Morphology, wall composition and evolution of the Haplophragmoididae (agglutinated foraminifera)

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ABSTRACT

Agglutinated quartz-siliceous foraminifera predominate within the West Siberian province in the Upper Jurassic, Cretaceous and Palaeogene. A notable increase in the representatives of the Family Haplophragmoididae Maync, 1952 is observed. Four stages are distinguished in the development of this family from the Carboniferous to Recent. Each stage is subdivided into two substages by the first appearance of new genera, their enlargement and decrease, or extinction.

INTRODUCTION

The investigated genera were identified by Podobina (1975, 1978) from the Superfamily Lituolidea Reuss, 1861, as the Family Haplophragmoididae Maync, 1952 of the new superfamily Haplophragmiidea Cushman, 1927 according to their wall composition and microstructure as well as other morphological features (coiling mode, chamber internal contours and others). The test of fossil representatives of this superfamily possesses a quartz-siliceous agglutinated wall. The morphology of this test depends on the chemical content. On the basis of the morphological characteristics of the tests indicated above, we propose to attribute the new superfamily to the Order Ammodiscida along with the previous lituolids and ammodiscids. The redefined superfamily Lituolidea consists of fewer genera in comparison to the Haplophragmiidea. It is represented by morphologically more complex tests with labyrinthic chambers, and their wall is of the calcareous secreted-agglutinated type with microgranular microstructure, rarely of the agglutinated type with rare-, middle- and completely agglutinated microstructure. Calcareous material predominates in the composition of the agglutinated material and cement in tests of the Lituolidea. This superfamily reached its acme in the Late Cretaceous and was found mainly in carbonate deposits. Podobina (1978, 1993) succeeded in investigating specimens of typical *Lituola nautiloidea* Lamarck and showed that this test had a secreted-agglutinated type of calcareous wall with a so-called microgranular microstructure.

The dependence of size and composition of agglutinated material on the character of sediment substratum is recognised. Tests found in sediments with an increased content of carbonate material include mainly calcite grains. The cement is also mainly calcareous. In tests from terrigenous sediments the agglutinated material is quartz and other stable minerals, glued by siliceous cement. The change in the wall composition and the microstructure of the agglutinated shells was used for facies investigations and palaeogeographical reconstructions (Podobina, 1966, 1995).

It should be noted that in Recent agglutinated tests cement is of organic origin, but during fossilisation the cement changed from organic to siliceous in terrigenous sediments where carbonate material was absent. We use the conventional term "quartz-siliceous" for the fossil agglutinated wall with siliceous cement and quartz agglutinate.

It is significant that many tests of genera such as *Trochamminoides, Labrospira, Cribrostomoides,* and others are planispirally enrolled but seldom coiled in a streptospiral arrangement. There is reason to believe that the Subfamily Recurvoidinae Alekseitchik, 1973 belongs to the Family Haplophragmoididae Maync, 1952. In our opinion, the subfamily Cyclammininae Marie, 1941 can be retained in the Haplophragmoididae because it is impossible to separate the following Late Cretaceous genera of Cyclammininae such as *Alveolophragmium, Cyclammina* from *Haplophragmoides, Asanospira* and other genera of the Haplophragmoidinae.

Methods

The composition, wall microstructure, and internal structure of the tests were investigated by the polishing method and studied with a polarising microscope and by the examination of complete tests in petrographic immersion liquids (Podobina, 1963, 1978). Almost all the genera of the family Haplophragmoididae have been investigated in

In: Hart, M.B., Kaminski, M.A., & Smart, C.W. (eds) 2000. Proceedings of the Fifth International Workshop on Agglutinated Foraminifera. *Grzybowski Foundation Special Publication*, 7, 397–401.

this manner. The grain composition and the agglutinate:cement ratio were determined on oriented thin-sections with a polarising microscope. This provided an opportunity to establish middle- or, more often, wholly agglutinated microstructure of agglutinated type of the wall in many genera of the studied family (Podobina, 1978, 1993).

