

## Notes on the Phylogeny and Classification of the Superfamily Verbeekinoidea : Studies of the Permian Verbeekinoidean Foraminifera- I

Ozawa, Tomowo  
Faculty of Science, Kyushu University

<https://doi.org/10.5109/1543907>

---

出版情報 : 九州大学理学部紀要 : Series D, Geology. 20 (1), pp.17-58, 1970-01-25. Faculty of  
Science, Kyushu University

バージョン :

権利関係 :



## Notes on the Phylogeny and Classification of the Superfamily Verbeekinoidea

(Studies of the Permian Verbeekinoidean Foraminifera-I)

By

Tomowo OZAWA

### Abstract

This paper is the introductory part of a series of paper entitled "Studies of the Permian Verbeekinoidean Foraminifera" and deals mainly with the phylogeny and classification of the superfamily. Diagnoses of all the genera of the Verbeekinoidea are given on the basis of the latest knowledge including new paleontologic data. Some comments are given to the genera *Lepidolina* and *Colania*, the validity of which has been still in dispute. New ideas on the phylogenetic relationship among the Neoschwagerinid species are also presented.

### Contents

	Page
Introduction .....	17
Historical review of the studies of the Verbeekinoidea .....	18
Paleoecology .....	22
Distribution .....	26
Dimorphism and polyvalence .....	30
A. Dimorphism .....	30
B. Polyvalence .....	32
Evolution of shell structure and phylogeny .....	33
A. Evolution of shell structure .....	33
B. Phylogeny .....	37
Classification of Verbeekinoidea .....	43
References .....	52

### Introduction

The superfamily Verbeekinoidea are a foraminiferal group which characteristically occurs from the Permian carbonate facies of the Tethys Sea Region, and have been dealt with by many biostratigraphers as useful guide fossils not only for the intercontinental but also interregional correlation of the Permian System of the Region. Morphologically species of this group have a very complicated shell as in the Alveolinids of the post-Upper Cretaceous ages.

Since GEINITZ's first description of "*Fusulina*" *verbeeki* from Sumatra in 1874, hundreds of papers have been published on the superfamily from the biostratigraphical, paleozoogeographical and paleontological standpoints. Nevertheless phylogenetic relationship and classification of the Verbeekinoidea remain as one of the most disputable parts in the studies of the Fusulinina. Taking the genus *Lepidolina* as an example, many different opinions have been expressed on the generic validity, and phylogenetic and stratigraphic problems in relation to *Yabeina* (LEE, 1933; YABE, 1948, 1964, 1966; KANMERA, 1954, 1957; MINATO and HONJO, 1959; HANZAWA and MURATA, 1963; TORIYAMA, 1967; ISHII and NOGAMI, 1964; HASEGAWA, 1965; KAHLER and KAHLER, 1966; etc.). There is not as yet general agreement about these problems. This is primarily due to the insufficient original description and scarcity of the later paleontologic study of the type specimens themselves. For these reasons it has been hoped to restudy the Verbeekinoidean species in detail from pure paleontologic standpoint. For these several years, I have been specially interested and engaged in evolutionary development of the group and examined rich material from many localities in the Japanese Islands, Southeast Asia and Pacific Northwest. In the course of this study I have found some important facts on the phylogenetic relation among the Neoschwagerinid species.

Before going into descriptive study of species, it seems necessary to revise the definition of several genera and to give a revised classification of the superfamily Verbeekinoidea. The main and ultimate aim of this serial study is to clarify the phylogeny among the Verbeekinoidean species through the descriptive studies of fossil populations of each species. Detailed descriptions of species of the superfamily are to be published in succeeding papers.

*Acknowledgements.*—I wish to express my sincere gratitude to Professor Ryuzo TORIYAMA and Associate Professor Kametoshi KANMERA for their invaluable advice and encouragement, for giving me an opportunity of studying their collections from the Akiyoshi Limestone and Kuma Massif, Japan, and for their kindness in reading the manuscript. I am much indebted to Professor Emeritus Teiichi KOBAYASHI who kindly gave me an opportunity to examine OZAWA's collections from the Akasaka and Akiyoshi Limestones. My sincere thanks are extended to Drs. Ken-ichi ISHII and Yasuo NOGAMI who gave me instructive advice and afforded me an opportunity of examining their collections from the Sisophon and Battambang Limestones in Cambodia. Deep thanks are also extended to Professors Tatsuro MATSUMOTO and Rokuro MORIKAWA, Associate Professor Tsugio SHUTO, Drs. Hisayoshi IGO, Juichi YANAGIDA, Itaru HAYAMI and Toshio KOIKE for their kind help and advice in various ways. I am indebted to Misses Seiko HAYAKAWA and Yuko WADA who have assisted me in preparing some illustrations and typescript.

### Historical review of the studies of the Verbeekinoidea

Studies of the Verbeekinoidea go way back to GEINITZ's first description of *Fusulina verbeeki*, the type-species of *Verbeekina* STAFF, 1909 from the Middle

Permian limestone of Padang Highlands, Boekit Besi, Sumatra in 1876. Since then, almost a century has passed and hundred works have been published on this foraminiferal group. Several papers were in fact epoch-making in the study of the Verbeekinoidea. For better understanding the present situation of the study it seems worth-while to review historical studies of the Verbeekinoidea.

DAWSON discovered *Loftusia* (= *Yabeina*) *columbiana* from Marble Canyon in British Columbia already in 1879. In 1883, SCHWAGER described *Schwagerina* (= *Verbeekina*) *verbeeki*, *Schwagerina* (= *Metadoliolina*) *lepida*, *S.* (= *M.*) *lepida* var. *ellipsoidalis* and *S.* (= *Neoschwagerina*) *craticulifera* with five schwagerinid species from China and Japan. The last named species was later designated by YABE (1903) as the type-species of *Neoschwagerina* YABE. SCHWAGER's specimens were recently restudied by NOGAMI (1965) based on the up to date knowledges.

During the first decade of this century, two important genera of the Neoschwagerinidae were introduced. VOLZ (1904) established *Sumatrina* based on *Sumatrina annae* VOLZ from the Middle Permian of Sumatra. HAYDEN (1909) introduced *Cancellina* as a subgenus of *Neoschwagerina*. His original description of the type-species of *Cancellina*, *Neoschwagerina primigena* HAYDEN from the Bamian Limestone of Afghanistan was insufficient, resulting in that this made some later authors misunderstand the diagnosis of the genus. He described many Verbeekinoidea species including *Yabeina inouyei* (= *Y. globosa*), *Neoschwagerina* (*Sumatrina*) *multiseptata*, *Doliolina ovalis* and *D. compressa*, which are the type-species of *Yabeina* DEPRAT, *Lepidolina* LEE, *Misellina* SCHENCK and THOMPSON and *Brevaxina* SCHENCK and THOMPSON, respectively. He was the first who gave an opinion on the phylogeny of the superfamily based on the similarity of shell morphology and their stratigraphic order of occurrence.

Similar monographs on the fusuline foraminifera from Indo-China were also presented by COLANI (1924) and GUBLER (1935). OZAWA (1925a, 1925b) published two important papers on the Fusulinina, of which the first (1925a) was a comprehensive and epoch-making work on the paleontology of the fusuline foraminifera. It is not too much to say that the essential framework of the phylogenetic relation among the verbeekinoidean species was pretty well established in this paper. He recognized four main bioseries in the verbeekinoidea species which have the common ancestor, *Doliolina claudiae*. The second paper dealt with the biostratigraphy of the Akiyoshi Limestone in Southwest Japan by means of the fusuline foraminifera. In 1927, he found a successive occurrence of the Neoschwagerinid species which display a serial evolutionary development in the Akasaka Limestone, and subdivided the limestone sequences into several species-zones on the basis of this fact. These two works were more or less stimulative to the subsequent biostratigraphic studies of these foraminifera. YABE and HANZAWA gave a tentative classification of the Fusulinina in 1932. They introduced a new genus *Pseudodoliolina* with *P. ozawai* from the Akasaka Limestone as the type-species. In 1933, LEE proposed the Neoschwagerinid genera *Colania* and *Lepidolina*. Unfortunately his descriptions were too insufficient to accept his proposal easily. *Colania* has long been regarded as a synonym of *Yabeina* or



*Lepidolina* by many authors. THOMPSON restudied the Permian fusuline fauna from the Bamian Limestone of Afghanistan that was once studied by HAYDEN, resulting in that knowledge on the Permian foraminiferal fauna in this area have been much increased. THOMPSON set up *Afghanella* based upon *Afghanella schencki* from this limestone. THOMPSON's comprehensive monograph on the fusuline genera appeared in 1948 that has been in fact very important for us to understand an outline of the fusuline foraminifera. So far as the verbeekinoidean genera are concerned, however, his opinion on phylogenetic relation among them is hardly accepted.

As KANMERA (1957) already noted THOMPSON erroneously regarded *cancellina* as the ancestor of *Neoschwagerina*, and gave a misleading diagnosis. At the same time, THOMPSON regarded *Pseudodoliolina* as a descendant of *Verbeekina*. In the same year, YABE presented a paper on the Neoschwagerinidae. His opinion on the phylogeny of the superfamily is well understood from the table given by him (YABE, 1948, p. 2).

From about fourth decade of this century, so many species of the Verbeekinoidea have been described in connection with the biostratigraphic studies of the Permian System in many provinces of the Tethys Sea Region. They are briefly summarized as follows:

Several verbeekinooid species which are intimately related to the Japanese or to East Asian faunas have been described from the Pacific Northwest of North America by American authors including THOMPSON, WHEELER and DANNER (1950), SKINNER and WILDE (1955, 1966) and DOUGLASS (1967). SOSNINA (1965) recorded several verbeekinoidean species from the Sikhote-Alin area of the Far East of Russia. In Japan a great number of works have been carried out on the superfamily by HUZIMOTO (1936) KANMERA (1954, 1957, 1963), TORIYAMA (1958), HONJO (1959), MORIKAWA (1960), MORIKAWA and SUZUKI (1961), NOGAMI (1961), SADA (1961, 1963), HANZAWA and MURATA (1963), HASEGAWA (1965), etc. Thus, our knowledge on the Verbeekinoidean faunas in Japan has been accumulated.

In Japan, the problem on *Lepidolina* has long been discussed in relation to the Upper Permian stratigraphy and the Permo-Triassic boundary in Japan. KANMERA (1954) fully described the Upper Permian fusuline fauna from the Kuma Formation in southern Kyushu. He recorded some interesting verbeekinoidean species comprising *Lepidolina kumaensis*, *Pseudodoliolina pseudolepida gravitesta*, the type-species of *Metadoliolina* ISHII and NOGAMI, 1961, and other species. On the basis of species assemblage he discriminated the *Lepidolina* fauna from the *Yabeina globosa* fauna, and set up the so-called *Lepidolina* Zone in the Upper Permian rocks, and regarded the zone as the highest fusulinian zone in Japan. NOGAMI (1959), SUYARI (1962), SADA (1963) and some other authors at first hold the opinion of KANMERA. On the contrary, HANZAWA and MURATA (1963) expressed the opposite opinion on this subject. They regarded the genus *Lepidolina* as a synonym of *Yabeina*, and stated that *Yabeina globosa* occupies the higher biostratigraphic horizon than "*Yabeina*" *multiseptata* and "*Y.*" *kumaensis*. They treated *Yabeina globosa* as the highest zonal indicator of the Neoschwa-

gerinidae. In their schema on the phylogeny of Verbeekinoiden species (HANZAWA and MURATA, 1963, p. 29), *Neoschwagerina minoensis* was placed in much lower horizons and was regarded as an ancestor of *Yabeina globosa*. This is probably not correct, because *N. minoensis* commonly associated with *Yabeina globosa* (OZAWA, 1927, p. 157; etc.). *Yabeina elongata* was regarded as a descendant of *Lepidolina multiseptata*, but it is nothing but the microspheric generation of the latter. Anyhow, their opinion on the phylogenetic relation among the species of the Verbeekinoidea cannot be warranted.

ISHII and NOGAMI (1964) studied a *Lepidolina* fauna based on many specimens collected from the Sisophon and Battambang Limestones, Cambodia. They described *Lepidolina multiseptata*, the type-species of the genus, in detail on the topotype specimens and showed variation of some biocharacters within the species, although there remained, as yet, some problems concerning the concept of subspecies and the treatment of dimorphism in the life cycle of the foraminifera. Having discussed the validity of the genus *Lepidolina* they regarded the genus as a synonym of *Yabeina* mainly based on the reason that the shell of the type-species of *Lepidolina* has an alveolar keriotheca. YABE (1964, 1965, 1966) expressed his own view on this subject in his serial papers entitled "*Lepidolina* Problems", and summarized biostratigraphical and paleontological knowledges concerning this problem. In the final paper cited he led the following conclusion:

1) *Lepidolina* represented well by *L. multiseptata* should be treated as a subgenus of *Yabeina*.

2) The *Yabeina* (s. s.) fauna is almost contemporaneous with the *Yabeina* (*Lepidolina*) fauna. Both are the representative faunas of the different lithofacies which are named by TORIYAMA (1967) as Kinshozan facies and Kuma facies, respectively. ISHII and SHIMIZU (1967) followed YABE's view. HASEGAWA (1965) described *Lepidolina kumaensis* from the Otani Conglomerate in the Hida Massif, Central Japan. He gave a brief note on *Yabeina* and *Lepidolina*, and pointed out the vagueness of the generic status of *Lepidolina*. It should be noted that he showed an interesting interpretation on the phylogenetic relationship of some neoschwagerinids which is somewhat similar to the conclusion presented in this paper. He regarded "*Gublerina elongata*" as a descendant of *Neoschwagerina colaniae*, although he suggested a probability that "*Gublerina elongata*" represents the microspheric forms of *Lepidolina multiseptata*. Thus, many discussions have been made by Japanese authors on the neoschwagerinid species.

From the Permian Limestone in South China, CHEN (1934, 1956), THOMPSON and FOSTER (1937) and SHENG (1963, etc.) described a large number of Verbeekinoidean species. Among them, SHENG's monograph of the fusulininan foraminifera from Kwangsi and its neighbouring areas is important in the consideration of the biostratigraphic relationship between the neoschwagerinid faunas and the *Palaeofusulina-Codonofusiella* fauna. Several species of the Verbeekinoidea were set up by him. Besides these contributions our knowledge on this superfamily in Southeast Asia has been accumulated by DEPRAT, COLANI, GUBLER, LANGE (1925), SAURIN (1958), ISHII and NOGAMI (1964), PITAKPAIVAN (1965), IGO (1966) and KANMERA and TORIYAMA (1968). In the paper cited above KAN-

MERA and TORIYAMA set up *Maklaya* for a primitive neoschwagerinid species-group including "*Cancellina*" *pamirica*.

During the last two decades, information on the verbeekinoidean faunas from Southwest Asia and Asia Minor has been much increased by several authors such as MIKLUKHO-MAKLAY (1955, 1957), LEVEN (1967, etc.), KALMIKOVA (1967), and SKINNER (1969). The verbeekinoidean fauna in the Southeast Europe has been clarified by KOCHANSKY-DEVIDÉ (1958, 1965) and KOCHANSKY-DEVIDÉ and RAMOVŠ (1955). The foraminiferal faunas in Sicily and Tunisia, the western extremity of the distribution of the Verbeekinoidea, were described by OZAWA and TOBLER (1929), DOUVILLÉ (1934) and SKINNER and WILDE (1966, 1967).

Compared with active works on the stratigraphic paleontology of the foraminifers, studies from the pure paleontologic standpoint were rather few in these four decades. SKINNER and WILDE (1954) studied the spirothecal structure of *Lepidolina multiseptata* and *Sumatrina annae*. KANMERA (1957) discussed about diagnostic features of *Cancellina* and primitive representatives of *Neoschwagerina*. MINATO and HONJO (1959) examined the axial septula of the neoschwagerinid species and gave their idea on their phylogenetic relationship based on the developmental pattern of the axial septula. Their view deviates far from those held by other authors. There are, however, still several problematical points to be discussed. MORIKAWA (1965) studied in some detail the parachomata of the verbeekinoid genera.

Recently GOBBETT (1968) reported an interesting paper dealt with paleozoogeography of the Verbeekinoidean foraminifers. Besides, the following paleontologists have expressed their views on the phylogeny of the Verbeekinoidean foraminifera; DEPRAT (1913), OZAWA (1925a, 1927), LEE (1933), GUBLER (1935), THOMPSON (1948), YABE (1948), KANMERA (1957), MIKLUKHO-MAKLAY, RAUSER-CHERNOUSOVA and ROZOVSKAYA (1958), MINATO and HONJO (1959), TORIYAMA (1960), MORIKAWA and SUZUKI (1961), SHENG (1963), HANZAWA and MURATA (1963) and HASEGAWA (1965).

### Paleoecology

As one of the main limestone builders, the fusuline foraminifers including the Verbeekinoidea abundantly occur in carbonate sediments of the Carboniferous and Permian Systems. Some of them are, however, known to occur in calcareous clastic sediments. For example, species of *Monodioxodina* which have a very slender shell usually occur in calcareous sandstone or arenaceous limestone. Some species of *Oketaella* have been recorded from calcareous shale (THOMPSON, 1954, p. 35-36). As will be mentioned below, the fusuline foraminifers are considered to have been very sensitive to microenvironments, which are indirectly interpreted by lithologic features of limestone, and the contained organic remains and their assemblage. As the result of adaptation to the microenvironments, many types of the fusuline foraminifers were developed. So far as has been known, a definite fusuline community is usually restricted to a certain rock-type. Some large,

subspherical or highly inflated fusiform schwagerinid species with a delicate spirotheca and septa, such as *Robustoschwagerina schellwieni* and *Acervoschwagerina endoi*, are predominant in micritic limestone which is interpreted to be a deposit under calm water environment. In this type of rock, their delicate shells are usually completely preserved. Species of *Nipponitella*, *Paradoxiella* and *Codonofusiella* have an uncoiled shell at the mature stage. These highly specialized or aberrant forms are mostly restricted to black-coloured, rather bituminous muddy limestone. Species of *Hidaella* which have a highly rugose spirotheca also occur in the similar lithofacies. These unusual species must have been much selective in their choice of a habitat. While, highly elongate schwagerinid species such as *Monodioxodina wanneri*, *M. matsubaishi*, *Parafusulina kaerimizensis*, *P. deliciosensis* and other species of a similar form are crowded commonly in arenaceous or well-sorted limestones with a sparry calcite matrix. Their elongate shells are often oriented in the same direction. Such occurrences are known in the Permian of Timor (THOMPSON, 1948, p. 7), Kitakami Massif (HUJIMOTO, 1956) and Akiyoshi Limestone (KAWANO, 1967, pl. 2) in Japan, the Primore Territory in Sikhote-Alin (SOSNINA, 1956, pl. 7), and other many localities. Their mode of occurrence and their state of preservation suggest the deposition in the place not far from their living sites. As has been mentioned by THOMPSON in the paper cited above, the oriented arrangement of shells and the lithologic features of the rocks in which they occur suggest that schwagerinid species such as *Monodioxodina wanneri* lived in a shallow sea environment where the wave action and/or submarine currents were fairly strong. As GOBBETT (1967, p. 83) noted, the shell-shape of foraminifers is in fact an important clue to their habitat. The thickness and rugosity of spirotheca, the mode of coiling of shells, the coarseness of alveoli in the keriothecal layer and the thickness of septa may more or less reflect environmental conditions in the habitat of fusuline foraminifera. In general the elongate species with a thick spirotheca and septa probably preferred agitated water condition. On the other hand, inflated, loosely coiled species with a thin spirotheca and septa probably selected less agitated calm water condition as their favorite habitat.

