* through the development of tests with uniserial chamber addition.

Ramified lineage *Arthrodendron* (Plate 1, Figure 8)

First reference: Ulrich 1904, p. 138. Unit of reference: *Aschemonella carpathica* Neagu 1964, p. 582, pl. 27, figs. 1–3, text-figs. 1: 5–8, 2: 2–4, 3: 1–3, 4: 1–6.
Scientific synonym: *Aschemocella*-Vialov 1966b, p. 31.
Morphology. Test is multilocular and branched or not, each branch presenting uniserially arranged chambers along a slightly twisted growth axis. The chambers are laterally compressed, with parallel sides or convex–concave shape in edge view; earlier chambers have a circular outline, whereas those of the adult branched portion of the test are distinctly elongated in the direction of growth. Chamber attachment is in lateral–peripheral position between the earlier ones, with a trend to becoming peripheral in the last-formed ones. The aperture is terminal and has a circular to elliptical outline; it is single in the tests that do not present branching and multiple in branched tests. The wall consists of finely agglutinated particles in a dominant siliceous matrix.
Stratigraphical interval: Upper Cretaceous–Paleocene (Campanian–Thanetian). Geographical distribution: EU (Italy, Romania, Spain), USA (Alaska), Ukraine, North Atlantic Ocean.

Ancestry. *Arthrodendron* descended from *Polyplacentammina* through the development of branched tests and chambers elongated in the direction of growth in the later stage.

IOS-6: condensed lineage *Bykovaeina* (Plate 1, Figure 9)

First reference: Suleymanov 1969a, p. 36. Unit of reference: *Bykovaeina divulgata* Suleymanov 1969a, p. 36, text–fig. 1.

Morphology. Test is unilocular, consisting of one chamber with a circular outline in lateral view. It is laterally compressed and lens-shaped in edge view. Periphery is acute, with carinate aspect, straight to gently folded. Wall is agglutinated, consisting of fine to moderately coarse particles in a matrix that was probably siliceous. There is no apparent aperture.

Stratigraphical interval: Upper Cretaceous (Santonian–Campanian). Geographical distribution: Kazakhstan.

Ancestry. *Bykovaeina* descended from *Thuramminoides* through the development of tests with an angular and keeled periphery.

IOS-7: condensed lineage *Tampicoides* (Plate 1, Figure 10)

First reference: this work; the name translates as "[the foraminifer of the] Tampico [Embayment]". Unit of reference: *Trochamminoides irregularis* White 1928, p. 307, pl. 28, fig. 1.

Test morphology. Test is free and multilocular, consisting of chambers added along an irregular coiling axis; the chambers are discoidal, with convex–concave shape and of about the same size. Sutures are distinct and incised. There is no apparent aperture on any of the chambers. The wall is agglutinated, consisting of fine to medium coarse particles bounded by cement.

Stratigraphical interval: Upper Cretaceous–Upper Oligocene (Campanian–Chattian). Geographical distribution: cosmopolitan.

Ancestry. *Tampicoides* descended from *Thuramminoides* through the development of multilocular tests in which the chambers are added along an irregular axis.

2.2. Nexus hyperamminas

(Fig. 2-2)

Description. The initiation of this nexus is marked by the development of bilocular tests with a relatively large proloculus and an elongated second chamber. The diversification is mostly apparent in the development of tests in which the second chamber increases in width at a higher rate, a coiling that can be loosely planispiral or trochospiral and an attached mode of life. The test wall is mostly agglutinated, but some units developed a completely organic wall through the loss of the agglutinated component, and another one of secreted microcrystalline calcite.

Stratigraphical interval: Lower Cambrian (upper Atdabanian)–Holocene.

Stalk: group of lineages *Hyperammina* (Plate 1, Figure 11)

First reference: Brady 1878, p. 433. Unit of reference: *Hyperammina elongata* Brady 1878, p. 433, pl. 20, fig. 2. Scientific synonym: *Bactrammina*-Eimer and Fickert 1899, p. 603. Nomenclatural synonym: *Arhyperammum*-Rhumbler 1913, p. 351.

Morphology. Test is free and consists of one large proloculus followed by a second chamber that has a cylindrical aspect or presents a gentle distal tapering. The two chambers are well-differentiated, with a conspicuous suture or present a subtle transition. Aperture is single, situated at the distal end of the tubular chamber, and in general presents a circular outline. Wall consists of fine to moderately coarse agglutinated particles of different nature, which are firmly or loosely bound together with a cement that frequently is organic.

Stratigraphical interval: Lower Cambrian (upper Atdabanian)–Holocene. Geographical distribution: cosmopolitan.

Ancestry. *Hyperammina* descended from *Thuramminoides* mainly through the development of bilocular tests.

IOS-1: directional branch-arenosiphons

Description. The early representatives of this directional branch have a straight to slightly curved growth axis, whereas planispirally coiled tests in the later stage occur in some of the later representatives.

Stratigraphical interval: Upper Ordovician–Lower Devonian (Sandbian–Emsian).

Directional lineage *Arenosiphon* (Plate 1, Figure 12)

First reference: Grubbs 1939, p. 544. Unit of reference: *Arenosiphon gigantea* Grubbs 1939, p. 544, pl. 61, figs. 1–3.

Morphology. Test is free, without a distinct proloculus and with a straight to curved growth axis. The chamber is elongated in the direction of growth. Test exterior can present transversal constrictions, and branching occurs rarely. Aperture is situated at the distal end of the elongated chamber, with a constricted aspect in some specimens. Test wall consists of well-sorted agglutinated particles, mostly quartz minerals.