Thanks to the introduction of numerical indices by the differentiation of the degree of evoluteness in planispiral shells it is possible to separate closely related generic taxa (Podobina, 1978). These indices provide the opportunity to separate similar genera such as *Trochamminoides*, *Labrospira*, *Haplophragmoides*, and others.

RESULTS AND DISCUSSION

The principal changes in the test morphology of the Haplophragmoididae are characterised by three features: the nature of the shell evoluteness, the change in apertural position, and the degree of complexity of the wall structure. By studying these forms from material collected in the territory of Western Siberia as well as from samples provided by scientists from many regions of the world, we came to the conclusion that the appearance of the first representatives of this family is in the Late Palaeozoic. Its radiation in the Late Jurassic, Cretaceous, and Palaeogene and its progressive decrease in numbers and diversity during the Neogene and the Quaternary are also observed. Reasons for the increasing number of individuals and specific diversity of individual genera in the Jurassic, Cretaceous, and Palaeogene periods are thought to be the favourable environmental conditions in epicontinental Boreal basins widely distributed at this time. As a result, these organisms serve as the basis for the studied foraminiferal assemblages. As Kh. Saidova's (1976) investigations have shown, some representatives of the family inhabit various depths in present-day marine basins. However, their diversity is insignificant. Morphologically more simple and long-lived genera such as *Labrospira*, *Haplophragmoides*, and *Recurvoides*, are the most adaptable to different conditions of existence in the modern basins.

Using the concept of parallel development, we have identified the appearance of definite morphological features at certain stratigraphic levels. These features are simultaneously shared by different species belonging to several genera, which led to considerable changes in their external appearance. Internal morphological features remained more stable, allowing separation of similar generic taxa of a given family after defining their composition and stratigraphic distribution. It is apparent that genera whose appearance changed considerably at definite stratigraphic levels can acquire some morphological features of their ancestors. Thus, the relatively large multichambered evolute shells of several genera (*Labrospira*, *Recurvoides*) typical for the Late Jurassic and Early Cretaceous of Western Siberia are represented in the Late Cretaceous by small, more compactly coiled forms with smaller numbers of chambers. Increasing size, evoluteness of the test, as well as the number of chambers in the final whorl [*Labrospira crassimargo* (Norman), *Recurvoides contortus* (Montfort) and others] are observed in Recent deposits of the Northern seas (Figure 1).

The principal morphological characters that distinguish the Family Haplophragmoididae from the similar Lituolidae and other families of the Order Ammodiscida are the following: chemical composition (quartz-siliceous), wall type (agglutinated), and the coiling of the spiral portion (from hemievolute to involute planispiral or streptoid) of the multichambered test. Agglutinated material is mainly quartz grains held together by siliceous cement, and this is typical for all fossil representatives of this family.

According to the American classification the following set of features was used for distinguishing the Superfamily Lituolaceae within the Suborder Textulariina: the multichambered character of tests, the spiral and straightened disposition of the chambers, their simple or complex structure; and a wall that is agglutinated, variable in composition, with calcareous, siliceous, and ferruginous cement (Loeblich & Tappan, 1964, 1987).

The scope of the Superfamily Lituolacea has been considerably widened by the inclusion of considerable variation in the character of spiral coiling and in the test structure, and in the diversity of the wall composition. The Family Lituolidae was established on the basis of the mode of coiling but also by the structure of the agglutinated wall. Tests having, in our opinion, secreted-agglutinated, and agglutinated types of calcareous wall, and agglutinated type of quartz-siliceous wall are also included. Alekseichik-Mitskevich (1973) proposed a classification of the Family Lituolidae using more specific characters. She considered the known difference between the wall types and separated agglutinated tests from microgranular calcareous ones (secreted-agglutinated, in our terminology) into the separate Family Haplophragmiidae Cushman, 1927. Supporting and developing Alekseichik-Mitskevich's idea, Podobina separated haplophragmoid tests with agglutinated quartz-siliceous wall into the Superfamily Haplophragmiidea. It was suggested that one had to take into account the composition of agglutinated material, being the result of the selected ability of protoplasm as one of basic taxonomic features of the superfamily. Quartz or other siliceous compounds (less than 25 %) predominate as agglutinate in the shell wall; organic (changed to siliceous) cement usually connects them. Organic cement, occupying a subordinate position in comparison to the agglutinated material, is observed in modern haplophragmoid genera.