Verbeekinoid species with subspherical to cylindrical shell occur chiefly in micritic limestone, less commonly in calcarenite with a sparry calcite matrix, and rarely in calcareous sandstone or conglomerate. In case they are found in clastic sediments, however, their shells are more or less broken as well exemplified by those in the conglomerate or conglomeratic sandstone intercalated in the Toyoma Slate in Kitakami Massif, Northeast Japan (SAITO, 1968) and of the Upper Permian in Southwest Japan (KANMERA, 1954 and others). It is undoubted that the verbeekinoideans found in conglomerate or sandstone were transported and deposited as pebbles at places far from their living sites. We have no positive evidence to show that verbeekinoidean species had lived in the places where such clastic sediments are accumulated. We can safely say that there were no verbeekinoidean species which had planktonic life at the mature stage, because their occurrence is restricted mostly to the limestone facies.

The ecology of the verbeekinoidean foraminifera may be well inferable from

the ecological evidence of the Alveolinid foraminifera which include living species, because these two foraminiferal groups represent a good example of a convergent evolution in foraminifera. WALLACE and SRB (1961, p. 56) explain the phenomenon of convergent evolution as follows; "When distantly related group of plants or animals occupy ecological niches that have many environmental characteristics in common, they may develop superficial resemblance." Close resemblance in shell morphology are in fact recognized between the species of the Verbeekinoideans and Alveolinids, although there is no genetic relation between them. For example, shell of *Misellina*, *Verbeekina* and *Sumatrina* or *Lepidolina* in the Verbeekinoideans are respectively isomorphic with those of *Ovalveolina*, *Multi-spirina* and *Alveolinella* or *Fasciolites* in the Alveolinids. REICHEL (1964) stated that "The fossil alveolinids are only found in neritic sediments where they may be associated with miliolids and calcareous algae. Many large species occur in great abundance and are therefore rock builders. *Alveolinella* lives in tropical seas at depth of 10 to 80 m."

The limestone in which the verbeekinoidean foraminifers occur often contains the Codiacean and Dasycladacean algae, and schwagerinid and endothylid foraminifera. Waagenophyllid corals and bryozoas are also commonly found with them. It is highly probable that the verbeekinoidean and alveolinid foraminifera occupied similar ecological niches in shallow warm water in the Permian and post-Upper Cretaceous respectively. GOBBETT (1967, p. 84) inferred the ecology of the verbeekinoidean foraminifera as follows: "at least some members of the Verbeekinoidea lived among algal meadows in warm, clear, sunlit waters of normal salinity, possibly as deep as 80 metres but frequency much shallower. This environment would probably not be subject to strong currents and would be the site of slow carbonate sedimentation brought about by organic activity and particularly by the growth of algae. The young stage of the Verbeekinids were probably epiplanktonic or planktonic." The verbeekinoidean species had probably these environments as their favorite habitat.

Species of *Misellina* are often associated with several species of schwagerinids such as *Pseudofusulina globosa*, *P. krafftii*, *P. fusiformis* and *Nagatoella orientis*. *Neoschwagerina simplex* and its allied species commonly occur with species of *Cancellina* such as *Cancellina nipponica* in micritic limestone in the lower Middle Permian. Some species of *Parafusulina* commonly coexist with them.

In Japan, the assemblage characterized by *Neoschwagerina simplex* and *Cancellina nipponica* is chiefly recognized in the outer zone of Japan including the Chichibu belts. While, *Parafusulina kaerimizensis* and its closely allied species which occupy the equivalent stratigraphic horizons to the *Neoschwagerina simplex* zone are found usually in swarms in huge limestone masses (the Akiyoshi, Taishaku, Atetsu Limestones, etc.) in the Inner Zone of Southwest Japan. The *Parafusulina kaerimizensis* faunule is almost devoid of the elements of the *Neoschwagerina simplex*-*Cancellina nipponica* assemblage, and is found in sparitic limestones which are considered to have deposited under very shallow and agitated water condition. As mentioned above, this environment was probably not favourable for species of Neoschwagerinids. Similar is the case in the assemblage

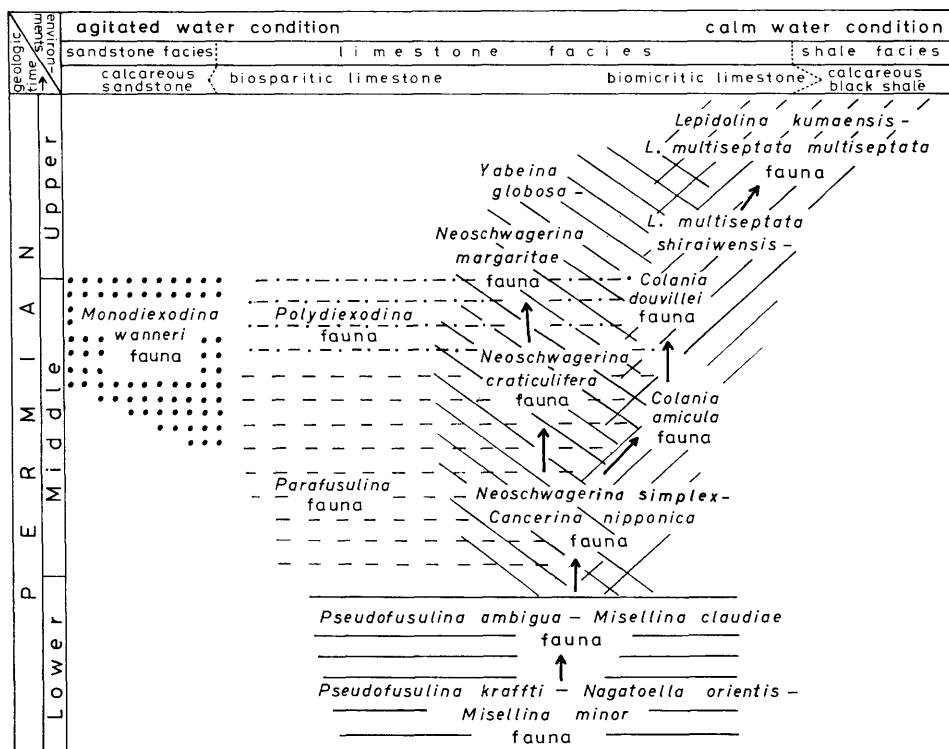


Fig. 1. Schematic diagram showing the development of the Neoschwagerinid faunas in connection with lithofacies.

containing *Neoschwagerina craticulifera* and that characterized by *Parafusulina japonica* in the middle Middle Permian. The typical representative of the latter is found in the Yamasuge Member of the Nabeyama Formation in the Kuzu area in Kwanto Province which is one of the reference sections of the so-called *Parafusulina* Zone of Japan. This fact may be explained by the difference of ecological adaptation between species of *Parafusulina* and those of *Neoschwagerina*.

Interesting interspecific ecological relationship is recognized among the neoschwagerinid species, especially between the species of the Neoschwagerininae, including genera *Maklaya*, *Neoschwagerina* and *Yabeina*, and those of the Lepidolininae composed of genera *Cancellina*, *Colania* and *Lepidolina*. Species of *Cancellina* commonly occur along with the primitive species of *Neoschwagerina* such as *N. simplex*. *Neoschwagerina craticulifera* which has long been recognized as a descendant of *Neoschwagerina simplex* commonly occurs in sparitic to micritic limestones. While, *Colania amicula* or its related species which are regarded as a descendant of the species group of *Cancellina nipponica* are mostly confined to micritic limestone. Association of species of *Neoschwagerina* and *Colania* is less common. Although *Colania douvillei* and *Neoschwagerina margaritae* are the good index fossils for the upper Middle Permian age, but their association is not common. *Yabeina globosa* and its allies are found more commonly in limestone masses than in lenticular limestones intercalated in thick piles of clastic sedi-

ments. On the other hand, *Lepidolina multiseptata* and its allies predominantly occur in small micritic limestone lenses intercalated in muddy sediments even in such small lenses as thick as 0.5 metre. As pointed out by KANMERA (1954) the association of *Yabeina globosa* and *Lepidolina multiseptata* has never been known, and the sediments characterized by the *Yabeina globosa* are very much different in facies from those of the *Lepidolina multiseptata* fauna. TORIYAMA (1967) proposed to call the two facies Kinshozan and the Kuma facies respectively. YABE mentioned that the Kuma facies far exceed in geographical distribution of the Upper Permian sediments in the Japanese Islands. Although the exact stratigraphic and chronologic relationship between the two facies has never been confirmed yet, YABE (1964) considered that, from the available data, a part of the *Lepidolina multiseptata shiraiwensis* zone is at least contemporaneous with the *Yabeina globosa* zone of the Kinshozan facies. I am in favour of YABE's view which is quite reasonable, and of the opinion that the faunal construction in the Japanese Upper Permian may be explained from the ecological aspect of the Neoschwagerinid species as well as chronological grounds. As compared with the species of Neoschwagerininae, those of Lepidolininae and Sumatrininae have delicate shell and are much abundantly found in micritic limestone deposited under calm water condition. In fact the segregation by the choice of ecological habitat, as mentioned above, exists between species of Neoschwagerininae and Lepidolininae. It is a remarkable fact that the prosperity of the Lepidolininae in the upper Middle to the Upper Permian is concordant with the decline of the Neoschwagerininae. This difference in ecological habitat and chronological prosperity between both subfamilies is noteworthy. This is one of main reasons I separate *Colania* and *Lepidolina* from the Neoschwagerininae in the present paper.

### Distribution

As well known, the verbeekinoidean foraminifers are restricted in distribution to the Tethys Sea Region including the west coast area of North America. GOBBETT (1967) has recently summarized their geographic distribution and mapped the localities where they occur. Further discussion on their general geographic distribution seems to be unnecessary, but short remarks are given here on the verbeekinoidean fauna in the Permian. GOBBETT recognized three groups of verbeekinoidean fauna, the *Misellina*, *Neoschwagerina* and *Yabeina* "Faunas" in ascending order. Up-to-date knowledge on the Permian verbeekinoidean fauna, however, may permit the following grouping or distinction in terms of representative species.

#### 1. *Misellina* fauna.

a) *Misellina minor* fauna.—Primitive species of *Misellina* are characteristic for the upper Lower Permian fauna. They are widespread in the Tethys Sea Region including Asia Minor, Pamir, Southeast Asia, South China, the Japanese Islands, Sikhote-Alin and the Pacific Northwest of North America. *Misellina*

(*Misellina*) *minor*, *M. (M.) ibukiensis*, *M. (M.) californica*, *M. (Brevaxina) compressa*, *M. (B.) otakiensis*, *M. (B.) dyhrenfurthi*, etc. are the representative species of this fauna. In addition to the species of *Misellina*, such schwagerinid species as *Pseudofusulina globosa*, *P. krafftii*, *P. fusiformis*, and *Nagatoella orientis* are contained in it.

b) *Misellina claudiae* fauna.—Advanced species of *Misellina* (*Misellina*) represented by *M. (M.) claudiae* and *M. (M.) ovalis* characterize the lowest Middle Permian fauna of Asia Minor, Pamir, Southeast Asia, South China, Sikhote-Alin and the Japanese Islands. Some schwagerinid species such as *Parafusulina ambigua* and *Nagatoella orientis* commonly occur in association with the above mentioned species of *Misellina*.

GOBBETT (1967) designated species of *Eoverbeekina*, *Pseudodoliolina*, *Presumatrina* and primitive species of *Neoschwagerina* as the constituents of the *Misellina* fauna. The species of these genera, however, occur in higher horizons than the strata containing species of *Misellina*, and are the members of the *Neoschwagerina* fauna. As defined above, only the assemblages characterized by species of *Misellina* are referred to the *Misellina* fauna.

## 2. *Neoschwagerina* fauna.

a) *Neoschwagerina simplex*—*Cancellina nipponica* fauna.—The lower Middle Permian fauna is characteristically represented by the *Neoschwagerina simplex*—*Cancellina nipponica* assemblage. Species of *Maklaya*, *Armenina*, *Cancellina*, *Presumatrina*, and primitive representatives of *Neoschwagerina* and *Pseudodoliolina* are members of this fauna. This fauna is known from the Asia Minor, Southeast Asia, South China, Sikhote-Alin, the Japanese Islands, and the Pacific Northwest of North America. Few species of *Parafusulina* are associated with this fauna.

b) *Neoschwagerina craticulifera* fauna.—The middle Middle Permian fauna is made up of advanced species of *Neoschwagerina* including *N. craticulifera*, *N. cheni*, *N. occidentalis* and *N. haydeni*, *Afghanella schencki*, *A. ozawai*, *P. pseudolepida*, *Verbeekina heimi*, *Verbeekina verbeeki*, etc. Large species of *Parafusulina* are also associated with these verbeekinoidean species. This fauna migrated into the Southeast Europe. At the end of the history of this fauna *Neoschwagerina margaritae*, *Colania douvillei*, *C. kwangsiana*, *Sumatrina annae*, and *Metadoliolina lepida* appear, and some species of *Polydioxodina* including *P. afghanensis* are accompanied.

## 3. *Yabeina* fauna.

The Upper Permian verbeekinoidean fauna comprises at least two groups, each of which is characterized by a particular assemblage of species. One is represented by *Yabeina globosa* and its related species, and the other by *Lepidolina multiseptata* and its allied species. As mentioned in the preceding chapter, the two groups are never associated with together and have long been in dispute whether they are coeval to each other or different in age.

a) *Yabeina globosa* fauna.—This fauna is characterized by species of *Yabeina* including *Y. globosa*, *Y. packardi*, *Y. cascadiensis*, *Y. syrtalis*, etc., *Neo-*



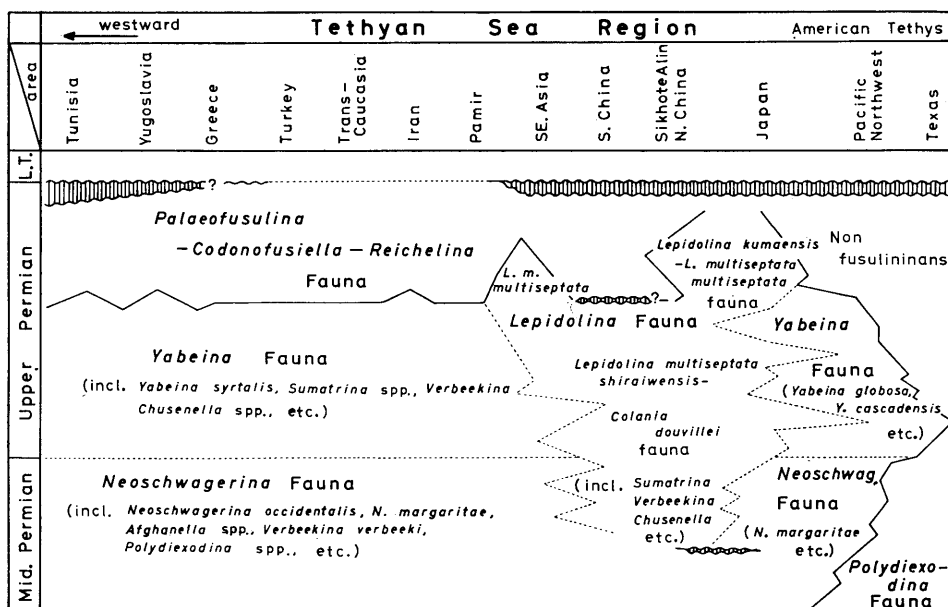


Fig. 2. Schematic diagram showing the distribution of faunas in the Upper Permian of the Tethyan Region.

Main data (Tunisia: SKINNER and WILDE, 1967; Yugoslavia: KOCHANSKY-DEVIDÉ, 1965, etc.; Greece: RENZ and REICHEL, 1945; Trans-Caucasia: RUZHENTSEV and SARYCHEVA, 1965; Iran: DOUGLAS, 1950, TARAZ, 1969; Pamir: LEVEN, 1967; Southeast Asia: DEPRAT, 1912, etc., GUBLER, 1935; South China: SHENG, 1963, etc.; North China and Sikhote-Alin: NODA, 1963, SOSNINA, 1960, etc.; Japan: KANMERA, 1954, 1967, YABE, 1964, 1965, ISHII and SHIMIZU, 1967, etc.; Pacific Northwest of North America: SKINNER and WILDE, 1966, etc.; Texas: SKINNER and WILDE, 1955)

*schwagerina katoi*, *N. minoensis*, *Verbeekina verbeeki*, and some other species. Some species of *Chusenella*, *Dunbarula*, *Paradoxiella*, and *Codonofusiella* are also members of this fauna. This fauna is usually rather simple in the constituent and is known from the Pacific Northwest of North America, the Japanese Islands, Southwest Asia, and North Africa.