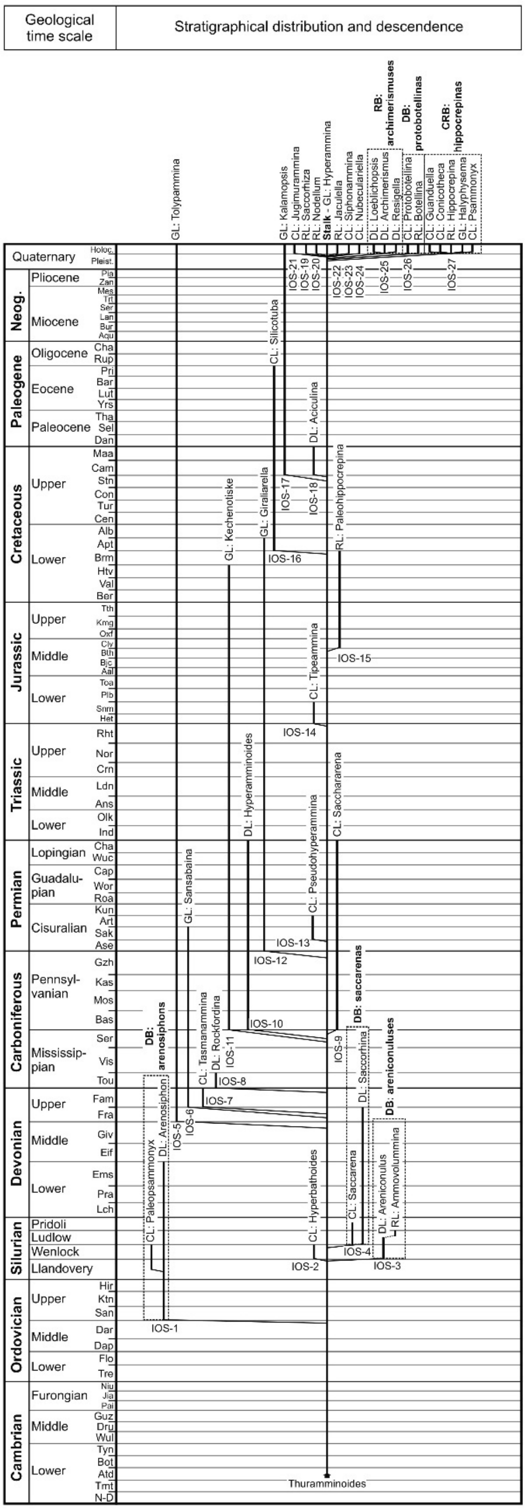

Fig. 2-2. Stratigraphical distribution and descendence of the representatives of the nexus hyperamminas.

Stratigraphical interval: Upper Ordovician–Lower Devonian (Sandbian–Emsian). Geographical distribution: USA (Illinois), EU (Baltic region).
Ancestry. *Arenosiphon* descended from *Hyperammina* through the reduction of the proloculus that became indistinct and the evolution of an elongated and slender second chamber.

Condensed lineage: *Paleopsammonyx* (Plate 1, Figure 13)

First reference: this work; the name translates as "the ancient *Psammonyx*". Unit of reference: *Psammonyx ceratospirillus* Mound 1968, p. 30, pl. 2, figs. 31–34, text–fig. 4.
Test morphology. Test is free, consisting of the small subspherical proloculus followed by the second elongated chamber that increases relatively rapidly in width. The second chamber is planispirally coiled forming one whorl and presents a

distinct lateral compression in the later ontogenetic stage. Aperture is elongated and constricted, at the distal end of the second chamber. Test wall is agglutinated, consisting mostly of inorganic particles bounded by cement.
Stratigraphical interval: Lower–Middle Silurian (upper Llandoverian–Wenlockian). Geographical distribution: USA (Indiana).
Ancestry. *Paleopsammonyx* descended from *Arenosiphon* through the development of a coiled second chamber, which is also laterally compressed in the later ontogenetic stages.

IOS-2: condensed lineage *Hyperbathoides* (Plate 1, Figure 14)

First reference: Ireland 1966, p. 224. Unit of reference: *Hyperbathoides schwalmi* Ireland 1966, p. 224, pl. 1, figs. 8–14.
Test morphology. Test is free, consisting of the subspherical proloculus followed by the second elongated chamber that presents two distinct morphological stages: it is irregularly coiled in the earlier ontogeny and uncoiled, with a straight growth axis, in the later stage. Aperture is simple, distal and with a constricted aspect. Test wall is agglutinated, consisting of fine and well-sorted clayey particles bounded by cement.
Stratigraphical interval: Middle Silurian (Wenlockian). Geographical distribution: USA (Kansas, Indiana).
Ancestry. *Hyperbathoides* is a descendant from *Hyperammina* through the development of an early stage of the elongated chamber with irregular coil.

IOS-3: directional branch-areniconuluses

Description. The early representatives of this directional branch have a straight second chamber, and an irregular and loosely trochospiral chamber in some of the later ones. The wall is agglutinated.
Stratigraphical interval: Middle–Upper Silurian (Wenlockian–lower Ludlowian).

Directional lineage *Areniconulus* (Plate 1, Figure 15)

First reference: Eisenack 1969, p. 200. Unit of reference: *Areniconulus bykovae* Eisenack 1969, p. 200, pl. 23, figs. 1–3, text–fig. 1.
Morphology. Test is free and consists of a small-sized proloculus followed by the second chamber that is elongated, presents weak constrictions and expands in width in the direction of growth. The growth axis changes direction throughout ontogeny conferring the test an irregular aspect, which is mostly apparent in the earlier portion. Aperture is simple and distal. Test wall consists of fine to moderately coarse agglutinated particles bounded by a cement of organic nature.
Stratigraphical interval: Silurian (Wenlockian–lower Ludlowian). Geographical distribution: EU (Baltic region).
Ancestry. *Areniconulus* descended from *Hyperammina* through the proloculus reduction and evolution of the elongated chamber that increases gradually in width.

Ramified lineage *Ammovolummina* (Plate 1, Figure 16)

First reference: Chernykh 1967, p. 39. Unit of reference: *Ammovolummina saumensis* Chernykh 1967, p. 41, pl. 3, figs. 2–4.
Scientific synonyms: *Serpenulina*-Chernykh 1967, p. 42; *Tolypamminoides*-Chernykh 1969a, p. 17; *Tubacera*-Chernykh in Pojarkov 1979, p. 42.
Test morphology. Test consists of the ovoid proloculus followed by the elongated second chamber that can be straight to curved or loosely trochospirally coiled. The second chamber increases in width at a relatively high rate resulting in a conical aspect. Aperture is simple, at the distal end of the elongated second chamber. The test surface can present weak growth lines. The test wall is agglutinated and consists of fine to moderately coarse particles bounded by cement.
Stratigraphical interval: Upper Silurian (Ludfordian). Geographical distribution: Russia.
Ancestry. *Ammovolummina* descended from *Areniconulus* through the development of a more twisted and elongated second chamber; notably, there is a gap spanning the lower Ludlowian in which the ranges of the two units do not overlap.

IOS-4: directional branch-saccarenas

Description. Directional lineage in which the tests branch distally and develop a wall of microcrystalline calcite with weak radial constrictions.
Stratigraphical interval: Upper Silurian–Upper Devonian (Ludlowian–Frasnian).

Condensed lineage *Saccarena* (Plate 1, Figure 17)

First reference: Chernykh 1969b, p. 138. Unit of reference: *Saccarena bitubulifera* Chernykh 1969b, fig. 2: J.
Morphology. Test is free and consists of the bulbous proloculus followed by the second chamber that presents a tubular aspect and is dichotomously branched. Aperture is simple in the early test portion before the second chamber branching and double in the adult part. The test wall is finely agglutinated, with the fine to moderately coarse grains bounded by siliceous cement.
Stratigraphical interval: Upper Silurian–Lower Devonian (Ludlowian–Emsian). Geographical distribution: Russia (Ural Mountains region).

Ancestry. *Saccarena* descended from *Hyperammina*, through the development of tests with a dichotomous branching in the distal portion.

Directional lineage *Saccorhina* (Plate 1, Figure 18)

First reference: Bykova 1955, p. 33. Unit of reference: *Saccorhina trivirgulina* Bykova 1955, p. 34, pl. 13, figs. 5–8.
Test morphology. Test is free and multilocular, consisting of the proloculus followed by uniserially added chambers in the early stage and bifurcating in the later one; the chamber from which the bifurcating portion of the test begins, has a subtriangular outline and is slightly flattened. The test presents transversal external constrictions in the early portion, which correspond to septa at the test interior. Aperture in the later stage is multiple, with simple openings at the distal ends of the bifurcated chambers. Test wall consists of microcrystalline calcite.
Stratigraphical interval: Upper Silurian–Upper Devonian (Ludlowian–Frasnian). Geographical distribution: Russia, EU (Germany, Poland).
Ancestry. *Saccorhina* descended from *Saccarena* through the development of multilocular tests with a wall of microcrystalline calcite.