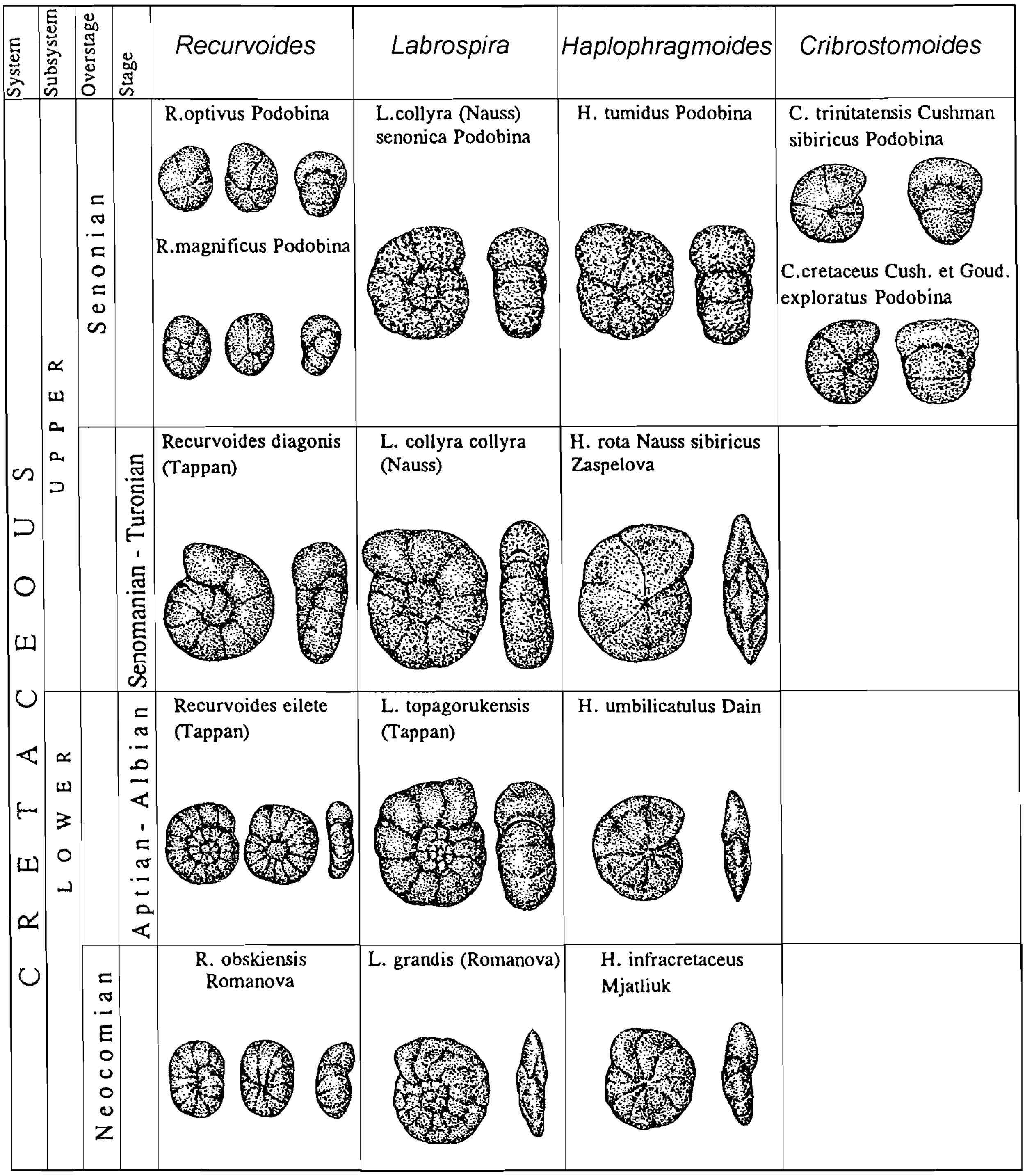

Figure 1. Lines of parallel development among some genera of Haplophragmoididae during the Cretaceous.