#### 4. *Lepidolina* fauna.

a) *Lepidolina multiseptata shiraiwensis*-*Colania douvillei* fauna.—Another group of the lower Upper Permian fauna is characterized by *Lepidolina multiseptata shiraiwensis*, *L. asiatica*, *Colania douvillei*, *C. kwangsiana*, *Sumatrana annae*, *S. longissima*, *Verbeekina verbeeki*, and some species of *Afghanella*, *Pseudodoliolina*, *Metadoliolina*, *Dunbarula*, and *Codonofusiella*. It is probably contemporaneous with the *Yabeina globosa* fauna.

b) *Lepidolina multiseptata multiseptata*-*L. kumaensis* fauna. — Highly evolved species of the Verbeekinoidea such as *Lepidolina multiseptata multiseptata*, *L. kumaensis*, *Metadoliolina gravitesta*, *M. dutkevitchi*, *M. multivoluta* and *Verbeekina douvillei* constitute the latest verbeekinoidean fauna. *Chusenella cambodiensis* and its allies are also dominant. Species of *Codonofusiella*, *Dun-*

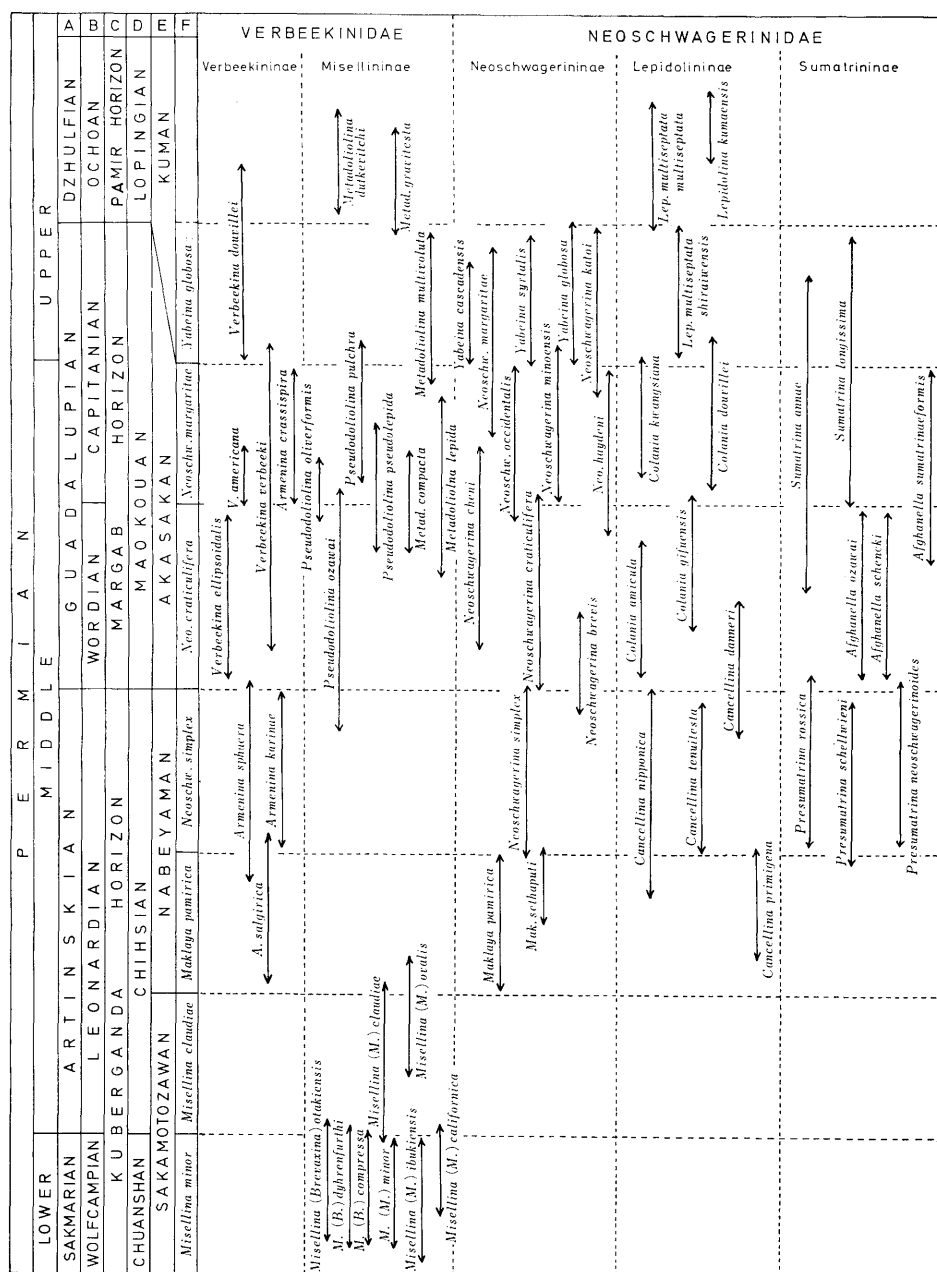


Fig. 3. Stratigraphic distribution of representative species of the Verbeekinoidea. [A: Permian subdivision by GLENISTER and FURNISH (1961) by means of Ammonoites, B-E: Permian subdivision in U. S. A., Central Asia, South China and Japan respectively, F: Zonal subdivision of the Permian System by the index species of the Neoschwagerininae].

*barula* and *Reichelina* commonly occur in association with the species listed above. This fauna is known from the limestone facies and the black shale facies of the lower to upper Upper Permian in the Eastern Asia embracing the Japanese Islands, Sikhote-Alin area, Northern Manchuria, South China, and Southeast Asia. At least a part of this fauna is contemporaneous with the *Codonofusiella-Palaeofusulina* fauna well distributed in the Upper Permian of South China, Indo-China, Asia Minor, Northern Africa and Southeast Europe (Fig. 2). No representative of the Sumatrininae (*Presumatrina*, *Afghanella* and *Sumatrina*) has so far been found in the Pacific Northwest of North America. The occurrences of the verbeekinoidean foraminifers are in fact sporadic in the marginal areas of the Tethys Sea Region, namely, Southeast Europe, North Africa, New Zealand and the Pacific Northwest of North America. It is concluded that the center of distribution of the verbeekinoidean foraminifers might have been in the areas covering the Japanese Islands, South China and Southeast Asia. The stratigraphic distribution of representative species of the Verbeekinoidea is shown in Fig. 3.

## Dimorphism and polyvalence

### A. Dimorphism

Analysis of life cycle of foraminifera is very important and essential subject in paleontology as well as in the studies of living species. LISTER (1895) was the first who explained the phenomenon of dimorphism in foraminifera on the basis of protozoan cytology. He found that two distinct types of shell occur in a species of *Elphidium* and that the dimorphism in shell size is the result of an alternation of the asexual and sexual phases. In dimorphism, megalospheric shells represent the gamout generation in the asexual phase, while, microspheric ones the shizont generation in the sexual phase. Further investigations on this biological subject were made by many protozoologists including MYERS (1940, etc.), Le CALVEZ (1938, etc.), GRELL (1957, etc.) and LEE (1963, etc.), and many invaluable facts have been elucidated. The dimorphism occurs in most species of foraminifera, but there are several species which show trimorphism in their life cycle. These phenomena are actually important not only for the taxonomy but also for the analysis of populations.

HAYDEN (1909), STAFF (1908), OZAWA (1925a), DUNBAR, SKINNER and ROBERT (1936), CIRY (1941), and some other paleontologists paid a special attention to the dimorphism in the Fusulinina. Subsequent authors, however, have not paid much attention to this phenomenon, and the main interest of the study has been focused to stratigraphic paleontology rather than pure paleontology. In the Verbeekinoidea, this phenomenon is recognizable in not a few species of the Neoschwagerinidae and the Verbeekinidae. In species of *Cancellina*, *Colania* and *Lepidolina* which constitute a definite phylogenetic group in the Neoschwagerinidae, the megalospheric shells can be easily distinguished from the microspheric ones in the size of proloculus and shell, the number of volutions and certain other shell features. I have made a biometric study on fossil populations of several

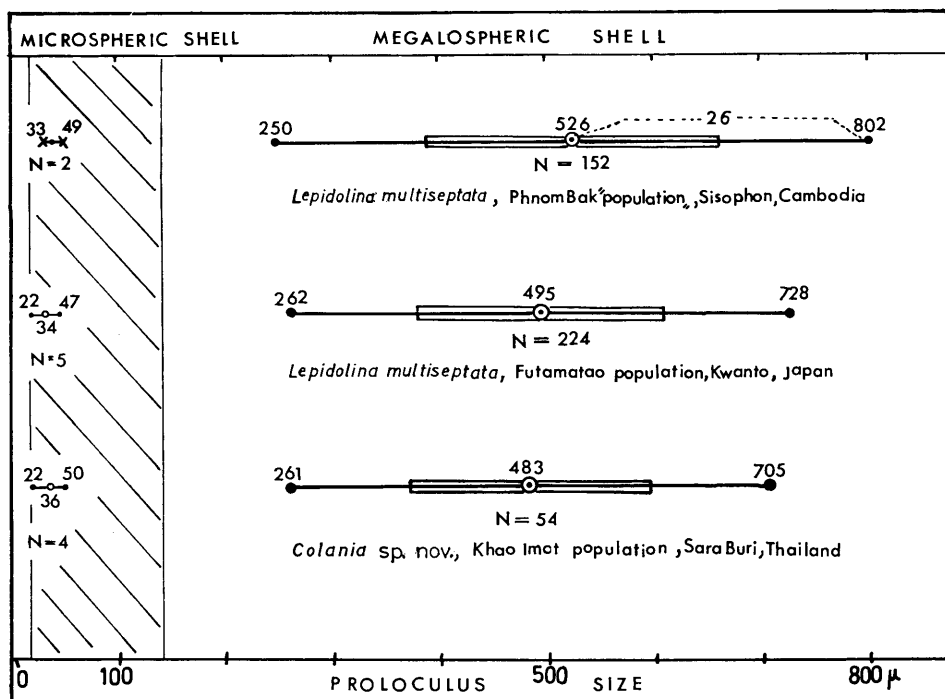


Fig. 4. Statistical analysis of dimorphism and variation in the proloculus size in three populations of two species of the Lepidolininae. The proloculus size range of most species of the Neoschwagerininae is restricted in the hatched area.

neoschwagerinid species and analyzed the dimorphism regarding the size of shell and proloculus, the number of volution and the mode of coiling of juvenile volutions. As the result of the study, some questions which have been thrown to us can be solved. As shown in Fig. 4, *Yabeina elongata*, the type-species of *Gublerina* MINATO and HONJO, which has a very large, elongate fusiform shell, represents shizont generation of *Lepidolina multiseptata*. That is, specimens of *Lepidolina multiseptata* including the holotype have a megalospheric shell and those referred to *Yabeina elongata* a microspheric shell. Similar relationship is also found in species of *Colania* which are regarded as the direct ancestor of species of *Lepidolina*. For instance, "*Neoschwagerina*" (= *Colania*) *douvillei* shows a distinct dimorphism (Pl. 7, Figs. 9 and 10) in shell and proloculus size. *Colania* sp. nov. (Pl. 1, Figs. 2, 6 and 7; Pl. 7, Figs. 5-7) from the Rat Buri Limestone of Thailand is another example which displays a dimorphic life cycle as in *Lepidolina multiseptata*. "*Yabeina probosis* CHEN" (1956, pl. 8, figs. 8-10) is undoubtedly a representative of microspheric generation of *Colania douvillei* or its allied species. These species occur with together. As already suggested by NOGAMI (1961) and ISHII (1966), *Yabeina* sp. A (NOGAMI, 1961, pl. 7, figs. 1-5) from the Atetsu Limestone in Southwest Japan is the microspheric representative of "*Yabeina*" (= *Lepidolina*) *shiraiwensis* OZAWA (NOGAMI's pl. 5, figs. 1-8) which coexists with the former in the same limestone. The same relationship is also shown in the following two examples. *Neoschwagerina* sp. A (NOGAMI, 1961,

pl. 3, fig. 7) is the microspheric generation of "*Neoschwagerina*" (= *Colania*) *douvillei*. *Neoschwagerina* sp. A (IGO, 1966, pl. 8, figs. 5–6) from the Jengka Pass in Pahang, Malaysia is also the microspheric specimens of "*Neoschwagerina*" (= *Colania*) *douvillei* OZAWA or "*Yabeina*" (= *Lepidolina*) *asiatica* ISHII.

On the other hand, microspheric and megalospheric shells in the species of *Maklaya*, *Neoschwagerina* and *Yabeina* are almost the same in size, and therefore the distinction of generations based on shell size is usually difficult. The difference is, however, seen in that the microspheric generation has a slightly smaller proloculus and endothyroid juvenile volutions. On the other hand the megalospheric shells are coiled planispirally throughout the growth (Pl. 4, Figs. 5 and 6). I have observed these two generations in the following species; *Misellina claudiae*, *Armenina* sp., *Neoschwagerina simplex*, *Neoschwagerina craticulifera* (Pl. 4, Figs. 6 and 7), *N. margaritae* and *Yabeina globosa*. Good examples which show these generations are seen in *Neoschwagerina brevis* THOMPSON, WHEELER and DANNAR (= *N. peculiaris* SKINNER and WILDE) and *Yabeina syrtalis* (DOUVILLÉ) which were illustrated by SKINNER and WILDE (1966, pl. 30, fig. 9, pl. 31, fig. 4; 1967, pl. 27, figs. 1–2). The dimorphism in the Sumatrininae and evolved species of the Verbeekinae is not well understood, because of rare occurrence of the microspheric specimens. Regarding the life cycle of these two subfamilies, further informations are necessary. Anyhow, as is understood from the above discussion, the analysis on polymorphism in life cycle is very important for taxonomy of the fusuline foraminifera as well as the other foraminiferal groups.

## B. Polyvalence

In the fusuline foraminifera, the polyvalent individuals are rarely found in some species of the Fusulinidae and Schwagerinidae. In the Verbeekinoidea, this phenomenon is especially abundant in species of the Lepidolininae (*Cancellina*, *Colania* and *Lepidolina*) and the Sumatrininae. It is rare in species of the Misellininae comprising the genera *Misellina* (s.l.), *Pseudodoliolina* and *Metadoliolina*. No polyvalent individuals have so far been known in the species of the Neoschwagerininae and Verbeekinae. The polyvalent individuals have been recognized in the following species:

*Cancellina nipponica* OZAWA; HANZAWA and MURATA (1963, pl. 12, fig. 8).

*Colania megaspherica* (DEPRAT); COLANI (1924, pl. 22, fig. 20).

*Lepidolina multiseptata* (DEPRAT); COLANI (1924, pl. 26, fig. 7), MORIKAWA (1956, pl. 34, fig. 9), TORIYAMA (1958, pl. 44, fig. 9), NOGAMI (1961, pl. 6, fig. 4), HANZAWA and MURATA (1963, pl. 5, fig. 3), WILDE (1965, pl. 18, fig. 4), OZAWA (Pl. 8, Figure 7 of this paper).

*Afghanella sumatrinaeformis* GUBLER; CHEN (1956, pl. 7, fig. 11).

*Sumatrina longissima* DEPRAT; COLANI (1924, pl. 20, figs. 21–22), TORIYAMA (1958, pl. 48, fig. 25).

*Pseudodoliolina ozawai* YABE and HANZAWA; TORIYAMA (ditto, pl. 39, fig. 31).

*Pseudodoliolina pulchra* SHENG; SHENG (1963, pl. 30, fig. 1).

*Colania douvillei* (OZAWA) from the Aikoyshi Limestone in Southwest Japan

and *Colania* sp. nov. (Pl. 1, Figs. 2, 6 and 7; Pl. 7, Figs. 5–7) from the Rat Buri Limestone in Thailand also contain polyvalent individuals. As well shown by *Lepidolina multiseptata* and other listed species the phenomenon of polyvalence seems to be closely related to the proloculus size. That is to say, it is much more common in species which have a large proloculus than in those with a small proloculus.

## Evolution of shell structure and phylogeny

### A. Evolution of shell structure

The evolutionary history of the verbeekinoid foraminifera is well represented by modification and progressive reduction of the keriothecal layer of the spirotheca, multiplication of septa and septula, progressive enlargement of shell. The following short remarks are given on these main evolutionary trends.

1. The shell becomes larger and the number of volutions increases. In the upper Lower Permian verbeekinoid species, mature specimens usually have only five to seven volutions and are about one millimeter or slightly more in size. For example, *Misellina ibukiensis* has six to seven volutions and is about 1 mm long. In the species of *Misellina* including the type-species, which occur in higher horizons, mature specimens attain a length of 2.5 mm or more and have more than eight volutions. Most of species of *Cancellina*, *Maklaya* and *Armenina* have a shell of 3 mm or more. The number of volution in these species usually exceeds ten. Many species of *Neoschwagerina*, *Colania*, *Verbeekina* and *Pseudodoliolina* have a much larger shell with more than thirteen volutions. The approximate size range and volution number of a representative species of these genera are given as follows; *Neoschwagerina craticulifera*: 14–16 volutions, 4–6 mm; *Verbeekina verbeeki*: 14–16 volutions, 4–8 mm; *Pseudodoliolina ozawai*: 13–15 volutions, 4 mm or more.

In the upper Middle Permian species, mature specimens have more than twenty volutions and attain a length of more than 10 mm. For instance, mature specimens of *Yabeina globosa*, the type-species of *Yabeina*, contain more than twenty volutions and are more than 11 mm. The most gigantic specimens are found in the microspheric generation of *Lepidolina multiseptata* (=“*Yabeina elongata*”) or of the species-group of *Colania kwangsiana* (Pl. 9, Fig. 4; Pl. 8, Fig. 5; Pl. 7, Fig. 7). In these species, the microspheric specimens have twenty-three or more volutions and exceed 25 mm in length. Thus, advanced species of the verbeekinoids have a shell more than fifteen times as long as the ancestral species.

2. The wall structure gradually becomes complicated through the development of septa and septula.

This is the most important tendency recognized in the evolutionary history of the Neoschwagerinidae. In the course of the development of septula, at least five stages are recognized, although all gradation or transition can be recognized in the development from the initial stage to the final stage, and therefore it is often difficult to distinguish strictly these stages. However, the following five

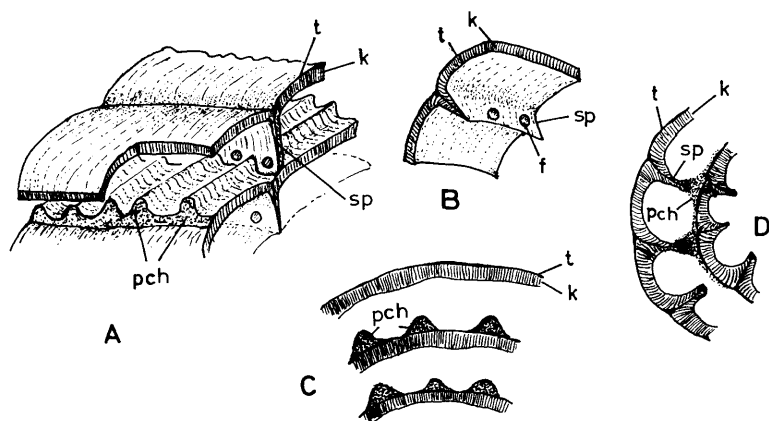


Fig. 5. Inner structures of the shell of *Misellina claudiae* (DEPRAT). A, Perspective view; B, Inner surface of the spirotheca; C, Part of axial section; D, Part of sagittal section. t, tectum; k, keriotheca; sp, septum; pch, parachomata; f, foramen.

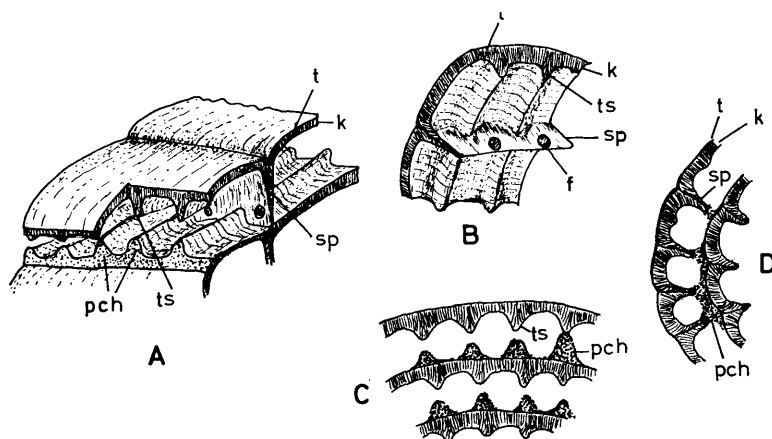


Fig. 6. Inner structures of the shell of *Maklaya pamirica* (LEVEN). A, Perspective view; B, Inner surface of the spirotheca; C, Part of axial section; D, Part of sagittal section. t, tectum; k, keriotheca; ts, primary transverse septulum; sp, septum; pch, parachomata; f, foramen.

stages may be differentiated with respect to the developmental pattern of septula.