IOS-5: group of lineages *Tolypammina* (Plate 1, Figure 19)

First reference: Rhumbler 1895, p. 83. Unit of reference: *Hyperammina vagans* Brady 1879a, p. 33, pl. 5, fig. 3.
Scientific synonym: *Serpulella*-Eimer and Fickert 1899, p. 674.
Test morphology. Test consists of a subspherical proloculus followed by a second chamber that is elongated and irregularly coiled. Aperture is single, simple and in the distal position. Test wall is agglutinated, consisting of particles bounded by various amounts of cement.
Stratigraphical interval: Upper Devonian (Frasnian)–Holocene. Geographical distribution: Cosmopolitan
Ancestry. *Tolypammina* descended from *Hyperammina* by adopting an attached mode of life and through the development of tests with an elongated and irregular second chamber.

IOS-6: group of lineages *Sansabaina* (Plate 1, Figure 20)

First reference: Loeblich and Tappan 1984b, p. 1159. Unit of reference: *Hyperammina elegantissima* Plummer 1945, p. 222, pl. 15, figs. 17–25.
Test morphology. Test is free and consists of a small proloculus that in some specimens is indistinct and a second elongated chamber that presents a weakly developed pseudoseptation, with the external constrictions that match those of the internal wall margin. The second chamber has a relatively low rate of increase in width and nearly parallel sides in the adult portion. Aperture is distal and presents a constricted aspect. The wall is agglutinated, consisting mostly of quartz particles bounded by a siliceous or organic cement.
Stratigraphical interval: Upper Devonian–Lower Permian (Famennian–Sakmarian). Geographical distribution: USA (Indiana, Kentucky, Montana, Ohio, Oklahoma), Australia, EU (Germany).
Ancestry. *Sansabaina* descended from *Hyperammina* through the reduction of the proloculus and development of a well-defined pseudoseptation in the second elongated chamber.

IOS-7: condensed lineage *Tasmanammina* (Plate 1, Figure 21)

First reference: Gutschick and Wuellner 1983, p. 312. Unit of reference: *Tasmanammina circumpeniformis* Gutschick and Wuellner 1983, p. 315, figs. 4: a–i, 7: a–f.
Morphology. Test is free and consists of one elongated chamber that can be straight to slightly curved. The chamber is closed at the proximal end with a tasmanitid algal cyst and open at the distal end where the simple aperture is situated. There is a considerable range of variability relative to the chamber width: in some specimens the width varies, whereas in others it remains rather constant. Test wall consists of relatively well-sorted quartz grains arranged in several layers; the agglutinated particles are bound with a siliceous cement.
Stratigraphical interval: Upper Devonian (Famennian). Geographical distribution: USA (Ohio).
Ancestry. *Tasmanammina* descended from *Hyperammina* through the loss of the proloculus and instead, the earliest portion of the test is sealed off with a tasmanitid algal cyst.

IOS-8: directional lineage *Rockfordina* (Plate 1, Figure 22)

First reference: Rauzer–Chernousova and Reytlinger 1986, p. 18. Unit of reference: *Reophax lacrymosa* Gutschick and Treckman 1959, p. 240, pl. 34, figs. 20–25, text–fig. 2: A–B.
Morphology. Test is free and consists of a relatively small proloculus that is slightly elongated in the direction of growth, followed by a second chamber that widens anteriorly. The second chamber presents well-developed transversal constrictions that correspond between the inner and outer wall margins, resulting in a conspicuous pseudoseptation. The segments between the two nearby constrictions are inflated posteriorly resulting in a pyriform aspect. Aperture has constricted aspect and is situated at the distal end of the test. The wall consists mostly of fine agglutinated particles, whereas particles of moderate size are rare and appear rather isolated at the wall surface.
Stratigraphical interval: Lower Mississippian (Tournaisian). Geographical distribution: USA (Indiana).
Ancestry. *Rockfordina* descended from *Hyperammina* through the development of tests with a well-developed pseudoseptation.

IOS-9: condensed lineage *Saccharарena* (Plate 1, Figure 23)

First reference: Loeblich and Tappan 1984b, p. 1159. Unit of reference: *Hyperammina spinescens* Cushman and Waters 1928a, p. 35, pl. 4, fig. 1.

Test morphology. Test is free, consisting of a large proloculus with a proximal spine, followed by a laterally compressed and elongated second chamber. The second chamber presents a discrete pseudoseptation and central longitudinal groove. Aperture is single and simple, and at the end of the second elongated chamber. Test wall consists of well-sorted and small-sized agglutinated particles, which are bounded by an organic or siliceous cement.

Stratigraphical interval: Pennsylvanian–Permian. Geographical distribution: USA (Texas), Australia, EU (Germany).

Ancestry. *Saccharаrena* descended from *Hyperammina* through the evolution of a discrete pseudoseptation, a central longitudinal groove on the second elongated chamber and a proximal spine attached to the proloculus.

IOS-10: directional lineage *Hyperamminoides* (Plate 1, Figure 24)

First reference: *Hyperamminella* Cushman and Waters 1928a, p. 36; it was changed to *Hyperamminoides* by Cushman and Waters (1928b, p. 112) to avoid synonymy with a homonym saccamminid foraminifer, and this change is accepted due to the relatively close morphologies of the two units. Unit of reference: *Hyperamminella elegans* Cushman and Waters 1928a, p. 36, pl. 4, figs. 3–4.

Test morphology. The test is free, consisting of a small proloculus followed by a second elongated chamber that has weak transversal or oblique constrictions, without a pseudoseptation. Aperture is simple and terminal. The wall consists of agglutinated small-sized and well-sorted particles, bounded by an organic or siliceous cement.

Stratigraphical interval: Pennsylvanian–Permian. Geographical distribution: USA (Texas), Australia.

Ancestry. *Hyperamminoides* descended from *Hyperammina* through the proloculus reduction, evolution of a strongly elongated second chamber with transversal or oblique constrictions and a small aperture situated in a terminal position.

IOS-11: group of lineages *Kechenotiske* (Plate 1, Figure 25)

First reference: Loeblich and Tappan 1984b, p. 1158. Unit of reference: *Hyperamminoides expansus* Plummer 1945, p. 223, pl. 16, figs. 1–6.

Test morphology. Test is free and consists of an indistinct proloculus followed by a second elongated chamber that expands rapidly in width. The second chamber can present weak transversal to oblique constriction without a pseudoseptation. Aperture is single and wide, at the distal end of the second elongated chamber. Test wall consists of fine to medium-coarse agglutinated particles bounded by a cement that was most likely of organic nature.

Stratigraphical interval: Pennsylvanian–Lower Cretaceous (Hauterivian). Geographical distribution: USA (Texas), Australia, EU (Austria, Germany, Romania), Russia.