Stages of development in the family Haplophragmoididae

Four stages can be distinguished in the development of the Haplophragmoididae. The first includes the period from the Carboniferous up to and including the Dogger. The first appearance of the planispiral genera *Trochamminoides*, *Labrospira*, and *Haplophragmoides* characterises this important stage in the development of the family. It is characterised by slow rates in the evolution of the first relatively primitive genera of this foraminiferal group (Figure 2).

Two substages are identified within the first stage. The beginning of the existence of planispiral genera: *Trochamminoides*, *Labrospira*, *Haplophragmoides*, and streptospiral *Recurvoides* are typical of the first substage (Carboniferous-Permian). The second substage (Triassic-Dogger) is characterised by the appearance of the first representatives of the genus *Thalmannammina*, probably since the Triassic .

The second stage – the Late Jurassic and Early Cretaceous – is characterised by the wide development of previously known genera - *Labrospira, Haplophragmoides, Recurvoides* and the appearance of the genus *Unitendina*. Two substages are recognised within this stage. The first of them (Late Jurassic) is marked by the further development of the pre-existing genera, including *Labrospira, Haplophragmoides, Recurvoides*. Representatives of *Haplophragmoides* are less diverse, but showed a significant increase in some provinces.

The third stage is from the Late Cretaceous to the Miocene. The appearance of such genera as *Cribrostomoides, Adercotryma, Recurvoidella, Asanospira, Hemicyclammina, Cyclammina* and others is a development within the first substage (Late Cretaceous), while the next substage is seen by the specialisation of features of the coiled, predominantly planispiral, genera. The second Palaeogene substage differs by the intensive development of the existing genera *Haplophragmoides, Labrospira, Cribrostomoides, Asanospira, Thalmannammina, Adercotryma, Recurvoidella, Cyclammina* and the appearance of new genera, such as *Budashevaella* and others in several subfamilies. Simultaneously, the expansion of such genera as *Cyclammina* and *Alveolophragmium*, which appeared in the Cretaceous, are typical.

The fourth stage – Miocene to Recent – in the development of the Haplophragmoididae is distinguished by the appearance of only new species. In its first Miocene substage the genus *Cyclammina* reached its acme in the North Pacific area. The second substage, including the period from the Pliocene up to the Recent is marked by the continuation of earlier genera such as *Trochamminoides, Labrospira, Haplophragmoides, Cribrostomoides, Cyclammina, Alveolophragmium* and others. The whole fourth stage is characterised mainly by the continuance of almost all genera excluding those which completed their development earlier. The ecology of some Haplophragmoididae genera is known from present-day oceans (bathyal and abyssal zones). In epicontinental basins of the Boreal and Arctic belts they developed at depths not more than 200 m, where they attain both large size and large numbers of individuals (Figure 2).

CONCLUSIONS

Several genera have been separated by Podobina from the Superfamily Lituolidea Reuss, 1861 as the Family Haplophragmoididae Maync, 1952 of the new Superfamily Haplophragmiidea Cushman, 1927 taking into account the chemical content of the quartz-siliceous agglutinated wall. Four stages in the development of the Haplophragmoididae can be identified. The first stage is that of the appearance of new genera and limited speciation; the second and the third ones are marked by the appearance and diversification of many genera. The fourth stage is marked by some extinctions and a slow rate of speciation.

Substages can be identified in each stage and are characterised by the appearance of new genera or by the further development of some pre-existing genera. They correspond to boundaries of epochs, particularly the Late Jurassic, the Early and Late Cretaceous, the Palaeocene and others.

ACKNOWLEDGEMENTS

The senior author thanks Prof. Malcolm Hart and the Grzybowski Foundation for financial support to attend IWAF-5 held in Plymouth, U.K.