The stage I (*Misellina claudiae* stage). No significant modification of the wall structure is recognized in this stage. This type of spirotheca is seen in all the species of *Misellina*, *Pseudodoliolina*, *Metadoliolina*, *Armenina*, and *Verbeekina* (Fig. 5).

The stage II (*Maklaya pamirica* stage). In this stage there appear incipient transverse septula formed by slight downward prolongation of the keriothecal layer. The lower end of the transverse septula is connected with the parachomata only immediately adjacent to the septa, leaving a large lateral passage in the central part of the chamber. Axial septula are not yet developed. Most of

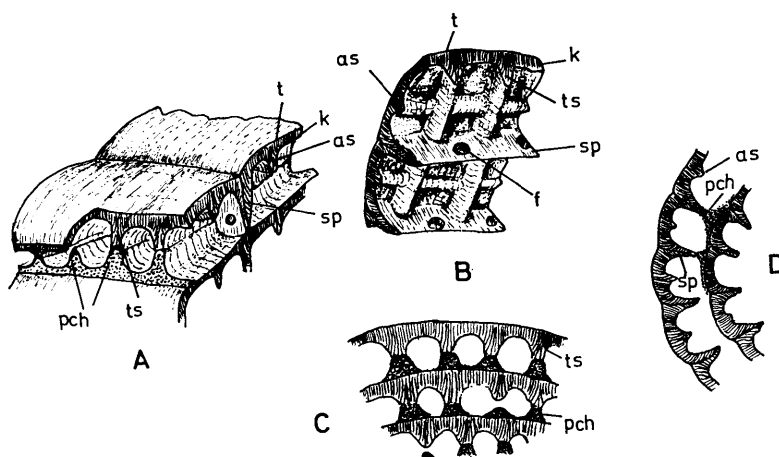


Fig. 7. Inner structures of the shell of *Neoschwagerina simplex* OZAWA. A, Perspective view; B, Inner surface of the spirotheca; C, Part of axial section; D, Part of sagittal section. t, tectum; k, keriotheca; ts, primary transverse septulum; as, axial septulum; sp, septum; pch, parachomata; f, foramen.

species of *Maklaya* and some small species of *Cancellina* (?) represent this stage (Fig. 6).

The stage III (*Neoschwagerina simplex* stage). The primary transverse septula are almost completely connected with the top of the parachomata, leaving a fairly large lateral passage in the central part of the chamber. The axial septula appear at least in the outer volutions. This stage of wall structure is found in the primitive species of *Neoschwagerina* including *N. simplex* and most species of *Cancellina*. Fig. 7 shows the wall structure of *Neoschwagerina simplex* OZAWA.

The stage IV (*Neoschwagerina craticulifera* stage). Adding to the primary transverse and axial septula, secondary transverse septula appear between the primary transverse septula in the outer part of shell. The advanced species of *Neoschwagerina* such as *N. craticulifera* and *N. margaritae* and most of species of *Colania* and *Presumatrina* assume this stage of wall structure (Fig. 8).

The stage V (*Yabeina globosa* stage). Secondary transverse septula are well developed even in the inner volutions. The septula and septa become thin and irregular. The wall structure is most complex in this stage as well represented by species of *Afghanella*, *Sumatrina*, *Yabeina*, and *Lepidolina* (Fig. 9).

The prolongation of the keriothecal layer is taken place not only transversely but also meridionally as seen in most species of *Cancellina*, *Neoschwagerina* and *Colania*. In the species of *Yabeina*, *Lepidolina*, *Afghanella* and *Sumatrina*, a chamberlet formed by the intersection of the primary transverse septula and axial septula is further subdivided into twofold or fourfold small partitions by the development of the secondary transverse septula.

3. The parachomata gradually increase in number, and become narrow and prominent. In general this tendency is well recognized, except for the species of



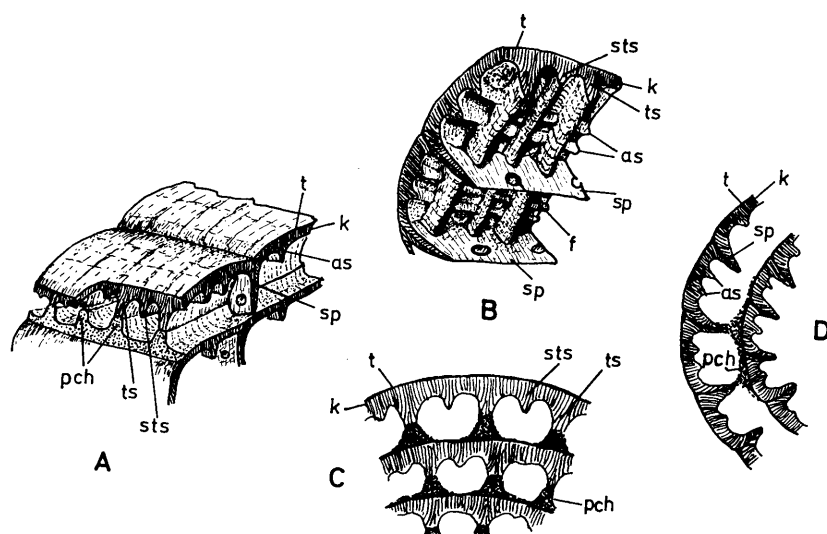


Fig. 8. Inner structures of the shell of *Neoschwagerina craticulifera* (SCHWAGER). A, Perspective view; B, Inner surface of the spirotheca; C, Part of axial section; D, Part of sagittal section. t, tectum; k, keriotheca; ts, primary transverse septulum; sts, secondary transverse septulum; as, axial septulum; sp, septum; pch, parachomata; f, foramen.

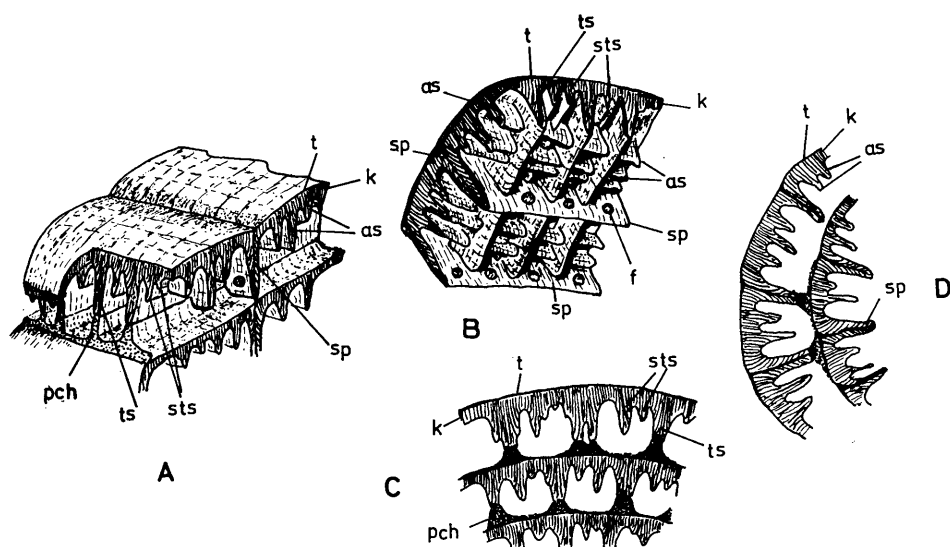


Fig. 9. Inner structures of the shell of *Yabeina globosa* (YABE). A, Perspective view; B, Inner surface of the spirotheca; C, Part of axial section; D, Part of sagittal section. t, tectum; k, keriotheca; ts, primary transverse septulum; sts, secondary transverse septulum; as, axial septulum; sp, septum; pch, parachomata; f, foramen.

*Armenina* and *Verbeekina*. In the species of the Neoschwagerinidae the parachomata become gradually more prominent and relatively narrower, being connected with the lower end of the transverse septula. In the *Pseudodoliolina-Metadoliolina* bioseries, the parachomata gradually become prominent, and the parachomata of *Pseudodoliolina pseudolepida*, *Metadoliolina dutkevitchi* and *M. multivoluta* which occur in the upper Middle to Upper Permian strata, extend to nearly the top of the chamber.

4. The number of the foramina increases. The number of the foramina rapidly increases throughout the ontogenetic and phylogenetic development. As the foramina increase, the number of the parachomata which alternate with foramina in position naturally increases.

5. The keriothecal layer of spirotheca gradually reduces its thickness. Although the thickness of the keriotheca essentially differs among the phylogenetic lineages in the verbeekinoids, it gradually decreases in every lineage. In species of *Misellina*, *Cancellina*, *Neoschwagerina*, and *Armenina* the keriothecal layer is clearly discerned beneath the tectum. However, the advanced species of *Verbeekina*, *Pseudodoliolina*, *Yabeina*, and *Lepidolina* have only a thin keriothecal layer which sometimes gives an appearance of a single layer. Especially in species of *Sumatrina*, the alveolar keriotheca can not be recognized in the spirotheca under the low magnification.

6. The shell-form changes from small subspherical to thickly fusiform or cylindrical.

The shell gradually changes from the small subspheric form as seen in species of *Misellina* and *Brevaxina* to large thickly fusiform or elongate fusiform as in species of *Metadoliolina*, *Pseudodoliolina*, *Yabeina*, *Lepidolina*, and *Sumatrina*.

## B. Phylogeny

A large number of species belonging to the Verbeekinoidea are known to occur successively in the Permian sequence of the Tethys Sea Region, and furnish details of evolutionary development of shell characters which afford us a key for tracing lines of descent at specific level. The biostratigraphic and paleontologic data obtained up to date demonstrate that the verbeekinoids diverged into several bioseries in their earliest stage of development almost simultaneously in upper Lower Permian age in the Tethyan Sea and its related region covering Asia Minor, Southeast Asia, the Japanese Islands, and the Pacific Northwest of North America. The ancestral species of the verbeekinoids are such minute and primitive species of *Misellina* (s.l.) as *Misellina* (M.) *minor*, *M. (M.) ibukiensis*, *M. (Brevaxina) compressa*, *M. (B.) otakiensis* and *M. (B.) dyhrenfurthi*. With respect to the ancestors of these earliest representatives of the Verbeekinoidea, our knowledge is very poor. THOMPSON (1948), MIKLUKHO-MAKLAY, RAUSER-CHERNOUSOVA and ROZOVSKAYA (1958) and RAUSER-CHERNOUSOVA (1963) are of the opinion that *Misellina* was derived from the Staffellidae. However, the Staffellidae can not be an ancestor of the verbeekinoids by the reasons mentioned in the next chapter (p. 44). Judging from the features of juvenile volutions of

species of *Misellina*, *Metadoliolina*, *Verbeekina*, *Neoschwagerina*, and other related genera, the Verbeekinoidea might have been derived from the Ozawainellidae. Species of *Eostaffella* may be the direct ancestor of the earliest members of *Misellina*.

*Maklaya*, *Cancellina*, *Armenina* and *Pseudodoliolina* had been derived directly from each of several ancestral species-groups of *Misellina* (s.l.) in lower Middle Permian times, and since then these genera independently evolved to form five main divergent lines. The five main lineages are as follows.

- (1) *Armenina-Verbeekina* bioseries.
- (2) *Pseudodoliolina-Metadoliolina* bioseries.
- (3) *Maklaya-Neoschwagerina-Yabeina* bioseries.
- (4) *Cancellina-Colania-Lepidolina* bioseries.
- (5) *Presumatrina-Afghanella-Sumatrina* bioseries.

The latter three lineages have septula which are the most important characteristic to distinguish them from the former two. These three lineages are grouped as the Neoschwagerinidae. Species of the *Maklaya-Neoschwagerina-Yabeina* bioseries have a shell with a thick spirotheca, broad and triangular or fan-shaped septa and septula, and are easily distinguishable from the other two groups (4, 5) in having much thicker and different shaped septa and septula, a thicker spirotheca, and a smaller proloculus even in the megalospheric specimens. This lineage is well traceable from the species-group of *Misellina* (*M.*) *claudiae* to that of *Yabeina globosa*.

Species of *Cancellina*, *Colania* and *Lepidolina* are very similar in shell morphology to species of *Presumatrina*, *Afghanella* and *Sumatrina*. In the later genera, however, septa and transverse septula are regular in shape and are short and thickened in their lower portion. *Presumatrina* resembles *Cancellina* in some important shell features and the former is considered to have been directly derived from the latter. *Presumatrina* is probably ancestral to both genera *Afghanella* and *Sumatrina*. Judging from the features of the spirotheca, septa, septula and parachomata, and stratigraphic order of occurrence, *Lepidolina* is a direct derivative from *Colania* which is, in turn, probably derived from *Cancellina*.

The phylogenetic relationships recognized in shell structures of the Verbeekinoidea are diagrammatically shown in Figs. 10 and 11.

Concerning with the life cycle, the *Cancellina-Colania-Lepidolina* bioseries shows distinct dimorphism in the size of shell and proloculus. The proloculi of megalospheric generation in this bioseries are very large. In this point, this bioseries is easily distinguished from the *Maklaya-Neoschwagerina-Yabeina* bioseries (Fig. 4). The microspheric specimens of the species of *Colania* (Pl. 7, Figs. 7 and 9) and *Lepidolina* (Pl. 8, Fig. 5; Pl. 9, Fig. 4) have large shell with more numerous volutions and a much smaller proloculus than the megalospheric specimens of the same species. These differences have been the main reason that most of the fusulinian paleontologists regarded the two types as the different species. Taking *Lepidolina multiseptata* as an example, as already discussed in the chapter of dimorphism, the microspheric individuals of this species have long been regarded as *Yabeina elongata* or the type-species of *Gublerina*. The speci-

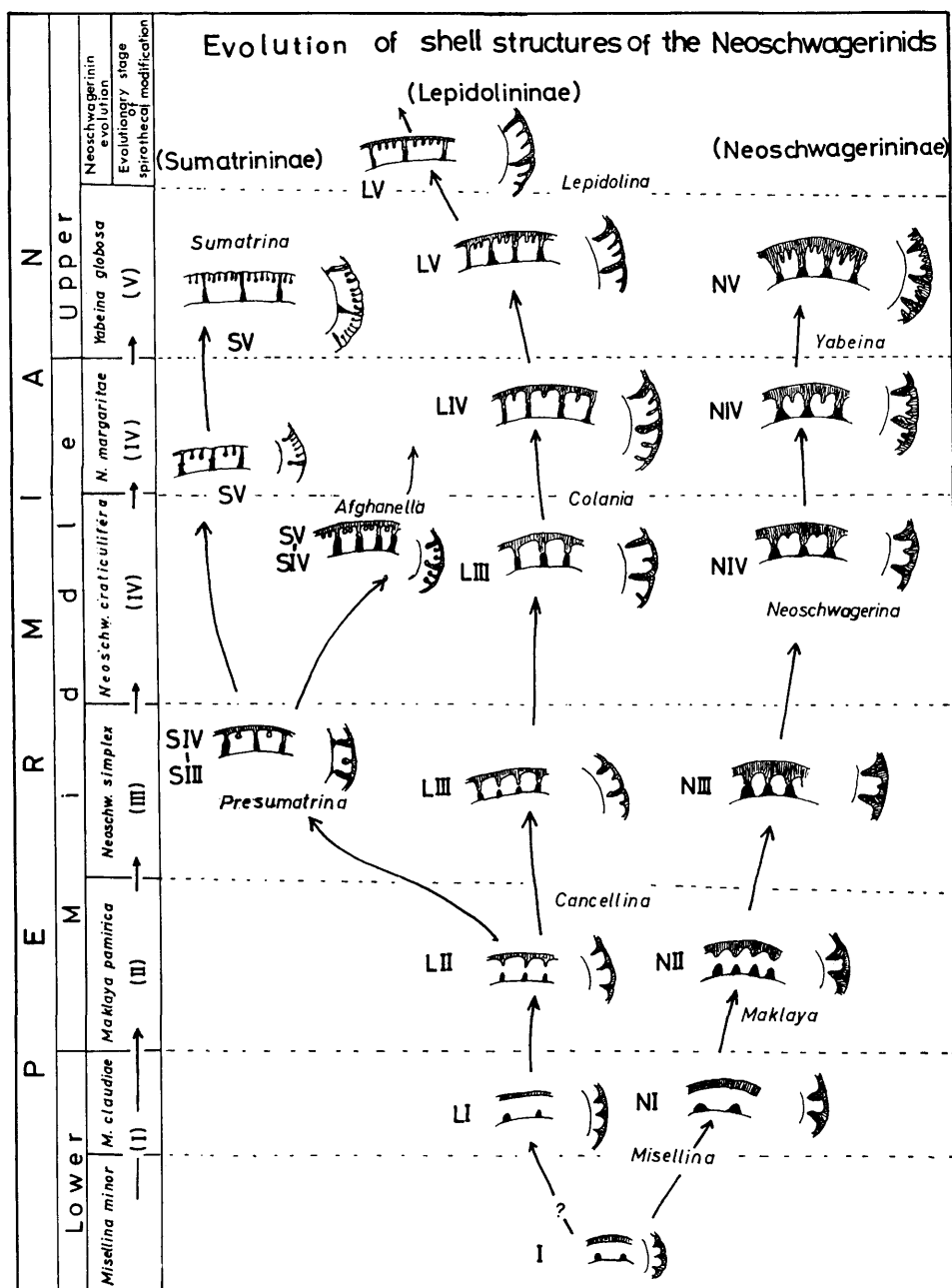


Fig. 10. Evolutionary development of shell structures and phylogeny of the Neoschwagerinidae.

mens referred to *Yabeina proboscis* CHEN and *Yabeina lantschichensis* TUMANSKAYA, the type-species of *Pseudoyabeina* TUMANSKAYA, represent merely the microspheric generation of *Colania douvillei* or *Lepidolina multiseptata*. Thus the *Cancellina-Colania-Lepidolina* bioseries constitutes a definite phylogenetic group in the Neoschwagerinidae. This may be also supported from the paleo-



Neoschwagerininae			ontogenetic development outer evolution				
Phylogenetic development ↑	specific name	☆	I	II	III	IV	V
	<i>Yabeina globosa</i>	V					
	<i>Neoschwagerina margaritae</i>	IV					
	<i>Neo. craticulifera</i>	IV					
	<i>Neo. simplex</i>	III					
	<i>Maklaya pamirica</i>	II					
	<i>Misellina claudiae</i>	I					
Lepidolininae			ontogenetic development* outer evolution				
Phylogenetic development ↑	specific name	☆	I	II	III	IV	V
	<i>Lepidolina kumaensis</i>	V					
	<i>L. multiseptata</i>	IV					
	<i>Colania douvillei</i>	IV					
	<i>Colania amacula</i>	III					
	<i>Cancellina nipponica</i>	II III					
	<i>Misellina ibukiensis</i>	I					
Sumatrininae			ontogenetic development* outer evolution				
Phylogenetic development ↑	specific name (or species group)	☆	I	II	III	IV	V
	<i>Sumatrina longissima</i>	V					
	<i>Sumatrina annae</i>	V					
	<i>Afghanella schencki</i>	V					
	<i>Presumatrina schellwieni</i>	IV					
	<i>Cancellina primigena</i>	III					

Fig. 12. Ontogenetic and phylogenetic relationship among the species of the Neoschwagerinidae in terms of the development of septula.