Ancestry. *Kechenotiske* descended from *Hyperammina* through the reduction of proloculus size and development of a second elongated chamber that expands rapidly in width.

IOS-12: group of lineages *Giraliarella* (Plate 1, Figure 26)

First reference: Crespin 1958, p. 56. Unit of reference: *Giraliarella angulata* Crespin 1958, p. 56, pl. 9, figs. 1–5.

Test morphology. Test is free and consists of an indistinct proloculus followed by a second elongated chamber that presents weak growth lines but no pseudoseptation. The second chamber has four, rarely three longitudinal acute ridges that confer the transverse section a rectangular to triangular shape; the chamber surface between two nearby ridges has an excavated aspect. Aperture has a circular outline and is situated in a terminal position. Test wall is cement dominated, with well-sorted and small-sized agglutinated particles.

Stratigraphical interval: Permian–Lower Cretaceous (Aptian). Geographical distribution: Australia, EU (France, Italy, Romania).

Ancestry. *Giraliarella* descended from *Hyperammina* through a considerable reduction of the proloculus that became indistinct and the evolution of acute longitudinal ridges running along the second elongated chamber.

IOS-13: condensed lineage *Pseudohyperammina* (Plate 1, Figure 27)

First reference: Crespin 1958, p. 55. Unit of reference: *Pseudohyperammina radiostoma* Crespin 1958, p. 55, pl. 8, figs. 1–7.

Test morphology. Test is free, with an indistinct proloculus and elongated second chamber that rapidly increases in width in the juvenile stage and presents parallel sides in the adult portion. The second chamber surface has growth lines but no pseudoseptation is apparent. Aperture is circular, in a terminal position, can be surrounded by a rim and presents radial groves that can extend over the entire anterior face. Test wall consists of two layers of agglutinated particles; both layers are finely agglutinated and include considerable amounts of cement.

Stratigraphical interval: Lower Permian (Sakmarian–Artinskian). Geographical distribution: Australia.

Ancestry. *Pseudohyperammina* descended from *Hyperammina* through the reduction of the proloculus, evolution of a wide second chamber with constrict and rimmed terminal aperture with radial groves and development of a double test wall.

IOS-14: condensed lineage *Tipeammina* (Plate 2, Figure 1)

First reference: Neagu 2004, p. 382. Unit of reference: *Rhabdammina elliptica* Deecke 1884, p. 23, pl. 1, fig. 1: a–b.

Test morphology. Test is free and consists of a small proloculus followed by an elongated second chamber that is slightly laterally compressed and rapidly expands in width throughout ontogeny. Aperture is simple, at the distal end of the second chamber. Test wall consists of agglutinated particles of organic and inorganic nature bounded by a siliceous cement. There are two layers within the wall: the inner layer consists of parallelly arranged sponge spicules, whereas the outer one consists of a mixture of sponge spicules and quartz grains.

Stratigraphical interval: Lower Jurassic (Hettangian–Sinemurian). Geographical distribution: EU (France, Germany, Romania).

Ancestry. *Tipeammina* descended from *Hyperammina* through the reduction in proloculus size, development of a double-layered wall and second chamber with a rapid width increase throughout ontogeny.

IOS-15: ramified lineage *Paleohippocrepina* (Plate 2, Figure 2)

First reference: this work; the name translates as "the ancient *Hippocrepina*". Unit of reference: *Hippocrepina depressa* Vašíček 1947, p. 243, pl. 1, figs. 1–2.

Test morphology. Test is free, with indistinct proloculus and consists of an elongated chamber that rapidly increases in width. The test is laterally compressed, with weak and irregular transversal constrictions. Aperture is single and simple, at the anterior end of the test. Test wall consists of small-sized and well-sorted particles bounded in a cement of siliceous nature.

Stratigraphical interval: Middle Jurassic–Lower Cretaceous (Callovian–Barremian). Geographical distribution: EU (Austria, France, Germany, Italy, Poland, Romania, Slovakia, Spain), North America (USA, Canada), Morocco, Ukraine and North Atlantic Ocean.

Ancestry. *Paleohippocrepina* descended from *Hyperammina* through the reduction of the proloculus and development of the elongated second chamber that rapidly increases in width throughout ontogeny.

IOS-16: condensed lineage *Silicotuba* (Plate 2, Figure 3)

First reference: Vialov 1966a, p. 9. Unit of reference: *Hyperammina grzybowskii* Dylążanka 1923, p. 65.

Morphology. Test is free and consists of an elongated proloculus, which is followed by an elongated second chamber with tubular aspect and external transversal constrictions. The aperture is situated at the distal end of the second chamber. The wall has a smooth aspect and consists mostly of siliceous cement, with small and rare agglutinated particles.

Stratigraphical interval: Upper Cretaceous–Eocene (Aptian–Priabonian). Geographical distribution: EU (Poland, Germany, Slovakia), Ukraine.

Ancestry. *Silicotuba* descended from *Hyperammina* through the proloculus elongation, external constrictions that occur on the second chamber and an almost completely siliceous test wall.

IOS-17: group of lineages *Kalamopsis* (Plate 2, Figure 4)

First reference: de Folin 1882, p. 320. Unit of reference: *Kalamopsis vaillanti* de Folin 1882, p. 320. Nomenclatural synonym: *Arkalomopsum*-Rhumbler 1913, p. 352.

Morphology. Test is free and consists of the proloculus followed by an elongated chamber with a distinct pseudoseptation. The elongated second chamber presents distinct transversal constrictions that define posteriorly inflated segments. Internally, the wall extensions are rather irregular and do not correspond to the constrictions of the external wall margin. Aperture has a constricted aspect and is situated at the open end of the elongated chamber. Test wall is cement-dominated, whereas the small, agglutinated particles occur in isolation.

Stratigraphical interval: Upper Cretaceous (Campanian)–Holocene. Geographical distribution: Atlantic Ocean and Western Tethys (Morocco, Poland, Romania, Slovakia).

Ancestry. *Kalamopsis* descended from *Hyperammina* through the development of tests with well-developed pseudoseptation, irregular wall extensions and a cement-dominated wall.

IOS-18: directional lineage *Aciculina* (Plate 2, Figure 5)

First reference: Vialov 1966b, p. 34. Unit of reference: *Aciculina parva* Vialov 1966b, p. 34, pl. 1, figs. 1–3, pl. 2, fig. 3, text–fig. 1. Nomenclatural synonym: *Aciculella*-Vialov 1968, p. 3; this name change is not accepted herein because this foraminifer cannot be reasonably confused for the homonym gastropod.

Test morphology. The test is free, consisting of a small proloculus followed by a strongly elongated second chamber with a needle-like aspect. Aperture is situated at the open end of the second elongated chamber. Test wall contains considerable amounts of siliceous cement and rare agglutinated particles.

Stratigraphical interval: Upper Cretaceous (Campanian–Maastrichtian). Geographical distribution: Ukraine.

Ancestry. *Aciculina* descended from *Hyperammina* through the elongation of the second chamber and the change of the test wall composition from particle- to cement-dominated.