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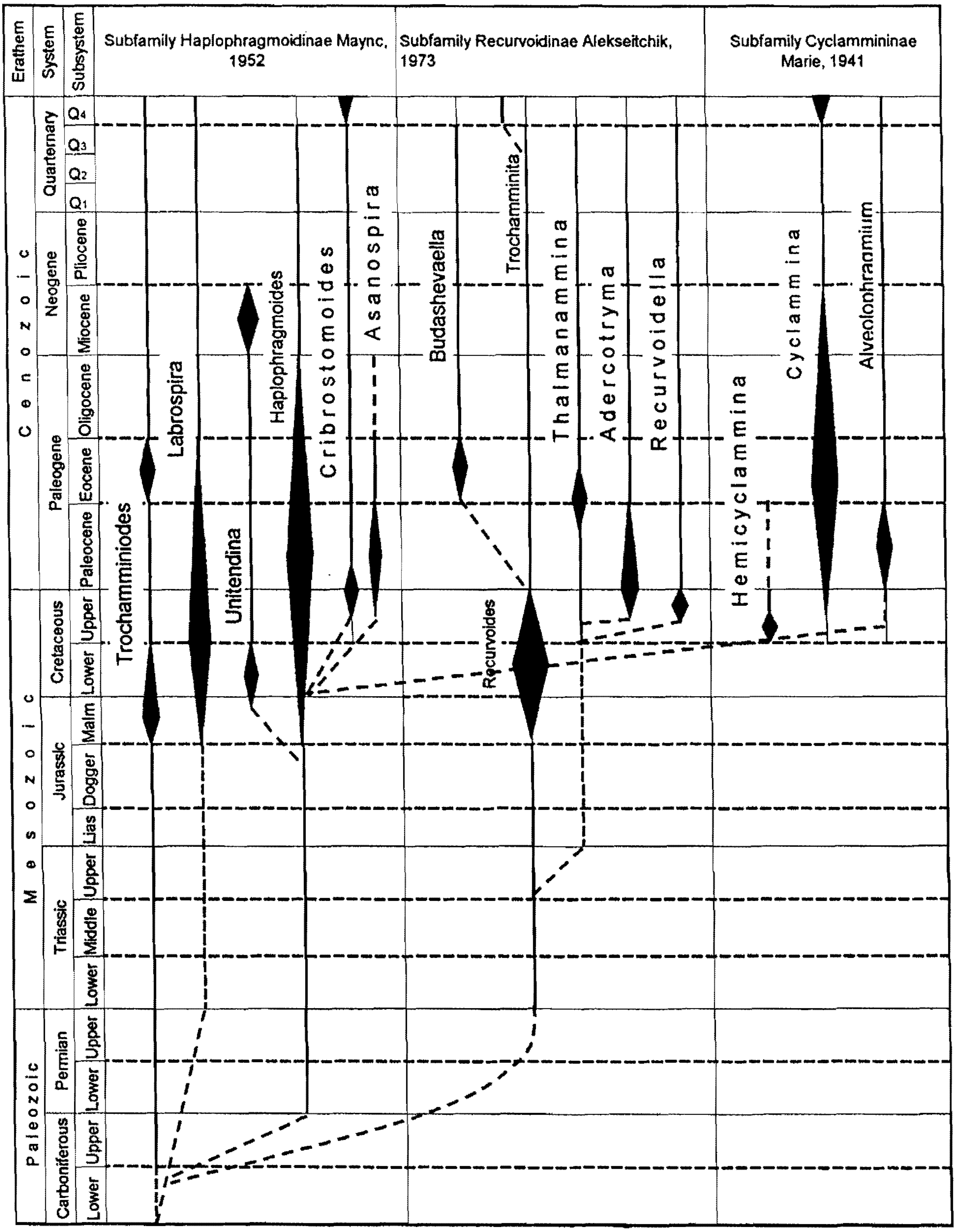

Figure 2. Proposed phylogenetic scheme of the Family Haplophragmoididae Maync, 1952.