(☆: Evolutionary stages recognized in the development of the septula; ★: Based on the megalospheric specimens).

ecological standpoint. Species of *Colania* and *Lepidolina* occur in the micritic limestone facies. While species of *Neoschwagerina* and *Yabeina* are predominant in the sparitic limestone facies (Fig.1). In chronological distribution, the prosperity of the *Maklaya*-*Neoschwagerina*-*Yabeina* bioseries is gradually replaced by that of the *Cancellina*-*Colania*-*Lepidolina* bioseries. Thus three phylogenetic groups are differentiated in the Neoschwagerinidae which is characterized



Species of *Armenina* and *Verbeekina* may be derivatives from the species-group of *Misellina* (*Brevaxina*) *otakiensis* and *M. (B.) dyhrenfurthi* which have poorly developed parachomata.

The ontogenetic development of species should be also taken into account for the consideration of phylogeny of the verbeekinoids. As shown in Fig. 12, phylogenetic development of the representative species is well retained in their ontogenetic development. As the stratigraphic sequence is followed upwards the features of the earlier stages are tend to be much reduced in the megalospheric specimens of highly evolved species. This tendency is more distinct in species of the *Cancellina-Lepidolina* and *Presumatrina-Sumatrina* lineages than in species of the *Maklaya-Yabeina* lineage. In *Yabeina globosa*, the secondary transverse septula first appear in the fourth or fifth volution. While in *Lepidolina multi-septata*, they do in the second or third volution. In *Sumatrina longissima* they appear in the first volution. This fact well coincides with the order of appearance in stratigraphic sequence of species having the secondary transverse septula in respective lineages. Species of *Presumatrina* have secondary transverse septula and appear already in the lower Middle Permian strata (Fig. 11).

On the basis of the above discussions from various viewpoints, the phylogenetic relationship of the species-groups of the Verbeekinoids are summarized as shown in Fig. 13.

### Classification of Verbeekinoidea

On the basis of the above discussion on the phylogenetic relationships, the new supraspecific classification of the Verbeekinoidea is summarized as follows.

#### Order Foraminiferida

##### Suborder Fusulinina von MÖLLER, 1878

##### Superfamily Verbeekinoidea STAFF and WEDEKIND, 1910

Shell large for foraminifera, subspherical to elongate fusiform or sub-cylindrical, shell involute and planispiral throughout growth except for juvenile stage. Distinct dimorphism recognizable in some genera. Septa plane. Advanced genera have primary transverse and axial septula. Secondary transverse septula appear between primary transverse septula in highly evolved members. Spirotheca consists of a tectum and an alveolar keriotheca. In later members, keriothecal layer decreases in thickness. Foramina numerous, occurring at base of septa. Parachomata present, alternate in position with foramina.

##### Family Verbeekinidae STAFF and WEDEKIND, 1910

Shell subspherical to elongate ellipsoidal having a straight axis of coiling and umbilicated to rounded poles. Septa plane and rather widely spaced. Spirotheca composed of a tectum and a keriotheca with fine alveoli. Foramina numerous. Parachomata exist. No septula present.

*Remarks.*—The following genera belong to the Verbeekinidae:



- Verbeekina* STAFF, 1909  
 (= *Paraverbeekina* MIKLUKHO-KAKLAY, 1955)  
*Armenina* MIKLUKHO-MAKLAY, 1955  
*Metadoliolina* ISHII and NOGAMI, 1961  
 (= *Neomisellina* SHENG, 1963)  
*Misellina* SCHENCK and THOMPSON, 1940  
 Subgenus *Misellina* SCHENCK and THOMPSON, 1940  
 Subgenus *Brevaxina* SCHENCK and THOMPSON, 1940  
*Pseudodoliolina* YABE and HANZAWA, 1932

The presence of the parachomata is the most important biocharacter in the verbeekinid species which have no septula. As concerns the parachomata, however, there are two groups which tend towards the opposite direction in development. One is the group comprising two genera *Armenina* and *Verbeekina*, in which the parachomata become degenerated as the lapse of geologic time. The other group is represented by *Misellina*, *Pseudodoliolina* and *Metadoliolina* in which the parachomata are enhanced. Thus, the former is classified as the subfamily Verbeekininae and the latter as the subfamily Misellininae.

*Eoverbeekina* has long been included in the Verbeekinidae by most of fusulinian paleontologists (THOMPSON, 1948, 1964; DUNBAR, 1948; MIKLUKHO-MAKLAY, RAUSER-CHERNOUSOVA and ROZOVSKAYA, 1958; SHENG, 1963; KAHLER and KAHLER, 1966; GOBBETT, 1967; etc.) but KANMERA (1957) excluded it from Verbeekinidae and considered that *Eoverbeekina* has been derived from *Sphaerulina*. Recently TORIYAMA and KANMERA (1968) set up two new genera, *Thailandina* and *Neothailandina* from the Permian Rat Buri Limestone in Thailand. They grouped them as Thailandininae and placed them tentatively in the Neoschwagerinidae. All the species of *Eoverbeekina*, *Chenia*, *Thailandina* and *Neothailandina* (called here *Eoverbeekina* group for briefness' sake), however, have a shell of highly recrystallized calcite as in those of *Staffella*, *Nankinella*, *Sphaerulina*, *Pisolina*, *Pseudoendothyra* and *Haoella*. In the case that species of these genera occur along with those of Verbeekinoids and Fusulinoids, the individual shells of the former are selectively suffered from secondary replacement. It is highly possible that the shells of the *Eoverbeekina* group were probably different from those of the Verbeekinoids and Fusulinoids and originally composed of aragonite, and that the aragonite crystals were transformed into calcite in the early stage of diagenesis or fossilization.

Anyhow, the *Eoverbeekina* group constitutes a distinct phylogenetic group in the fusuline foraminifera.

#### Subfamily Verbeekininae STAFF and WEDEKIND, 1910

Shell subspherical, having a straight axis of coiling and umbilicated to rounded poles. Septa plane and widely spaced. Spirotheca composed of a tectum and a keriotheca with very fine alveoli. Parachomata discontinuous, uneven in height in earlier members, and rudimentary in the advanced members. Small foramina present at base of septa.

*Verbeekina* STAFF, 1909(=*Paraverbeekina* MIKLUKHO-MAKLAY, 1955)*Type-species.*—*Fusulina verbeeki* GEINITZ

Shell medium to large, subspherical to short ellipsoidal; involute except for juvenile stage which have Eostaffelloid coiling. Inner volutions tightly coiled, like Staffelloid in shape, latter volutions expand rapidly. Spirotheca thin for shell size, composed of a tectum and a keriotheca with very fine alveoli. Parachomata rudimentary. Foramina small and semicircular. Septa thin and very widely spaced.

*Remarks.*—In 1955, *Paraverbeekina* was proposed by M.-MAKLAY with *P. pontica* as the type-species. Later three species were added by SHENG (1963) to the genus *Paraverbeekina*. Except the slight difference of shell profile, no essential difference is recognized between species referred to *Paraverbeekina* and those of *Verbeekina*. Therefore *Paraverbeekina* is regarded as a junior synonym of *Verbeekina*.

*Armenina* MIKLUKHO-MAKLAY, 1955 emend. SHENG 1963[*Armenia* COOGAN, 1959 (nomen vanum)]*Type-species.*—*Armenina karinae* MIKLUKHO-MAKLAY

Shell small to moderate and subspherical to spherical, having slightly umbilicated to rounded poles. Shell form changes from *Brevaxina*-like form in inner few volutions with a short axis of coiling to subspherical one in outer volutions. Shell tightly coiled in inner volutions and gradually increases in height in outer volutions. Proloculus minute. Spirotheca thick, composed of a tectum and a finely alveolar keriotheca. Parachomata well developed throughout length of shell, but discontinuous and uneven in height.

## Subfamily Misellininae MIKLUKHO-MAKLAY, 1958

Shell subspherical to subcylindrical, possessing a straight axis of coiling. Septa plane. Proloculus large in megalospheric specimens. Parachomata well developed throughout length of shell, narrow, high and uniform in size. Foramina numerous, occurring at base of septa. Spirotheca composed of a tectum and a keriotheca with fine alveoli. Height of volution nearly constant throughout length of shell.

*Misellina* SCHENCK and THOMPSON, 1940(=*Moellerina* SCHELLWIEN, 1898; *Doliolina* SCHELLWIEN, 1902)*Type-species.*—*Doliolina ovalis* DEPRAT

Shell small to moderate, subspherical to oval, planispiral except for juvenile volutions of microspheric specimens. Spirotheca of two layers, a tectum and an alveolar keriotheca. Parachomata massive and well developed throughout length of shell. Circular to semicircular foramina occur at base of septa. No septula exist.

*Remarks.*—*Misellina* (s.l.) is the ancestral stock to the Neoschwagerinidae and the Verbeekinidae. As KANMERA and TORIYAMA (1968) noted, they comprises at least three or four species-groups, each of which respectively has some diagnostic characters that are retained in their descendants such as *Armenina*, *Pseudodolilolina*, *Cancellina*, and *Maklaya*. For instance, *Misellina* (*Brevaxina*) *dyhrenfurthi* DUTKEVITCH, *Misellina* (*Brevaxina* ?) *otakiensis* HAJIMOTO and other allied species of *Misellina* are considered to be ancestral to species of *Armenina* or *Verbeekina*. *Misellina ovalis* (DEPRAT), the type-species of the genus, is very similar in shell form and natures of the parachomata to early species of *Pseudodolilolina* or *Metadolilolina*.

Species of *Maklaya* may be directly derived from the species group of *Misellina* comprising *M. claudiae* and *M. aliciae*. Because of rare occurrence of species of *Misellina*, our knowledge concerning the classification of these varied species-groups is still incomplete. Two distinct groups are, however, easily discriminated as the followings.

Subgenus *Misellina* SCHENCK and THOMPSON, 1940

*Type-species.*—*Dolilolina ovalis* DEPRAT

Shell small to moderate, ellipsoidal, having a straight axis of coiling and rounded to bluntly pointed poles. Spirotheca and septa relatively thick. Parachomata broad, high and continuous throughout length of shell. Proloculus of megalospheric specimens large for shell-size. Septa relatively thick.

Subgenus *Brevaxina* SCHENCK and THOMSON, 1940

*Type-species.*—*Dolilolina compressa* DEPRAT

Shell small, nautiloid to staffelloid having umbilicated poles and a short axis of coiling. Except for inner volutions which are evolute, shell involute. Height of volution rather rapidly increases. Parachomata small and widely spaced. Spirotheca and septa thin.

*Metadolilolina* ISHII and NOGAMI, 1961

(= *Neomisellina* SHENG, 1963)

*Type-species.*—*Pseudodolilolina pseudolepida gravitesta* KANMERA

Shell moderate to large, ellipsoidal to subcylindrical, having rounded poles and a straight axis of coiling. Volution numerous. Inner one or two volutions usually discoidal, having a short axis of coiling. Proloculus minute. Spirotheca thick, composed of a tectum and a thick keriotheca with fine alveoli. Thin film sometimes covers inner surface of keriotheca. Dimorphism well recognized. Parachomata massive and well developed throughout the length of shell. Septa plane, thick, and widely spaced.

*Pseudodolilolina* YABE and HANZAWA, 1932

*Type-species.*—*Pseudodolilolina ozawai* YABE and HANZAWA

Shell ellipsoidal to cylindrical, having a straight axis of coiling and rounded poles. Shell uniformly expands. Proloculus medium to large. Spirotheca thin, composed of a tectum and an extremely thin dense layer which is analogous to the alveolar keriotheca of other Verbeekinid genera. Parachomata well developed throughout length of shell, high, and triangular to elongate hemispherical in section. Foramina numerous.

#### Family Neoschwagerinidae DUNBAR and CONDRA, 1928

Shell medium to large for the Verbeekinoid foraminifera, thick fusiform to subspherical, having numerous, closely coiled volutions, a straight to a slightly shifting axis of coiling and bluntly to pointed poles. Distinct dimorphism in shell- and proloculus-size recognizable in some members. Septa short and closely spaced. Septula characteristic of this family. In early members only axial and primary transverse septula developed. Secondary transverse septula appear in advanced members. Parachomata well developed throughout length of shell. Spirotheca of two layers, a tectum and an alveolar keriotheca, but keriotheca extremely thin in advanced members.

*Remarks.*—The presence of septula is the most important characteristic of the family. Concerning the natures of the septula, three distinct lineages are recognized in the genera of this family. They are *Maklaya-Neoschwagerina-Yabeina*, *Cancellina-Colania-Lepidolina*, and *Presumatrina-Afghanella-Sumatrina* bioseries, respectively. Each of them is here treated as a subfamily of the Neoschwagerinidae.

#### Subfamily Neoschwagerininae DUNBAR and CONDRA, 1928

Shell medium to large, subspherical to inflated fusiform, planispiral and involute except for juvenile stage of microspheric generation. Size of shell and proloculus between megalospheric and microspheric generations not so distinct. Two generations usually discriminated only by mode of coiling in juvenile volutions and slight difference in proloculus-size. Septa thick and relatively closely spaced. Spirotheca thick, composed of a tectum and a thick keriothecal layer with fine alveoli. Axial and primary transverse septula thick and triangular or fan-shaped. They are incipient in development in the earliest members. Secondary transverse septula appear in the latest members, and thick and short. Parachomata relatively thick and low, usually join with lower ends of septula, leaving a lateral passage in central part of chamber. Foramina present at base of septa; circular and regularly spaced.

The following three genera are included in this subfamily.

Genus *Maklaya* KANMERA and TORIYAMA, 1968

Genus *Neoschwagerina* YABE, 1903

Genus *Yabeina* DEPRAT, 1914

#### *Neoschwagerina* YABE, 1903

(=? *Crimellina* TUMANSKAYA, 1953; *Metaschwagerina* MINATO and HONJO, 1958)

*Type-species.*—*Schwagerina craticulifera* SCHWAGER

Shell moderate, subspherical to fusiform, having bluntly pointed to rounded poles, a straight to slightly shifting axis of coiling and numerous volutions. Proloculus of megalospheric specimens moderate in size. Microspheric generation is distinguishable from megalospheric one by the different mode of coiling of juvenile volutions and the slight difference of proloculus-size. Spirotheca thick, composed of a tectum and a fine alveolar keriotheca. Primary transverse septula broad and triangular or fan-shaped in cross section. Axial septula thick and short. Secondary transverse septula appear in outer volutions of evolved species including the type-species. Parachomata massive and low, usually connected with lower end of primary transverse septula.

*Maklaya* KANMERA and TORIYAMA, 1968  
*Type-species.*—*Cancellina pamirica* LEVEN

Shell small, subspherical, having bluntly to rounded poles. Except for juvenile volutions of microspheric generation, shell planispiral and involute. Spirotheca thick, composed of two layer, a tectum and a thick alveolar keriotheca. Septa thick and short. Primary transverse septula incipiently developed, broad and short, and not yet connected with lower end of parachomata. Neither axial nor secondary septula present. Parachomata broad and low. Foramina occur at base of septa.

*Yabeina* DEPRAT, 1914  
 [= *Jabeina* MIKLUKHO-MAKLAY, 1953; SOSNINA; 1965 (nomen vanum)]  
*Type-species.*—*Neoschwagerina (Yabeina) inouyei* DEPRAT, 1914  
 (= *Neoschwagerina globosa* YABE, 1906)

Shell large, inflated fusiform to fusiform, with bluntly pointed poles and numerous volutions. Shell uniformly expands. Proloculus very small for shell-size. Difference in size of shell and proloculus between megalospheric and microspheric generations not distinct. Spirotheca moderate to thin, composed of a tectum and an alveolar keriotheca. Septa relatively thin and numerous. Axial septula thick and variable in shape, not equal in length. Primary transverse septula elongate triangular to irregular in shape. Secondary transverse septula well developed especially in outer volutions, short and irregular. Parachomata relatively narrow and low, connected with lower end of septula. Foramina numerous, present at base of septa.

#### Subfamily Lepidolininae MIKLUKHO-MAKLAY, 1958

MIKLUKHO-MAKLAY (1958) first grouped genera *Lepidolina* and *Yabeina* as the Lepidolininae. KAHLER and KAHLER (1966) regarded Lepidolininae as a synonym of Neoschwagerininae, and following the opinions of HANZAWA and MURATA (1963) and ISHII and NOGAMI (1964). They treated *Lepidolina* as a synonym of *Yabeina*. As already insisted in the preceding chapter, species referred to *Lepidolina* are phylogenetically derived not from species of *Yabeina* but from *Colania*. Based on this fact, *Lepidolina*, *Colania* and *Cancellina* are sepa-

rated from the Neoschwagerininae. In this paper these genera are grouped as the Lepidolininae in the sense entirely different from that used by M.-MAKLAY.

Shell moderate to very large for verbeekinoid foraminifera, inflated fusiform to subcylindrical, having a straight to slightly shifting axis of coiling and bluntly pointed to rounded poles. Distinct dimorphism in size of shell and proloculus recognized. Compared with megalospheric specimens, microspheric ones usually have a much larger and elongate shell with a large number of volutions and a very small proloculus. Proloculus of megalospheric shell very large, and this feature is much accelerated in advanced genera. Spirotheca thin, composed of a tectum and a thin alveolar keriotheca. Septa also thin and widely spaced. Septula thin and short. Axial and primary transverse septula present in shells of earlier members. Secondary transverse septula appear in advanced members. Parachomata narrow and high. Foramina numerous, occur at base of septa.

*Lepidolina* LEE, 1933 emend.

[=*Pseudoyabeina* TUMANSKAYA, 1954; *Gublerina* MINATO and HONJO, 1959; *Kumaella* CHISAKA, 1960 (nomen nudum)]

*Type-species.*—*Neoschwagerina* (*Sumatrana*) *multiseptata* DEPRAT

Shell very large for verbeekinoid foraminifera, inflated fusiform to elongate fusiform, having a straight to shifting axis of coiling and bluntly pointed to rounded poles. Dimorphism distinct; megalospheric shell has very large proloculus, while microspheric shell is very large and elongate and have numerous volutions and a very small proloculus. Spirotheca very thin, composed of a tectum and a lower thin keriothecal layer with fine alveoli. Axial and primary transverse septula very thin and short. Secondary transverse septula well developed, thin and short. Axial and secondary transverse septula irregular in length and thickness. Secondary septula closely spaced and its lower parts slightly thickened by deposits related to parachomata. Chomata well developed, very narrow and high, connecting with lower end of primary transverse septula. Foramina small and numerous, occurring at base of septa.