IOS-19: ramified lineage *Saccorhiza* (Plate 2, Figure 6)

First reference: Eimer and Fickert 1899, p. 670. Unit of reference: *Hyperammina ramosa* Brady 1879a, p. 33, pl. 3, figs. 14–15.

Scientific synonym: *Pseudoschizammina*-Saidova 1975, p. 24.
Morphology. Test is free and consists of a bulbous proloculus followed by a mostly dichotomously branched second chamber. The second chamber can present bulbous structures especially towards the distal part. Aperture is double or multiple, with simple openings at the distal ends of the branching second chamber. The wall consists of fine to moderately coarse agglutinated particles, with dominant sponge spicules that confer the test surface a "hairy" aspect; the agglutinated particles are bounded by an organic cement, less frequently a siliceous one.
Stratigraphical interval: Holocene. Geographical distribution: cosmopolitan.
Ancestry. *Saccorhiza* descended from *Hyperammina* through the development of tests with a dichotomously branched second chamber and a wall in which the siliceous spicules are relatively rare.

IOS-20: ramified lineage *Nodellum* (Plate 2, Figure 7)

First reference: Rhumbler 1913, p. 443, 473. Unit of reference: *Reophax membranacea* Brady 1879a, p. 53, pl. 4, fig. 9. Scientific synonyms: *Xenothekella*-Saidova 1970a, p. 145; *Chitinosiphon*-Thalmann and Bermúdez 1954, p. 53. Nomenclatural synonym: *Arnodellum*-Rhumbler 1913, p. 443, 473.
Test morphology. The test is free and bilocular, consisting of the proloculus followed by the elongated second chamber that increases slowly in diameter and presents transversal constrictions. Aperture is single, rounded, slightly constricted and situated at the distal end of the last-formed chamber. The wall is organic and proteinaceous.
Stratigraphical interval: Holocene. Geographical distribution: Atlantic Ocean, Pacific Ocean.
Ancestry. *Nodellum* descended from *Hyperammina* through the loss of the agglutinated component in the wall.

IOS-21: condensed lineage *Jugimurammina* (Plate 2, Figure 8)

First reference: Zheng in Zheng and Fu 2001, p. 682. Unit of reference: *Jugimurammina stellapertura* Zheng in Zheng and Fu 2001, p. 683, pl. 113, figs. 6–10, pl. 117, fig. 1.
Morphology. The test is free and consists of the proloculus and the second chamber that is elongated, has a tubular aspect and presents an external pseudoseptation. The lumen of the second chamber presents four to five serrated or crenulated longitudinal ridges. Aperture is single, with a stellate aspect that is the result of the development of internal longitudinal ridges. Test wall is agglutinated and consists of fine agglutinated particles bounded by a variable amount of cement.
Stratigraphical interval: Holocene. Geographical distribution: West Pacific Ocean.
Ancestry. *Jugimurammina* descended from *Hyperammina* through the development of a slender elongated second chamber with weak external pseudoseptation and internal longitudinal ridges that result in the formation of an aperture with stellate outline.

IOS-22: ramified lineage *Jaculella* (Plate 2, Figure 9)

First reference: Brady 1879a, p. 35. Unit of reference: *Jaculella acuta* Brady 1879a, p. 35, pl. 3, figs. 12–13.
Nomenclatural synonym: *Arjaculum*-Rhumbler 1913, p. 352.
Test morphology. Test is free, with an indistinct proloculus followed by an elongated chamber that increases slowly in width. The aperture is simple, at the distal end of the elongated chamber and presents a constricted aspect. Test wall consists of moderately coarse agglutinated particles.
Stratigraphical interval: Holocene. Geographical distribution: cosmopolitan.
Ancestry. *Jaculella* descended from *Hyperammina* through the reduction of the proloculus size and development of the second chamber that slowly increases in width throughout ontogeny.

IOS-23: condensed lineage *Siphonammina* (Plate 2, Figure 10)

First reference: Geslin and others 2004, p. 113. Unit of reference: *Siphonammina bertholdii* Geslin and others 2004, p. 113, pl. 2–4, figs. 1–19.
Test morphology. The test is free and consists of the proloculus that is lost in ontogeny due to its organic nature and the second chamber, which is elongated and has a tubular aspect. The aperture is simple, and at the distal end of the second elongated chamber that is bordered by a thin rim and surrounded by a ring-like structure that confers on it a constricted aspect. The wall is agglutinated, with calcite minerals, bounded by organic cement.
Stratigraphical interval: Holocene. Geographical distribution: Atlantic Ocean (off Bermuda).
Ancestry. *Siphonammina* descended *Hyperammina* through the development of a ring–like structure that surrounds the aperture and loss of the test mineralization over the proloculus.

IOS-24: condensed lineage *Nubeculariella* (Plate 2, Figure 11)

First reference: Awerinzew 1911, p. 8. Unit of reference: *Nubeculariella birulai* Awerinzew 1911, p. 8, fig. 3.
Test morphology. Test is attached, consisting of one chamber that in general has a tubular aspect; the closed end is slightly swollen, whereas the opened one is flared. Aperture is single and simple, at the flaring end of the test. The wall is agglutinated consisting of poorly sorted particles bounded by a pseudochitinous cement.
Stratigraphical interval: Holocene. Geographical distribution: Arctic Ocean.
Ancestry. *Nubeculariella* descended from *Hyperammina* by adopting an attached mode of life and development of tests with a smaller proloculus and a wider aperture that is bordered by a flaring wall.

IOS-25: ramified branch-archimerismuses

Description. This ramified branch includes units in which the test presents well-defined pseudoseptation with corresponding internal constrictions or well-developed septa; the wall is mostly agglutinated, but the agglutinated component can be lost.
Stratigraphical interval: Holocene.

Directional lineage *Archimerismus* (Plate 2, Figure 12)

First reference: Loeblich and Tappan 1984b, p. 1161. Unit of reference: *Hyperammina subnodosa* Brady 1884, p. 259, pl. 23, figs. 11–14.
Morphology. Test is free and consists of the subglobular proloculus followed by a second elongated chamber that has a tubular aspect. The second chamber presents external transversal constrictions and a well-defined pseudoseptation, with the defined segments presenting occasionally a slightly inflated proximal zone. The aperture has a constricted aspect and is situated at the anterior end of the second chamber. Wall is formed of fine to moderately coarse agglutinated particles bounded by relatively large amounts of cement. A thin internal organic layer of proteinaceous nature occurs.
Stratigraphical interval: Holocene. Geographical distribution: Atlantic and Pacific Oceans.
Ancestry. *Archimerismus* descended from *Hyperammina* mainly through the development of a pseudoseptation.

Directional lineage *Loeblichopsis* (Plate 2, Figure 13)

First reference: Hofker 1969, p. 19. Unit of reference: *Reophax cylindrica* Brady 1884, p. 299, pl. 32, figs. 7–9.
Test morphology. The test is free and subcylindrical, consisting of the proloculus followed by the second chamber that presents weak external transversal constrictions corresponding to well-developed internal septa. The aperture is small, rounded and constricted. The wall is agglutinated.
Stratigraphical interval: Holocene. Geographical distribution: North Atlantic Ocean, Indian Ocean.
Ancestry. *Loeblichopsis* descended from *Archimerismus* through the formation of a well-developed internal septation and a reduction of the transversal constrictions resulting in a test with subcylindrical external aspect.