*Remarks.*—*Lepidolina* has the most evolved shell structures in the Verbeekinoidea and occupies the uppermost horizon of the Verbeekinoid biostratigraphy. It is similar to *Sumatrana* and *Yabeina* at first glance. It is, however, distinguished from *Sumatrana* by the different shape and the irregularity of septula, the spirothecal structure and by having a much larger shell with numerous volutions. While it is distinguished from *Yabeina* by having a larger proloculus in the megalospheric generation, a larger, elongate shell of the microspheric generation, and the essential difference in the thickness and shape of septa and septula.

*Cancellina* HAYDEN, 1909

[=*Neoschwagerina* (*Minoella*) HONJO, 1959]

*Type-species.*—*Neoschwagerina* *primigena* HAYDEN

Shell small to moderate, ellipsoidal to fusiform having a relatively large proloculus in megalospheric specimens. Spirotheca thin, composed of a tectum

and a thin keriotheca. Septa thin and widely spaced. Primary transverse septula thin and short, and widely spaced. Axial septula incipiently developed. No secondary septula present. Parachomata narrow and high, usually extending to lower end of transverse septula. Small semicircular foramina present at base of septa.

*Colania* LEE, 1933 emend.

(=*Gifuella* HONJO, 1959)

*Type-species.*—*Colania kwangsiana* LEE

Shell medium to very large for Verbeekinoid foraminifera, fusiform to elongate fusiform. Dimorphism distinct; megalospheric shell has a large proloculus, while microspheric one very large, elongate, and have a minute proloculus and numerous volutions. Septa thin and widely spaced. Spirotheca thin, composed of a tectum and a keriotheca. Axial septula well developed, thin and short, and irregular in length and width. Primary transverse septula slender, connecting with top of parachomata. Secondary transverse septula not well developed, but one or two septula seen in outer volutions. Parachomata narrow and high. Foramina numerous, occurring at base of septa.

*Remarks.*—*Colania* was proposed by LEE (1933) with *C. kwangsiana* LEE as the type-species of the genus. He gave the following diagnosis, "..... There is a group of forms in which the inner whorls are perfectly Neoschwagerinoid conforming to the type of *N. craticulifera*. But as we trace to the outer whorls the alveolar structure in the septa becomes gradually indistinct, and finally they turn out to be entirely opaque projections. At the same time, the keriotheca in the spiral wall thins down until it completely disappears. This consolidation of spiral or transverse septa is accompanied by the introduction of transverse septula and an axial septa immediately behind each antetheca. The axial septa is posteriously followed by one or two semipartitions or septula which generally remains alveolar.

It is neither just nor convenient to refer this group of forms either to *Neoschwagerina* or to *Yabeina*. They represent an intermediate stage in the evolutionary series. For this transitional type I propose the generic name *Colania*."

Thus LEE regarded *Colania* as the transitional group between *Neoschwagerina* and *Yabeina*. The type-species was, however, based upon some ill-oriented specimens, and his original illustrations and description of the type-species were so insufficient that the diagnosis of *Colania* remained ambiguous. Many later authors have regarded *Colania* as a mere synonym of *Yabeina* or *Lepidolina*.

In 1959, HONJO proposed *Gifuella* for the neoschwagerinid species which have thin transverse septula, designating *Gifuella gifuensis* as the type-species. He included *Neoschwagerina douvillei* OZAWA in *Gifuella*. *Gifuella gifuensis* and *Neoschwagerina douvillei* are, however, very similar to species of *Colania*, especially to *Colania* sp. illustrated by LEE (1933) in the nature of septa and septula. Recently SHENG (1963) described the type-species of *Colania* based on a large number of specimens from the type locality of the species, the Maokow Limestone

in Kwangsi, South China. Shell-characters of *Colania kwangsiana* are well understood from SHENG's description and illustrations. Fortunately I had an opportunity to study some neoschwagerinid species from the Rat Buri Limestone in central Thailand which are very similar to *Colania kwangsiana* and other allied species described by SHENG. The species from Thailand displays a dimorphism and a lot of large specimens which represent the microspheric generation are found along with many smaller megalospheric specimens with a large proloculus. I have found a similar dimorphism in the specimens of *Neoschwagerina douvillei* from the Akiyoshi Limestone in Southwest Japan. On the basis of these observations, I have reached the conclusion that *Colania kwangsiana*, "*Gifuella*" *gifuensis*, "*Neoschwagerina*" *douvillei* are neither referable to *Neoschwagerina* nor *Yabeina*, but constitute the transitional group between *Cancellina* and *Lepidolina* in the evolutionary stage, because they show much resemblance in essential biocharacters with species of *Lepidolina* including *L. multi-septata*. From these reasons, the generic name *Colania* should be employed for the transitional species-group between *Cancellina* and *Lepidolina*. The revised diagnosis of *Colania* has been given above. To be noted here is that *Gifuella* is a synonym of *Colania*.

#### Subfamily Sumatrininae KÄHLER and KÄHLER, 1946

The following genera constitute this subfamily.

*Afghanella* THOMPSON, 1946

*Presumatrina* TUMANSKAYA, 1950

*Sumatrina* VOLZ, 1904

Shell medium, inflated fusiform to cylindrical, having bluntly pointed poles and a straight to slightly shifting axis of coiling. Proloculus of megalospheric generation large for shell-size.

Spirotheca very thin, composed of a tectum and a thin keriotheca. Spirotheca decreases in thickness from earlier member to latest member which has a very thin keriothecal layer. Septa thin and relatively long, and widely spaced. Primary transverse septula thin and short, and widely spaced. Secondary transverse septula and axial septula short and thin, club-shaped, uniform in size and shape, and regularly spaced. Parachomata well developed and high. Foramina numerous.

*Sumatrina* VOLZ, 1904

(=*Pseudolepidolina* TUMANSKAYA, 1953)

*Type-species*.—*Neoschwagerina* (*Sumatrina*) *annae* VOLZ

Shell medium and elongate fusiform to cylindrical, having a straight to slightly shifting axis of coiling, a small number of volutions, and a relatively large proloculus. Spirotheca extremely thin, composed of a tectum and an extremely thin keriotheca. Septa long and thin, and widely spaced. Primary transverse septula thin and short. Secondary transverse septula also thin and uniform in size and shape, their lower part thickened, and club-shaped in



cross-section. Two to four secondary transverse septula exist between primary transverse septula. Parachomata massive and high, connecting with lower end of primary transverse septula. Foramina numerous, occurring throughout the length of shell.

*Afghanella* THOMPSON, 1946

(=*Pseudosumatrina* TUMANSKAYA, 1950)

*Type-species*.—*Afghanella schencki* THOMPSON

Shell inflated fusiform to typical fusiform, having a straight axis of coiling and a moderate to large proloculus. Spirotheca thin, composed of a tectum and a keriotheca. Septa thin and long, and widely spaced primary transverse septula short and thin, and uniform in size and shape. Secondary transverse septula thin and short. Lower part of septula thickened by secondary deposits related to parachomata. Parachomata well developed, and narrow and high. Foramina semicircular.

*Presumatrina* TUMANSKAYA, 1950

[=*Praesumatrina* R.-CHERNOUSOVA and FURSENKO, 1959;

MIKLUKHO-MAKLAY, 1963; R.-CHERNOUSOVA, 1963;

SOSNINA, 1965; LEVEN, 1967 (nomen vanum)]

*Type-species*.—*Doliolina schellwieni* DEPRAT

Shell small to medium for neoschwagerinid foraminifera, elongate fusiform to typical fusiform, having a straight to slightly shifting axis of coiling and bluntly pointed to rounded poles. Spirotheca thin, composed of a tectum and a thin keriotheca. Septa thin and widely spaced. Axial septula developed between septa. Transverse septula thin and short, and uniform in size and shape. Its lower part thickened, connecting top of parachomata. One secondary transverse septulum appears between each pair of primary transverse septula in outer volutions. Proloculus large for shell-size. Parachomata well developed and narrow and high.

## References

- BANDY, O. L. (1964): General correlation of foraminiferal structure with environment. In J. IMBRIE and N. NEWELL [Editors] *Approaches to paleoecology*, 75–90, John Wiley and Sons, New York.
- CHEN, S. (1934): Fusulinidae of South China, Part 1. *Palaeont. Sinica*, [B], 4, (2), 1–185, pls. 1–16.
- (1956): Fusulinidae of South China, Part 2. *Ibid.*, [N. S., B], (6), 1–71, pls. 1–14.
- CHISAKA, T. (1960): On some Permian Fusulinids from the Takagami Conglomerate, Choshi Peninsula, Chiba Prefecture, Japan. *Jour. Coll. Arts and Sci. Chiba Univ.*, 3, (2), 235–254, pls. 1–9.
- (1960): Verbeekinae, Neoschwagerininae and Sumatrininae from Japan. “*Fossils*” (*Kaseki*), *Palaeont. Soc. Japan*, (1), 17–28. (in Japanese).
- (1962): Fusulinids from the vicinity of Maiya town, Kitakami Mountainland, and Upper Permian fusulinids of Japan. *Jour. Coll. Arts and Sci. Chiba Univ.*,

- [*Nat. Sci.*], 3, (4), 519–551, pls. 1–8.
- CIRY, R. (1941): Les Fusulinidés de Turquie. *Annales Palaéontologie*, 29, 53–78, pl. 3.
- COLANI, M. (1924): Nouvelle contribution à l'étude des Fusulinidés de l'Extrême-Orient. *Indochine Service Géol., Mém.* 11, (1), 1–191, pls. 1–29.
- COOGAN, A. H. (1958): Russian Fusulinid genera. *Jour. Paleont.*, 32, (2), 304–311, 2 text-figs.
- DAWSON, G. M. (1879): On a new species of *Loftusia* from British Columbia. *Quart. Jour., Geol. Soc. London*, 35, 69–75, pl. 6.
- DEPRAT, J. (1912): Étude des Fusulinidés de Chine et d'Indochine et classification des calcaires à fusulinés. *Mém. Surv. Géol. l'Indochine*, 1, (3), 1–76, pls. 1–9.
- (1913): Étude des Fusulinidés de Chine et d'Indochine et classification des calcaires (II<sup>e</sup> Mémoire). Les Fusulinidés des calcaires carbonifériens et permien du Tonkin, du Laos et du Nord-Annam. *Ditto*, 2, (1), 1–74, pls. 1–10.
- (1914): Étude des Fusulinidés du Japon, du Chine et d'Indochine et classification des calcaires à fusulines (III<sup>e</sup> Mémoire). Étude comparative des Fusulinidés d'Akasaka (Japon) et des fusulinidés de Chine et d'Indochine. *Ditto*, 3, (1), 1–45, pls. 1–8.
- (1915): Étude des Fusulinidés de Chine et d'Indochine et classification des calcaires carbonifériens et permien du Tonkin, du Laos et du Nord-Annam. *Ditto*, 4, (1), 1–30, pls. 1–3.
- DOUGLAS, J. A. (1950): The Carboniferous and Permian faunas of the South Iran and Iranian Baluchistan. *Paleont. Indica, Mem. Geol. Surv. Indica*, [N. S.], 22, (7), 57 pp., pls. 1–5.
- DOUGLASS, R. C. (1967): Permian Tethyan Fusulinids from California. *Professional Paper, Geol. Surv. U.S.A.*, 593-A, A1–A13, pls. 1–6.
- DOUTKEVITCH, G. A. and KHAVAKOV, A. B. (1934): Permian fauna of Fusulinidae found in Sections of Kara-Su and Kuberganda in East Pamir. *Acad. Sci., U.S.S.R., Tadjik Complex Exped., 1932, Geol. Pamir*, 8, 53–104, pls. 1–3.
- DOUVILLÉ, M. H. (1906): Les calcaires à fusulines de l'Indo-Chine. *Soc. Géol. France, Bull.*, [4], 6, 588–602, pls. 17–18.
- (1934): Le Permien Marin de l'Extrême-Sud Tunesien, II Les Fusulinidés de la Tunisie. *Mém. Serv. Carte Géol. Tunisie*, [N. S.], (1), 75–90, pls. 1–3.
- DUNBAR, C. O. (1932): *Neoschwagerina* in the Permian fauna of British Columbia. *Roy. Soc. Canada, Trans.*, [3], 26, (4), 45–49, pl. 1.
- (1948): Fusuline Foraminifera. In J. A. CUSHMAN [Editor] *Foraminifera*, 142–170, pls. 10–12, 44–45.
- GEINITZ, H. B. (1876): Zur Geologie von Sumatra. I. Zur Geologie von Sumatra's Westküste. *Palaontographica*, 22, 399–404.
- GOBBETT, D. J. (1967): Palaeozoogeography of the Verbeekinidae (Permian Foraminifera). In C. G. ADAMS and D. V. AGER [Editors] *Aspects of Tethyan Biogeography. Systematics Assoc. Publ.*, (7), 77–91.
- GRELL, K. G. (1957): Untersuchungen über die Fortpflanzung und Sexualität der Foraminiferen. 1. *Rotaliella roscoffensis*. *Archiv Protistenkunde*, 102, (2), 147–164, pls. 1–11.
- GUBLER, J. (1935): Les Fusulinidés du Permien de l'Indochine, leur structure et leur classification. *Soc. Géol. France, Mém.*, [N. S.], 11, (26), 1–173, pls. 1–8.
- GUNG, F. (1966): Some new species of Fusulinids from the Upper Permian of Ganze district, Pinnan Province, Kweichow. *Acta Paleont. Sinica*, 14, (1), 80–89, pl. 1.
- HANZAWA, S. and MURATA, M. (1963): The paleontologic and stratigraphic considerations on the Neoschwagerininae and Verbeekininae, with the descriptions of some fusulinid foraminifera from the Kitakami Massif, Japan. *Sci. Rep. Tohoku Univ., (geology)*, 35, (1), 1–31, pls. 1–20.
- HASEGAWA, Y. (1965): "*Lepidolina*" from the Otani Conglomerate, Central Japan. "*Earth Science*" (*Chikyu Kagaku*), (76), 25–33, pls. 1–3.
- HAYDEN, H. H. (1909): Fusulinidae from Afghanistan. *India Geol. Survey Records*, 38, 230–256, pls. 17–22.

- HONJO, S. (1959): Neoschwagerinids from the Akasaka Limestone. *Jour. Fac. Sci., Hokkaido Univ.*, [4], 10, (1), 111-161, pls. 1-12.
- HUZIMOTO, H. (1936): Stratigraphical and Palaeontological Studies of the Titibu System of the Kwantō-mountainland. Part 2, Palaeontology. *Sci. Rep. Tokyo Bunrika Daigaku*, [C], (2), 32-125, pls. 1-26.
- (1956): A new species of *Parafusulina* from the Kitakami massif, Japan. *Trans. Proc. Palaeont. Soc. Japan*, [N. S.], (21), 157-160, pl. 25.
- IGO, H. (1960): *Yabeina* from the Omi limestone, Niigata Prefecture, Central Japan. *Sci. Rep., Tohoku Univ.*, [2], (Geol.), Spec. vol. 4, 335-343, pl. 36.
- (1964): Permian Fusulinids of Nyukawa, Central Japan, Part 1. Some Fusulinids from the Shiroy and Kono Formations. *Jour. Paleont.*, 38, (4), 637-649, pls. 103-106.
- (1966): Some Permian Fusulinids from Pahang, Malaya. In T. KOBAYASHI and R. TORIYAMA [Editors] *Geol. Paleont. Southeast Asia*, 3, (33), 30-38, pls. 4-9. Tokyo Univ. Press, Tokyo.
- ISHII, K. (1966): On some Fusulinids and other foraminifera from the Permian of Pahang, Malaya. *Jour. Geosci., Osaka City Univ.*, 9, Art. 4-V, 131-136, pls. 5-6.
- (1966): Permian of the western part of Cambodia—On the stratigraphy of Sisophon and Battambang limestone in Cambodia. "*Fossils*" (*Kaseki*), *Palaeont. Soc. Japan*, (12), 29-39. (in Japanese).
- and NOGAMI, Y. (1966): On the new genus *Metadoliolina*. *Trans. Proc. Palaeont. Soc. Japan*, [N. S.], 44, 161-166, pl. 25.
- and ——— (1962): On *Yabeina shiraiwensis* OZAWA and *Yabeina yasubensis* TORIYAMA. *Fac. Sci., Osaka City Univ.*, 6, Art. 2, 59-67, pls. 1-2.
- and ——— (1964): Contribution to the Geology and Paleontology of Cambodia. Part 1. Permian Fusulinids. *Fac. Sci., Osaka City Univ.*, 8, Art. 2, 9-37, pls. 1-8.
- and SHIMIZU, D. (1967): *Palaeofusulina-Colaniella* fauna of the Permian Maizuru Group, Japan. "*Fossils*" (*Kaseki*), *Palaeont. Soc. Japan*, (15), 26-30.
- ISHIZAKI, K. (1963): Verbeekinae from the inferred Upper Wolfcampian Limestone in the west of Ryoseki, Kochi Prefecture. *Trans. Proc. Palaeont. Soc.*, [N. S.], (50), 51-64, pl. 9.
- KAHLER, F. and KAHLER, G. (1966): Über die Doppelschalen der Fusuliniden. *Ecologiae Geol. Helv.*, 59, (1), 33-38.
- and ——— (1966-67): Fusulinida (Foraminiferida). In F. WESTPHAL [Editor] *Fossilium Catalogues*, Pars 111-114, Dr. JUNK-Publishers, Hague, Netherlands.
- KALMIKOVA, M. A. (1967): Permian Fusulinids of Darvas. *Vsesoiuzny Nauchno-Issled. Geol. Inst., Ministerstva Geologii S.S.S.R. (VSEGEI)*, [N. S.], 116, 116-221, pls. 1-31.
- KANMERA, K. (1954): Fusulinids from the Upper Permian Kuma Formation, Southern Kyushu, Japan. With special reference to the Fusulinid Zone in the Upper Permian of Japan. *Mem. Fac. Sci., Kyushu Univ.*, [D], 4, (1), 1-38, pls. 1-6.
- (1957): Revised Classification of *Cancellina* and *Neoschwagerina*, and Evolution of Sumatrininae and Neoschwagerininae. *Ibid.*, 6, (1), 47-64, pls. 19-20.
- (1963): Fusulines of the Middle Permian Kozaki Formation of Southern Kyushu. *Ibid.*, 14, (2), 79-141, pls. 11-19.
- (1967): Biostratigraphic position of the Kuman stage with special reference to the international correlation. "*Fossil*" (*Kaseki*), *Palaeont. Soc. Japan*, (15), 31-39. (in Japanese).
- and TORIYAMA, R. (1968): Fusulinacean fossils from Thailand. Part III. *Maklaya*, new generic designation for Neoschwagerinids of the group of *Cancellina pamirica* LEVEN. In T. KOBAYASHI and R. TORIYAMA [Editors], *Geol. Paleont. Southeast Asia*, 5, 31-46, pls. 4-5, Tokyo Univ. Press, Tokyo.
- KANUMA, M. (1960): Stratigraphical and paleontological studies of the southern part of the Hida Plateau and the northeastern part of the Mino Mountainland, Central Japan. Part II. Paleontology. *Bull. Tokyo Gakuhei Univ.*, 11, 55-73,

pls. 10-13.

- KAWANO, M. (1961): Stratigraphical and paleontological studies of the Paleozoic formations in the western part of the Chugoku Massif. *Bull. Fac. Educ., Yamaguchi Univ., Mathematics and Sci.*, 11, Special Number, 1-133, pls. 1-15.
- (1967): On the limestone in the Neighbourhood of Managa-take of the Akiyoshi Plateau. *Bull. Akiyoshi-dai Sci. Museum*, (4), 1-6, pls. 1-2.
- KOBAYASHI, M. (1957): Paleontologic study of the Ibukiyama Limestone, Shiga Prefecture, Central Japan. *Sci. Rep. Tokyo Kyoiku Daigaku*, [C], 48, 247-311, pls. 1-10.
- KOCHANSKY-DEVIDÉ, V. (1958): Die Neoschwagerinenfaunen der südlichen Crna Gora (Jugoslawien). *Geol. vjesin.* 11, 45-76, pls. 1-4.
- (1965): Die Fusuliniden foraminiferen aus dem Karbon und Perm im Velebit und in der Lika (Kroatien) Mittleres und Oberes Perm. *Acta Geol.*, 5, 101-150, pls. 1-13.
- and RAMOVŠ, A. (1955): Die Neoschwagerinenschichten und ihre Fusuliniden-fauna bei Bohinjska Bela und Bled (Julische Alpen, Slowenien, NW-Jugoslawien). *Slov. Akad.*, 4, 359-424, pls. 1-8.
- KOIKE, T., HASHIMOTO, W. and SATO, T. (1968): Fusulinid-bearing limestone pebbles found in the Agbahag Conglomerate, Mansalay, Oriental Mindoro, Philippines. *Geol. Palaeont. Southeast Asia*, 4, 198-210, pls. 31-32.
- KONISHI, K. (1952): Permian Microfossils in the Dodo Conglomerate of the Yasuba-type. *Trans. Proc. Paleont. Soc. Japan*, [N. S.], (5), 155-165, pl. 14.
- (1964): Geologic notes on Tonaki-jima and Width of Motobu Belt, Ryukyu Islands. *Sci. Rep. Kanazawa Univ.*, 9, 169-188, pls. 1-3.
- LANGE, E. (1925): Eine mittelpermische Fauna von Guguk Bulat (Padanger Oberland, Sumatra). *Geol.-mijnb. Genootsch. Nederland en Kolonien Verh.*, *Geol. Ser.*, 7, 157-239, pls. 1-5.
- LEE, J. J., FREUDENTHAL, H. D., MULLER, W. R., KOSOY, V., PIERCE, S. and GROSSMAN, R. (1963): Growth and physiology of foraminifera in the laboratory: Part 3—Initial studies of *Rosalina floridana* (CUSHMAN). *Micropaleont.*, 9, (4), 449-466, pls. 1-3.
- LEE, J. S. (1933): Taxonomic criteria of Fusulinidae with notes on seven new Permian genera. *Mem. National Research Inst. Geol.*, (14), 1-21, pls. 1-5.
- LEVEN, E. Ya. (1967): Stratigraphy and Fusulinids of the Pamir Permian deposits. *Acad. Sci. U.S.S.R., Geol. Inst., Transact.* 167, 5-215, pls. 1-39.
- LISTER, J. J. (1895): Contributions to the life history of the Foraminifera. *Philosoph. Trans. Royal Soc., London*, [B], 186, 401-453, pls. 6-9.
- LOEBLICH, A. R. and TAPPAN, H. (1961): Suprageneric classification of the Rhizopoda. *Jour. Paleont.*, 35, (2), 245-330.
- MIKLUKHO-MAKLAY, A. D. (1955): New data on Permian fusulinids of the southern part of the U.S.S.R. *Acad. Sci. U.S.S.R., DOKLADY*, [N. S.], 105, 573-576.
- (1957): Some fusulinids from the Permian of Crimea. *Series Geol. Sci.*, 9, 93-159, pls. 1-14.
- (1958): Systematics of highly advanced fusulinids (Superfamily Verbeekinoidea). *Bull. Leningrad Univ.*, Number 12, *Ser. Geol. Geograph.*, 2, 5-14.
- (1963): *The Upper Paleozoic System of Central Asia*. Leningrad Univ. Publication, 1-328.
- , PAUSER-CHERNOUSOVA, D. M. and ROZOVSKAYA, S. F. (1958): Systematics and phylogeny of Fusulinida. *Acad. Sci. U.S.S.R.*, 2 (*Voprosy Mikropaleontologii*), 5-21.
- MINATO, M. and HONJO, S. (1959): The axial septula of some Japanese Neoschwagerininae with special remarks of the phylogeny of the subfamily Neoschwagerininae DUNBAR and CONDRA, 1928. *Jour. Fac. Sci. Hokkaido Univ.*, [4], 10, (2), 305-336, pls. 1-6.
- and KOCHANSKY-DEVIDÉ, V. (1964): Über die Axialseptula einiger Neoschwagerinenarten aus Jugoslawien. *Geol. Vjesnik, Zagreb*, 17, 143-147.
- MORIKAWA, R. (1960): Fusulinids from the Iwaizaki limestone. *Sci. Rep. Saitama*

- Univ.*, [B], 3, (3), 274-299, pls. 46-53.
- (1965): Solidgraphic Study of Fusulinid Foraminifera (2)—Subfamily Verbeekiniinae in Japan—. *Ditto.*, [B], 5, (1), 15-27, pls. 2-5.
- and SUZUKI, Y. (1961): Fusulinids from the Akasaka Limestone (Part 2). *Ditto.*, [B], 3, (1), 43-70, pls. 4-22.
- MYERS, E. H. (1937): The present state of our knowledge concerning the life cycle of the foraminifera. *Zoölogy*, 24, 10-17.
- (1960): Observations on the origin and fate of flagellated gametes in multiple tests of *Discorbis* (Foraminifera). *Jour. Mar. Biol. Ass. United Kingdom*, [N. S.], 24, 201-225, pls. 1-3.
- NODA, M. (1956): Stratigraphical and palaeontological studies of the Toman Formation in the Kaishantun and Kamisanbo Districts. *Rep. Earth Sci., Dep. General Educ., Kyushu Univ.*, (2), 1-22, pls. 1-6.
- NOGAMI, Y. (1958): Fusulinids from the Maizuru Zone, Southwest Japan, Part 1. Ozawainellinae, Schubertellinae and Neoschwagerininae. *Mem. Coll. Sci. Univ. Kyoto*, [B], 25, (2), 97-114, pls. 1-2.
- (1961): Permishe Fusuliniden aus dem Atetsu-Plateau sudwestjapans. Teil 2, Verbeekiniinae, Neoschwagerininae u. a., *Ditto.*, 28, (2), 159-228, pls. 1-7.
- (1965): Neu-Untersuchung der von SCHWAGER beschriebenen Fusuliniden aus China und Japan. 1. Fusuliniden aus China. *Paläont. Z.*, 39, 1/2, 51-71, 9-11.
- ORLOV, Yu. A. (1959): *Fundamentals of Paleontology*, General Part and Protozoa, Publication Acad. Sci. U.S.S.R.
- OZAWA, Y. (1925a): On the classification of Fusulinidae. *Jour. Coll. Sci. Imperial Univ. Tokyo*, 45, Art. 4, 1-26, pls. 1-4.
- (1927): Stratigraphical studies of the Fusuline limestone of Akasaka, Province of Mino. *Ditto.*, [2], 3, 121-164, pls. 34-46.
- PITAKPAIVAN, K. (1965): Fusulines of the Rat Buri Limestone of Thailand. *Mem. Fac. Sci. Kyushu Univ.*, [D], 17, (1), 3-69, pls. 1-6.
- RAUSER-CHERNOUSOVA, D. M. (1963): Einige fragen zur evolution der Fusulinideen. In KOENIGSWALD, G. H. R., BUNING, W. L. and WAGNER C. W., [Editors] *Evolutionary trends in Foraminifera*. 45-65, Elsevier Publishing Co.
- REICHEL, M. (1964): Alveolinidae. In MOORE, R. C. [Editor] *Treatise on Invertebrate Paleontology*, Part C, Protista 2, C503-510a.
- RUZHENTSEV, V. E. and SARYCHEVA, T. G. [Ed.] (1965): The development and change of marine organisms at the Palaeozoic-Mesozoic boundary. *Transact. Palaeont. Inst., Acad. Sci. U.S.S.R.*, 108, 1-312, pls. 1-58.
- SADA, K. (1961): *Neoschwagerina* from the Yukawa group in the Atetsu Limestone Plateau. *Jour. Sci. Hiroshima Univ.*, [C], 4, (1), 117-129, pls. 11-14.
- (1963): *Neoschwagerina* from the Joé Limestone, Hiroshima Prefecture, West Japan, with a note on *Neoschwagerina margaritae* DEPRAT. *Geol. Rep. Hiroshima Univ.*, (12), 541-552, pl. 58.
- and YOKOYAMA, T. (1966): Upper Permian Fusulinids from the Taishaku Limestone in West Japan. *Trans. Proc. Palaeont. Soc. Japan*, [N. S.], 63, 303-315, pls. 33-34.
- SAITO, Y. (1968): Geology of the Younger Paleozoic System of the Southern Kitakami Massif, Iwate Prefecture, Japan. *Sci. Rep. Tohoku Univ.*, [2], 40, (2), 79-139, pls. 18-19.
- SAKAGAMI, S. (1958): Fusulinids from the Upper Permian Conglomerates of the northern part of Itsukaichi, Tokyo-to, Japan. *Jour. Hokkaido Gakugei Univ.*, 9, (2), 72-97, pls. 1-4.
- SAURIN, E. (1958): Fusulinidés du Phnom Cau Lan (Cambodia). *Khoa-Hoc Dai-Hoc Duong (Fac. Sci.)*, 223-231, pls. 1-2, Saigon.
- SCHENCK, H. G. and THOMPSON, M. L. (1940): *Misellina* and *Brevazina*, new Permian fusulinid Foraminifera. *Jour. Palaeont.*, 14, (6), 584-589.
- SCHWAGER, C. (1884): Carbonische Foraminiferen aus China und Japan. In RICHTHOFEN, F., *China*, 4, 106-159, pls. 15-18.
- SHENG, J. C. (1958): Some Fusulinids from the Maokou Limestone of Chinghai

- Province, Northwestern China. *Acta Palaeont. Sinica*, 6, (3), 268-291, pls. 1-4.
- (1963): Permian Fusulinids of Kwangsi, Kueichow and Szechuan. *Palaeontologia Sinica*, [N. S., B], (10), 1-247, pls. 1-36.
- SKINNER, J. W. (1969): Permian Foraminifera from Turkey. *Univ. Kansas Paleont. Contrib.*, Paper 36, 1-14, pls. 1-32.
- and WILDE, G. L. (1954): Fusulinid wall structure. *Jour. Paleont.*, 28, (4), 445-451, pls. 45-52.
- and ——— (1955): New Fusulinids from the Permian of West Texas. *Ditto.*, 29, (6), 927-940, pls. 89-95.
- and ——— (1966): Permian Fusulinids from Pacific Northwest and Alaska. *Univ. Kansas Paleont. Contrib.*, Paper 4, 1-60, pls. 1-49.
- and ——— (1966): Permian Fusulinids from Sicily. *Ditto.*, Paper 8, 1-16, pls. 1-20.
- and ——— (1967): Permian Foraminifera from Tunisia. *Ditto.*, Paper 30, 1-22, pls. 1-32.
- SOSNINA, M. I. (1956): Materialy po Paleontology. Novye cemeystva i rody. *Trudy Vsyegyei*, [N. S.], 12, 15-29, pls. 1-7.
- (1960): Microfaunistic zone in the Carboniferous and Permian deposits of the Sikhote-Alin. Mezhdunarodnyy Geologicheskyy Kongress, 21 sessiya, *Doklady Sovyetskikh Geologov*. 65-68, 1 pl.
- (1965): Some Permian Fusulinids and Lagenids from Sikhote-Alin. *Gosud. Geol. Komitet, S.S.S.R., Vses. Nauchno-Issledov. Geol. Inst.* [N. S.], 115, Biostrat. Sbornik, 1, 142-159, pls. 1-5.
- SUGI, T. (1960): Restudy of *Verbeekina sphaera* OZAWA. *Trans. Proc. Palaeont. Soc. Japan*, [N. S.], 39, 311-329, pl. 36.
- SUYARI, K. (1962): Geological and paleontological studies in Central and Eastern Shikoku, Japan. Pt. 2. Paleont., *Tokushima Univ., Jour. Gakugei, Nat. Sci.*, 12, 1-64, pls. 1-12.
- THOMPSON, M. L. (1946): Permian Fusulinids from Afghanistan. *Jour. Palaeont.*, 20, 140-157, pls. 23-26.
- (1948): Studies of American Fusulinids. *Univ. Kansas Palaeont. Contrib.*, Protozoa, Art. 1, 1-184, pls. 1-38.
- (1954): American Wolfcampian Fusulinid. *Ditto.*, Art. 5, 1-226, pls. 1-52.
- (1964): Fusulinacea. In MOORE, R. C. [Editor] *Treatise on Invertebrate Paleontology* Part C, Protista 2, C358-436, Geol. Soc. America and Kansas Univ. Press.
- and FOSTER, C. L. (1937): Middle Permian Fusulinids from Szechuan, China. *Jour. Palaeont.*, 11, 126-144, pls. 23-25.
- , WHEELER, H. and DANNER, W. R. (1950): Middle and Upper Permian fusulinids of Washington and Oregon. *Cushman Lab. Foram. Contrib.*, 1, 46-63, pls. 3-8.
- TORIYAMA, R. (1942): The Fusulinids of the Yasuba conglomerate in the province of Tosa. *Jap. Jour. Geol. Geogr.*, 18, (4), 137-247, pls. 24-25.
- (1954): A gigantic fusulinid species from the Kitakami Massif, northeastern Japan. *Trans. Proc. Palaeont. Soc. Japan*, [N. S.], 15, 179-182, pl. 24.
- (1958): Geology of Akiyoshi, Pt. 3. Fusulinids of Akiyoshi. *Mem. Fac. Sci. Kyushu Univ.*, [D], 7, 1-264, pls. 1-48.
- (1960): Tentative classification of the Fusulinid Foraminifera. "Fossils" (*Kaseki*), *Palaeont. Soc. Japan*, (1), 34-39. (in Japanese).
- (1967): Permian System. In K. ASANO et al. [Editors] "Historical geology" (*Chishigaku*), 1, 224-305, Asakura Pub. Co., Tokyo. (in Japanese).
- and KANMERA, K. (1968): Fusulinacean fossils from Thailand, Pt. 2. Two new Permian genera from Thailand. *Geol. Palaeont. Southeast Asia*, 4, 29-44, pls. 6-8.
- and SUGI, T. (1959): Permian fusulinids from Central Thailand. *Mem. Fac. Sci. Kyushu Univ.*, [D], 9, (1), 17-32, pls. 1-3.
- TUMANSKAYA, O. G. (1950): O vysshikh fusulinidakh iz verkhnepermiskikh otolozhe-

- niy, S.S.S.R., *B. MOIP otd. geol.*, t. 25, 4. 77-97, pls. 1-7. (cited in M.-MAKLAY, A. D., (1957)).
- VIEN, L. T. (1959): Étude de Fusulinidés du Haut-Laos, du Cambodge et du Sud Viêt-Nam. *Ann. Fac. Sci. Saigon*, 99-120, pls. 1-2.
- WALLACE, B. and SRB, A. M. (1961): *Adaptation. Foundations of modern biology*, 113 pp., Prentice-Hall.
- WILDE, G. L. (1965): Abnormal growth conditions in Fusulinids. *Contrib. Cushman Found. Foram. Research*, 16, Part 3, 121-124, pls. 18-20.
- YABE, H. (1906): A contribution to the genus *Fusulina*, with notes on a Fusulina-Limestone from Korea. *Jour. Coll. Sci. Imperial Univ. Tokyo*, 21, Art. 5, 1-36, pls. 1-3.
- (1948): Neoschwagerininae DUNBAR and CONDRA, *Proc. Acad. Tokyo*, 24, (9), 1-9.
- (1964): *Lepidolina* Problem, *Proc. Japan Acad.*, 40, (3), 214-219.
- (1964): Problems on the genus *Lepidolina* (Part 1). "Fossils" (Kaseki), *Palaeont. Soc. Japan*, (8), 134-139. (in Japanese).
- (1965): Problems on the genus *Lepidolina* (Part 2). *Ditto.*, (9), 36-55.
- (1966): Problems on the genus *Lepidolina* (Supplement). *Ditto.*, (12), 47-55.
- and HANZAWA, S. (1932): Tentative Classification of the Foraminifera of the Fusulinidae. *Proc. Imperial Acad. Japan*, 8, (2), 40-43.
- YAMAGIWA, N. and ISHII, K. (1958): *Yabeina* from Omura Island, Shima, Mie Prefecture. *Jubilee Pub. Commem. Prof. H. FUJIMOTO*, 58-64, pls. 3-4.

Tomowo OZAWA

Notes on the Phylogeny and Classification of  
the Superfamily Verbeekinoidea

Plates 1~9



## Plate 1

## Explanation of Plate 1

All figures are  $\times 20$

### Neoschwagerininae

Fig. 1. *Neoschwagerina craticulifera* (SCHWAGER)

Tangential section showing the structure of septula. Akasaka Limestone, Central Japan. (Late Dr. OZAWA's collection).

Fig. 3. *Yabeina globosa* (YABE)

Axial section showing the structure of septula. Akasaka Limestone, Central Japan. (After OZAWA, 1927).

Figs. 8, 9. *Neoschwagerina brevis* THOMPSON, WHEELER and DANNER ( $=N. peculiaris$  SKINNER and WILDE). 8, enlarged figure of a part of a sagittal section of a megalospheric specimen showing juvenile volutions and proloculus. 9, enlarged figure of a part of an axial section of a microspheric specimen showing juvenile volutions and proloculus.

### Sumatrininae

Fig. 5. *Sumatrina longissima* DEPRAT

Tangential section of a mature specimen showing the structure of septula. Khao Imot, Rat Buri Limestone, Sara Buri area, Thailand.