Directional lineage *Resigella* (Plate 2, Figure 14)

First reference: Loeblich and Tappan 1984b, p. 1158. Unit of reference: *Nodellum moniliforme* Resig 1982, p. 977, pl. 1, figs. 1–2.
Morphology. The test is free, consisting of the proloculus followed by a second elongated chamber with well-defined pseudoseptation resulting in a uniserial aspect. The segment shape is variable, ranging from pyriform and inflated posteriorly to subcylindrical and with anterior and posterior quasi–hemispherical terminations. The aperture has a constricted aspect and is situated at the opened end of the second elongated chamber. The wall is proteinaceous.
Stratigraphical interval: Holocene. Geographical distribution: Pacific Ocean.
Ancestry. *Resigella* descended from *Archimerismus* through the development of the inner organic layer and the loss of the agglutinated component of the test wall.

IOS-26: directional branch-protobotellinas

Description. This directional branch shows the development of relatively large tests with constrictions developed at first within the test interior and then at the exterior. In addition, there is a distinct trend to develop an internal labyrinthine structure.
Stratigraphical interval: Holocene.

Condensed lineage *Protobotellina* (Plate 2, Figure 15)

First reference: Heron–Allen and Earland 1929a, p. 326. Unit of reference: *Protobotellina cylindrica* Heron–Allen and Earland 1929a, p. 326, pl. 2, figs. 9–13.
Morphology. Test is free, consisting of the proloculus and elongated chamber with tubular aspect. The second chamber has well-defined internal transversal constrictions that are weak or absent towards the external margin of the test. Aperture is constricted and situated at the distal end of the second chamber. Wall is relatively thick, consisting of agglutinated particles and sponge spicules, which are bounded by small amounts of cement. The agglutinated sponge spicules extend towards the test interior and across the aperture.
Stratigraphical interval: Holocene. Geographical distribution: Atlantic Ocean.
Ancestry. *Protobotellina* descended from *Hyperammina* through the development of tests with transversal constrictions that can have a correspondent at the external margin of the wall.

Ramified lineage *Botellina* (Plate 2, Figure 16)

First reference: Carpenter and others 1870, p. 443. Unit of reference: *Botellina labyrinthica* Brady 1881a, p. 48. Nomenclatural synonym: *Arbotellum*-Rhumbler 1913, p. 351.
Morphology. The test is free and consists of the proloculus followed by the second tubular chamber that presents distinct transversal constrictions on both inner and outer wall margins. Aperture is simple, at the distal end of the tubular

chamber; it can present a constricted aspect. Wall consists of inorganic particles and mostly sponge spicules in a siliceous or organic cement. The sponge spicules often extend into the test's internal cavities and together with additional particles result in a labyrinthic aspect to the test interior.
Stratigraphical interval: Holocene. Geographical distribution: cosmopolitan.
Ancestry. *Botellina* descended from *Protobotellina* mainly through the development of tests with constrictions on both sides of the wall.

IOS-27: complexly ramified branch-hippocrepinas

Description. This branch includes units with agglutinated walls that expand distally in diameter. The diversification is apparent in the loss of the wall's agglutinated component, the development of a loosely planispirally coiled second chamber and the development of a porous apertural plate; an attached mode of life was rarely adopted.
Stratigraphical interval: Holocene.

Ramified lineage *Hippocrepina* (Plate 2, Figure 17)

First reference: Dawson and Parker in Dawson 1870, p. 86. Unit of reference: *Hippocrepina indivisa* Dawson and Parker in Dawson 1870, p. 87, fig. 2. Nomenclatural synonym: *Arhippocrepum*-Rhumbler 1913, p. 351.
Test morphology. Test is free, with small-sized proloculus followed by a second elongated chamber with circular outline that expands rapidly in size. The second chamber has weakly developed external transversal constrictions. Aperture is situated at the distal end of the test, has a constricted aspect and can be surrounded by a delicate lip. Test wall is agglutinated, consisting mostly of quartz grains bounded by an organic or siliceous cement.
Stratigraphical interval: Holocene. Geographical distribution: cosmopolitan.
Ancestry. *Hippocrepina* descended from *Hyperammina* mainly through the development of tests with a smaller proloculus, a second chamber with a higher rate of width increase and an aperture bordered by a delicate lip.

Condensed lineage *Conicotheca* (Plate 2, Figure 18)

First reference: Gooday and others 2008, p. 416. Unit of reference: *Conicotheca nigrans* Gooday and others 2008, p. 416, figs. 14–16.
Test morphology. Test is free, with indistinct proloculus and an elongated chamber that increases in width anteriorly. Aperture is simple, at the distal end of the test, and has a constricted aspect. The test wall is organic.
Stratigraphical interval: Holocene. Geographical distribution: West Pacific Ocean.
Ancestry. *Conicotheca* descended from *Hippocrepina* through the development of tests with an organic wall.

Condensed lineage *Guanduella* (Plate 2, Figure 19)

First reference: Brönnimann and Zaninetti 1984, p. 65. Unit of reference: *Guanduella cribrata* Brönnimann and Zaninetti 1984, p. 65, pl. 6, fig. 12, text–fig. A: 1–3.
Test morphology. Test is free and unilocular, consisting of an elongated chamber with conical aspect; there is no apparent proloculus. Aperture is wide and situated at the distal end of the chamber; it is protected by a secreted plate with larger pores. Test wall consists of a mixture of particles of organic and inorganic provenance bounded by an organic cement.
Stratigraphical interval: Holocene. Geographical distribution: South Atlantic Ocean (off Brazil).
Ancestry. *Guanduella* descended from *Hippocrepina* through a considerable reduction of the agglutinated component of the test wall and the development of a secreted apertural plate.

Group of lineages *Halyphysema* (Plate 2, Figure 20)

First reference: Bowerbank 1862, p. 1105. Unit of reference: *Halyphysema tumanowiczii* Bowerbank 1862, p. 1105, pl. 53, fig. 3. Scientific synonym: *Gastrophysema*-Haeckel 1877, p. 24. Nomenclatural synonym: *Arhaliphysemum*-Rhumbler 1913, p. 352.
Test morphology. Test is attached, consisting of an elongated chamber that can be in the shape of an elongated cone, cylindrical or clavate and branched in occasional specimens. The test is attached to the substrate by a complex and subdivided basal root-like structure. Aperture is single to multiple in the case of the tests with distal branching. The wall is agglutinated, consisting mostly of sponge spicules, foraminiferal tests and inorganic particles bounded by cement.
Stratigraphical interval: Holocene. Geographical distribution: cosmopolitan.
Ancestry. *Halyphysema* descended from *Hippocrepina* by adopting an attached mode of life, development of a complex attachment structure and occasional branching in the distal portion of the test.

Condensed lineage *Psammonyx* (Plate 2, Figure 21)

First reference: Döderlein 1892, p. 145. Unit of reference: *Psammonyx vulcanicus* Döderlein 1892, p. 145. Nomenclatural synonym: *Arpsammonyxum*-Rhumbler 1913, p. 386.
Test morphology. Test is free, consisting of the proloculus followed by the elongated second chamber that increases rapidly in width; the second chamber is loosely planispirally coiled, forming up to two whorls. The test is laterally compressed and presents shallow constrictions in the adult portion. The aperture is oval-shaped, bordered by a thin rim and situated on the anterior face of the elongated chamber towards the periphery. The wall is agglutinated.

Stratigraphical interval: Holocene. Geographical distribution: West Pacific Ocean (off Japan).
Ancestry. *Psammonyx* descended from *Hippocrepina* through the development of a planispirally coiled second chamber with a higher rate of width increase.

2.3. Nexus rhabdamminas

(Fig. 2-3)

Description. This nexus initiated with the development of tests in which elongated extensions mostly with tubular aspect emerge from the fusiform proloculus. The diversification is marked by the development of tests with a larger proloculus that is often referred to as the central chamber, an increase in branch length and branching complexity and less frequently in their reduction. Most of the units present a free test, but an attached mode of life was adopted several times in the group's history. The wall is mostly agglutinated, with the development of a calcitic microcrystalline wall in one directional branch and a loss of the agglutinated component recorded in a relatively small number of later lineages.
Stratigraphical interval: Middle Cambrian–Holocene.

Stalk: group of lineages *Rhabdammina* (Plate 2, Figure 22)

First reference: M. Sars in Carpenter 1869, p. 60. Unit of reference: *Rhabdammina abyssorum* M. Sars in Carpenter 1869, p. 60. Nomenclatural synonym: *Arrhabdammum*-Rhumbler 1913, p. 351.
Test morphology. Test is free and consists of the proloculus that has an elongated to fusiform shape from which radiate two to five elongated tubular extensions with a circular transverse section. The radiating tubes can present distal branching. Apertures are simple openings at the ends of the radiating tubes. The wall consists of agglutinated particles, which are moderately coarse to coarse, and bounded by relatively small amounts of cement, which can be organic, ferruginous or siliceous.
Stratigraphical interval: Middle Cambrian–Holocene. Geographical distribution: cosmopolitan.
Ancestry. *Rhabdammina* descended from *Hyperammina* through the development of bidirectional to multidirectional growth and therefore, the proloculus does not occupy a peripheral position.

IOS-1: directional lineage *Lakites* (Plate 2, Figure 23)

First reference: Nestell and Tolmacheva 2004, p. 257. Unit of reference: *Lakites ordovicus* Nestell and Tolmacheva 2004, p. 257, pl. 1, figs. 1–4, pl. 10, fig. 1.
Scientific synonym: *Saccamminita*-Kaminski and Perdana 2019, p. 60.
Test morphology. Test is free and consists of an elongated and fusiform proloculus with two short extensions that in general are asymmetrically developed. Aperture is double, with simple openings at the distal ends of the two tubular extensions. Test wall is agglutinated, consisting of a variety of inorganic particles bounded by organic cement.
Stratigraphical interval: Lower Ordovician–Lower Silurian (Floian–Llandoverian). Geographical distribution: Russia, Saudi Arabia.
Ancestry. *Lakites* descended from *Rhabdammina* through the development of tests with two asymmetrically developed extensions from the fusiform proloculus.

IOS-2: condensed lineage *Paleoastrorhiza* (Plate 2, Figure 24)

First reference: this work; the name translates as "the ancient *Astrorhiza*". Unit of reference: *Astrorhiza constans* Bell 1996, p. 80, fig. 5: C–D.
Test morphology. Test is free, consisting of a large and flattened central chamber with subpolygonal outline from which five to six extensions with tubular aspect emerge in the same plane. Apertures are multiple, consisting of simple openings at the distal ends of the tubular extensions. The wall is agglutinated, consisting mostly of quartz minerals bounded with a relatively small amount of cement.
Stratigraphical interval: Lower Devonian (Emsian). Geographical distribution: Australia.
Ancestry. *Paleoastrorhiza* descended from *Rhabdammina* through the increase in the proloculus relative to the test size and an increase in the number of extensions with tubular aspects emerging from it.

IOS-3: condensed lineage *Cylindrammina* (Plate 2, Figure 25)

First reference: Bell 1996, p. 84. Unit of reference: *Cylindrammina stolonifera* Bell 1966, p. 84, fig. 6: A–B.
Test morphology. Test is free, consisting of an inflated central chamber with cylindrical-twisted shape from which emerge two to ten relatively thin tubular extensions that are not situated in the same plane. Apertures are multiple, with simple openings at the ends of the extensions with tubular aspects. Test wall is agglutinated, consisting mostly of small-sized and well-sorted quartz minerals.
Stratigraphical interval: Lower Devonian (Emsian). Geographical distribution: Australia.
Ancestry. *Cylindrammina* descended from *Rhabdammina* through the development of a large-sized central chamber that has a cylindrical-twisted shape and numerous extensions with tubular aspect.

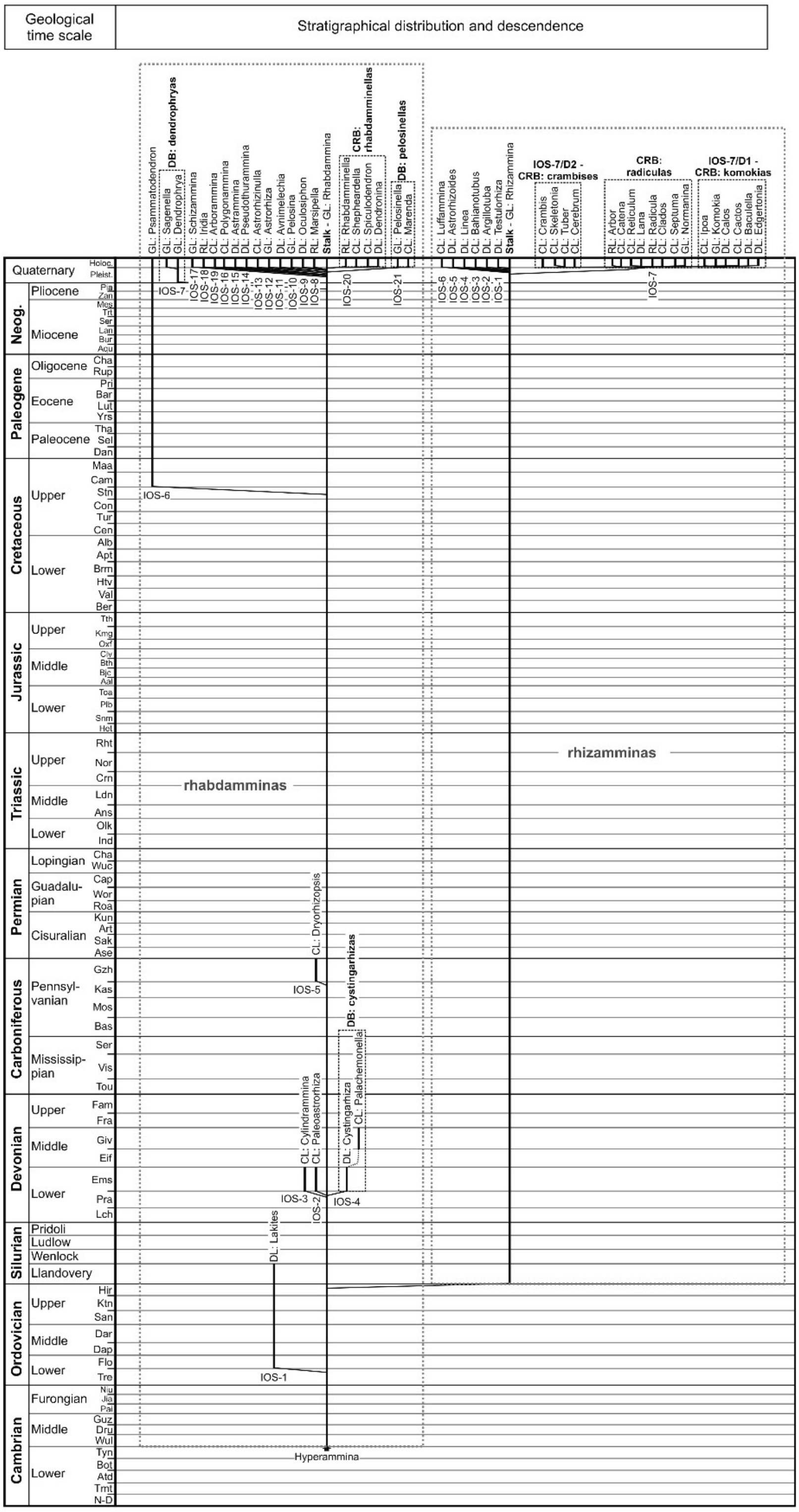

Fig. 2-3. Stratigraphical distribution and descendence of the representatives of the nexuses rhabdamminas and rhizamminas.

IOS-4: directional branch-cystingarhizas

Description. The most apparent morphological changes in this directional branch are the development of tests with a larger central chamber from which emerge tubular extensions, each bearing a distal aperture, followed by a modification of the wall from agglutinated to calcitic microcrystalline.
Stratigraphical interval: Lower–Middle Devonian (Emsian–Givetian).

Directional lineage *Cystingarhiza* (Plate 2, Figure 26)

First reference: Bell 1996, p. 81. Unit of reference: *Cystingarhiza mawsonae* Bell 1996, p. 82, fig. 5: I–J.

Test morphology. Test is free, consisting of a large-sized, spherical or subspherical central chamber from which emerge two to six extensions with tubular aspect; the tubular extensions are not situated in the same plane. Apertures are multiple, with simple openings at the distal ends of each of the tubular extensions. Test wall is agglutinated, consisting mostly of quartz minerals.
Stratigraphical interval: Lower Devonian (Emsian). Geographical distribution: Australia.
Ancestry. *Cystingarhiza* descended from *Rhabdammina* through the development of a spherical or subspherical central chamber and the development of extensions with tubular aspect that are not situated in the same plane.

Condensed lineage *Palachemonella* (Plate 2, Figure 27)

First reference: Beckman 1953, p. 265. Unit of reference: *Palachemonella torleyi* Beckman 1953, p. 265, Pl. A, figs. 1–14, pl. B, figs. 1–5, text–fig. 6.
Test morphology. Test is free and unilocular, with an irregular to slightly elongated chamber. Apertures are multiple, rounded to oval openings at the end of elongated, subcylindrical projections. Test wall is relatively thick and consists of microcrystalline calcite.
Stratigraphical interval: Middle Devonian (Givetian). Geographical distribution: EU (Germany).
Ancestry. *Palachemonella* descended from *Cystingarhiza* through the development of a wall of microcrystalline calcite. Notably, the stratigraphical intervals of the two units do not overlap and there is a gap spanning the lower part of the Middle Devonian which separates them.

IOS-5: condensed lineage *Dryorhizopsis* (Plate 2, Figure 28)

First reference: Henbest 1963, p. 23. Unit of reference: *Dryorhizopsis cadyi* Henbest 1963, p. 23, pl. 2, figs. 5–6.
Test morphology. Test is attached and consists of the proloculus from which radiate elongated extensions that attach to the substrate along their length and are longer in one direction and shorter in the opposite one; some of the extensions can branch distally. Apertures are multiple, represented by simple openings at the distal ends of the radial extensions. Test wall is agglutinated, consisting of small-sized particles bounded by a chitinous cement.
Stratigraphical interval: Upper Pennsylvanian (Gzhelian). Geographical distribution: USA (Texas).
Ancestry. *Dryorhizopsis* descended from *Rhabdammina* by adopting an attached mode of life and having branching occurring at the distal ends of the elongated extensions.

IOS-6: group of lineages *Psammatodendron* (Plate 2, Figure 29)

First reference: Norman in Brady 1881b, p. 404. Unit of reference: *Psammatodendron arborescens* Norman in Brady 1881b, p. 404.
Scientific synonym: *Dendrophryna*-Vialov 1996a, p. 9.
Test morphology. The test is attached and consists of a basal structure with ellipsoidal or irregular outline from which emerges a second tubular chamber that dichotomously branches upwards. Apertures are multiple, with simple openings at the distal ends of the branches. The wall is agglutinated, consisting mostly of quartz grains bounded by an organic cement.
Stratigraphical interval: Upper Cretaceous (Campanian)–Holocene. Geographical distribution: Western Tethys (Romania), North Atlantic Ocean.
Ancestry. *Psammatodendron* descended from *Rhabdammina* mainly through the development of tests in which the basal attachment structure is a vestige of the ancestral proloculus.

IOS-7: directional branch-dendrophryas

Description. This directional branch consists of units that adopted an attached mode of life and present a gradual increase in the branching complexity.
Stratigraphical interval: Quaternary (Pleistocene–Holocene).

Group of lineages *Dendrophrya* (Plate 3, Figure 1)

First reference: Wright 1861, p. 122. Unit of reference: *Dendrophrya erecta* Wright 1861, p. 122, pl. 4, fig. 4. Nomenclatural synonyms: *Ardendrophyrum*-Rhumbler 1913, p. 345.
Test morphology. Test is attached to the substrate with a hemispherical structure from which originates an elongated and irregularly branched chamber. Apertures are multiple, with simple openings situated at the ends of the tapering branches. Test wall consists of two layers; the inner layer is organic and pseudochitinous, whereas the outer one is agglutinated, consisting of organic and inorganic particles.
Stratigraphical interval: Quaternary (Pleistocene–Holocene). Geographical distribution: cosmopolitan.
Ancestry. *Dendrophrya* descended from *Rhabdammina* by adopting an attached mode of life and developing a hemispherical attachment structure that is a vestige of the ancestral proloculus.

Group of lineages *Sagenella* (Plate 3, Figure 2)

First reference: Brady 1879a, p. 41. Unit of reference: *Sagenella frondescens* Brady 1879a, p. 41, pl. 5, fig. 1.
Nomenclatural synonyms: *Sagenina*-Chapman 1900, p. 4 (this name change is not accepted herein because this foraminifer cannot be reasonably confused with the homonym bryozoan); *Arsagenum*-Rhumbler 1913, p. 345.