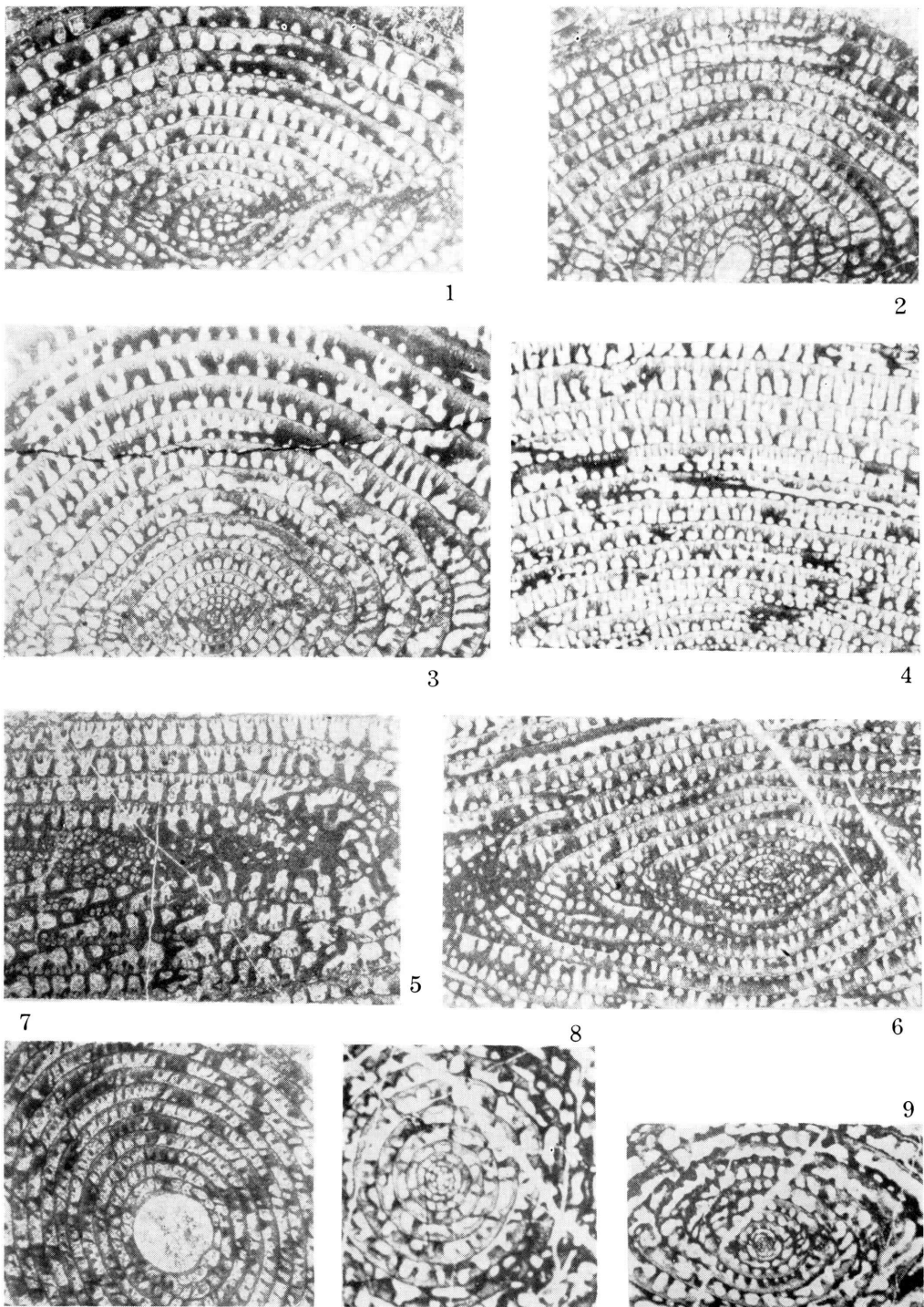
### Lepidolininae

Figs. 2, 6-7. *Colania* sp. nov.

2, axial section showing the structure of septula. 6, enlarged figure of a part of an axial section of a microspheric specimen showing juvenile volutions and proloculus. 7, enlarged figure of a part of a sagittal section of a megalospheric specimen showing juvenile volutions and proloculus. Khao Imot, Rat Buri Limestone, Sara Buri area, Thailand.

Fig. 4. *Lepidolina multiseptata multiseptata* (DEPRAT)

Enlarged figure of a part of an axial section of a microspheric specimen showing structure of septula. Futamatao Formation, southeastern part of Kwanto Mountains, Central Japan.



## Plate 2

## Explanation of Plate 2

All figures are  $\times 10$ , unless otherwise stated

### Verbeekinae

Genus *Verbeekina* STAFF, 1909

Fig. 1. *Verbeekina verbeeki* (GEINITZ)

Type-species of *Verbeekina*. Axial section, Akiyoshi Limestone, Southwest Japan. (After TORIYAMA, 1958).

Fig. 2. *Verbeekina* sp. cf. *V. akasakensis* THOMPSON

Axial section. Khao Imot, Rat Buri Limestone, Thailand.

Fig. 3. *Verbeekina* sp.

Axial section. Khao Imot, Rat Buri Limestone, Thailand.

Genus *Armenina* MIKLUKHO-MAKLAY, 1955

Fig. 4. *Armenina crassispira* (CHEN)

Axial section. Maokou Limestone, South China. (After SHENG, 1963).

Fig. 5. *Armenina wangi* SHENG

Axial section of the holotype from the Maokou Limestone, South China. (After SHENG, 1963).

Fig. 6. *Armenina salgirica* M.-MAKLAY

Axial section. Margab Horizon, Pamir. (After LEVEN, 1967).

Figs. 7, 8. *Armenina sphaera* (OZAWA)

7, axial section. 8, sagittal section. 7 and 8, from the Akasaka Limestone, Central Japan. (After OZAWA, 1927).

Fig. 9. *Armenina asiatica* LEVEN

Axial (slightly diagonal) section. Kuberganda Horizon, Pamir. (After LEVEN, 1967).

Fig. 10. *Armenina* sp. nov.

Axial section. Primitive species of *Armenina*. Nariki Formation, Kwanto Mountains, Central Japan.

### Misellinae

Genus *Misellina* SCHENCK and THOMPSON, 1940

Subgenus *Misellina* (*Brevaxina*) SCHENCK and THOMPSON, 1940

Fig. 11. *Misellina* (*Brevaxina*) *otakiensis* (HUZIMOTO)

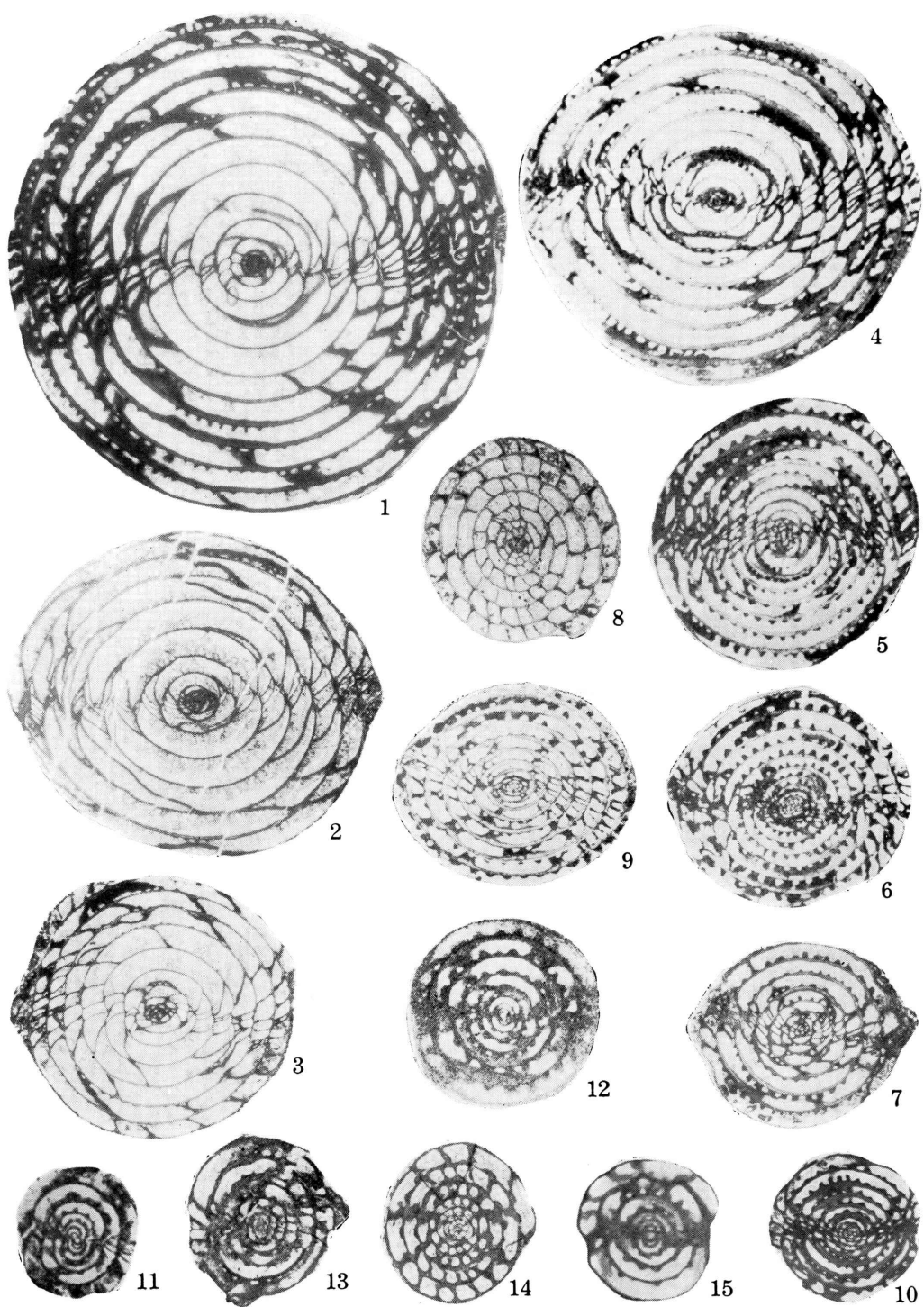
Axial section,  $\times 18$ . Kuberganda Horizon, Pamir. (After LEVEN, 1967).

Figs. 12-14. *Misellina* (*Brevaxina*) sp. nov.

12 and 13, axial sections. 14, sagittal section. All specimens are  $\times 20$ . 12, from the Nariki Formation, Kwanto Mountains, Central Japan. 13 and 14, from the Raidenyama Formation, Kwanto Mountains.

Fig. 15. *Misellina* (*Brevaxina*) *dyhrenfurthi* (DUTKEVICH)

Axial section, ( $\times 20$ ) from the upper part of the Darwas Horizon, Darwas, Southern Russia. (After KALMIKOVA, 1967).



## Plate 3

### Explanation of Plate 3

All figures are  $\times 10$ , unless otherwise stated

#### Miselliniinae

Genus *Metadoliolina* ISHII and NOGAMI, 1961

Fig. 1. *Metadoliolina dutkevitchi* SOSNINA

Axial section. Upper Permian of Sikhote-Alin. (After SOSNINA, 1965).

Fig. 2. *Metadoliolina compacta* (CHEN).

Axial section. Upper part of the Maokou Limestone, South China. (After SHENG, 1963).

Figs. 3, 4. *Metadoliolina gravitesta* (KANMERA).

Type-species of *Metadoliolina*. 3, axial section of the holotype. 4, sagittal section. Upper Permian Kuma Formation, southern Kyushu, Japan. (After KANMERA, 1954).

Fig. 5. *Metadoliolina* sp. cf. *M. dutkevitchi* SOSNINA

Axial section. Upper Permian Kuma Formation, southern Kyushu, Japan.

Fig. 6. *Metadoliolina multivoluta* (SHENG)

Axial section. Upper Permian Futamatao Formation, Kwanto Mountains, Central Japan.

Genus *Pseudodoliolina* YABE and HANZAWA, 1932

Figs. 7, 8. *Pseudodoliolina pseudolepida* (DEPRAT)

7, axial section. 8, sagittal section. Khao Imot, Rat Buri Limestone, Sara Buri area, Thailand.

Figs. 9–11. *Pseudodoliolina ozawai* YABE and HANZAWA

Type-species of *Pseudodoliolina*. 9, axial section from the Kuberganda Horizon, Pamir. (After LEVEN, 1967); 10, axial section from the Nariki Formation, Kwanto Mountains, Central Japan; 11, sagittal section from the Akasaka Limestone, Central Japan. (Late Dr. OZAWA's collection).

Fig. 12. *Pseudodoliolina oliverformis* THOMPSON, WHEELER and DANNER

Axial section. Twin Lakes areas, northwestern Washington, U.S.A. (After THOMPSON, WHEELER and DANNER, 1950).

Fig. 13. *Pseudodoliolina* sp.

Primitive species of *Pseudodoliolina*. Axial section. Rat Buri Limestone, Changwat Sara Buri, Central Thailand. (KANMERA and TORIYAMA's collection).

Genus *Misellina* SCHENCK and THOMPSON, 1940

Subgenus *Misellina* SCHENCK and THOMPSON, 1940

Figs. 14, 15. *Misellina* sp.

Primitive species of *Misellina*. 14, tangential section; 15, axial section,  $\times 20$ . Raidenyama Formation, Kwanto Mountains, Central Japan.

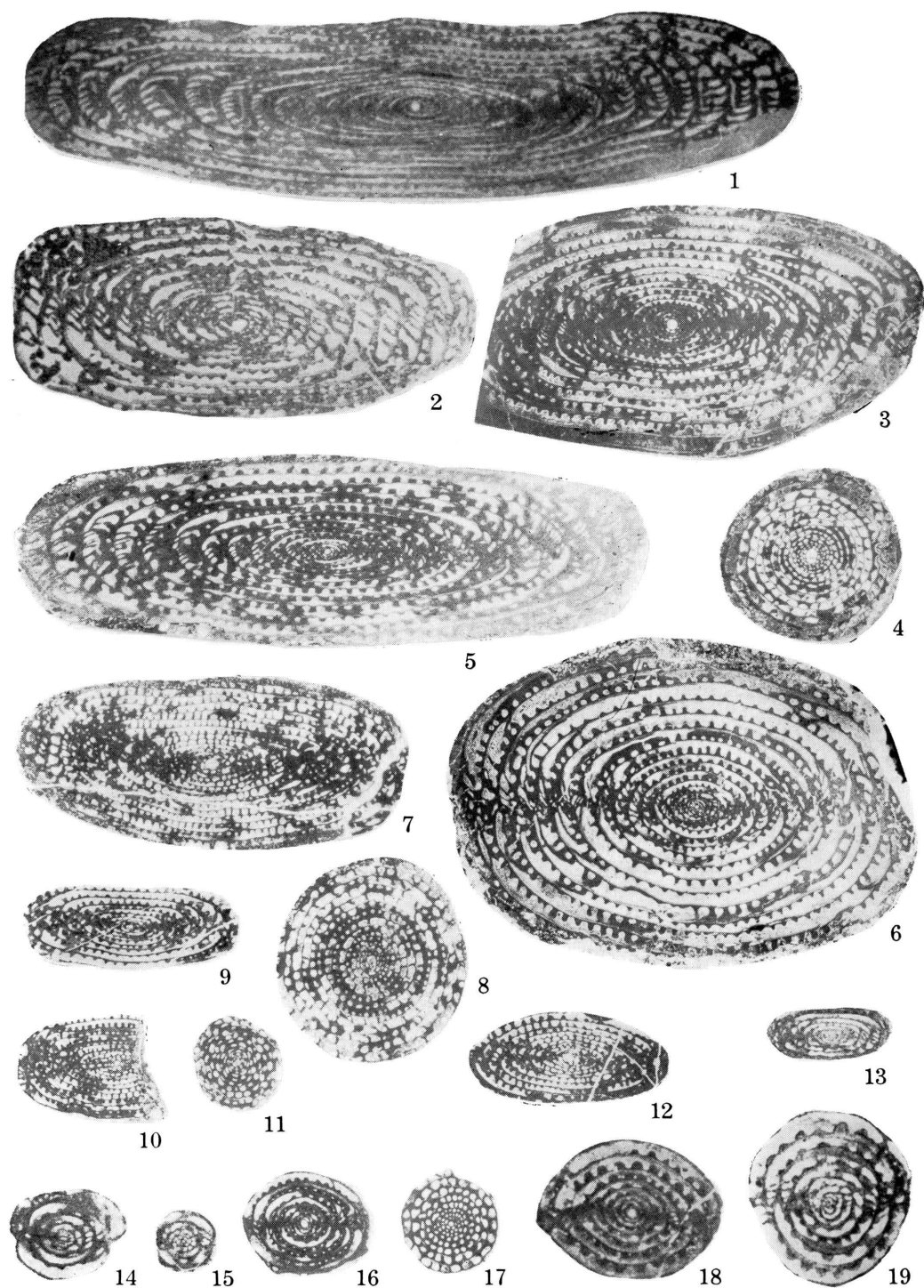
Figs. 16–18. *Misellina claudiae* (DEPRAT)

16, axial section, 17, sagittal section from the Nariki Formation, Kwanto Mountains, Central Japan.  $\times 10$ ; 18, axial section,  $\times 15$ . Lowest part of the Chihhsia Limestone, South China. (After LEE, 1933).

Fig. 19. *Misellina olgae* LEVEN

Axial section,  $\times 15$ . Artinsk Horizon of Pamir. (After LEVEN, 1967).





## Plate 4

## Explanation of Plate 4

All figures are  $\times 10$

### Neoschwagerininae

Genus *Neoschwagerina* YABE, 1903

Figs. 1-3. *Neoschwagerina margaritae* DEPRAT

Advanced species of *Neoschwagerina*. 1, axial section from the Akasaka Limestone, Central Japan. (After OZAWA, 1927); 2, axial section, 3, sagittal section. 2, 3 from the Nariki Formation, Kwanto Mountains, Japan.

Fig. 4. *Neoschwagerina cheni* SHENG

Axial section. Nariki Formation, Kwanto Mountains, Japan.

Fig. 5. *Neoschwagerina occidentalis* KOCHANSKY-DEVIDÉ and RAMOVŠ (= *N. pinguis* SKINNER).

Axial section of a megalospheric specimen from the Permian limestone, near Ankara, Turkey. (After SKINNER, 1969).

Figs. 6-8. *Neoschwagerina craticulifera* (SCHWAGER)

Type-species of *Neoschwagerina*. 6, axial section of a megalospheric specimen 8, sagittal section of a megalospheric specimen. 6, 8, from the Akasaka Limestone, Central Japan. (6, after DEPRAT, 1914; 8, after OZAWA, 1927); 7, axial section of a microspheric specimen from the Nariki Formation, Kwanto Mountains, Central Japan.

Figs. 9-11. *Neoschwagerina simplex* OZAWA

Primitive species of *Neoschwagerina*. 9, axial section. 10, sagittal section. 9 and 10, from the Raidenyama Formation, Kwanto Mountains, Central Japan; 11, sagittal section from the Akasaka Limestone, Central Japan. (After OZAWA, 1927).

Genus *Maklaya* KANMERA and TORIYAMA, 1968

Figs. 12, 13. *Maklaya pimirica* (LEVEN)

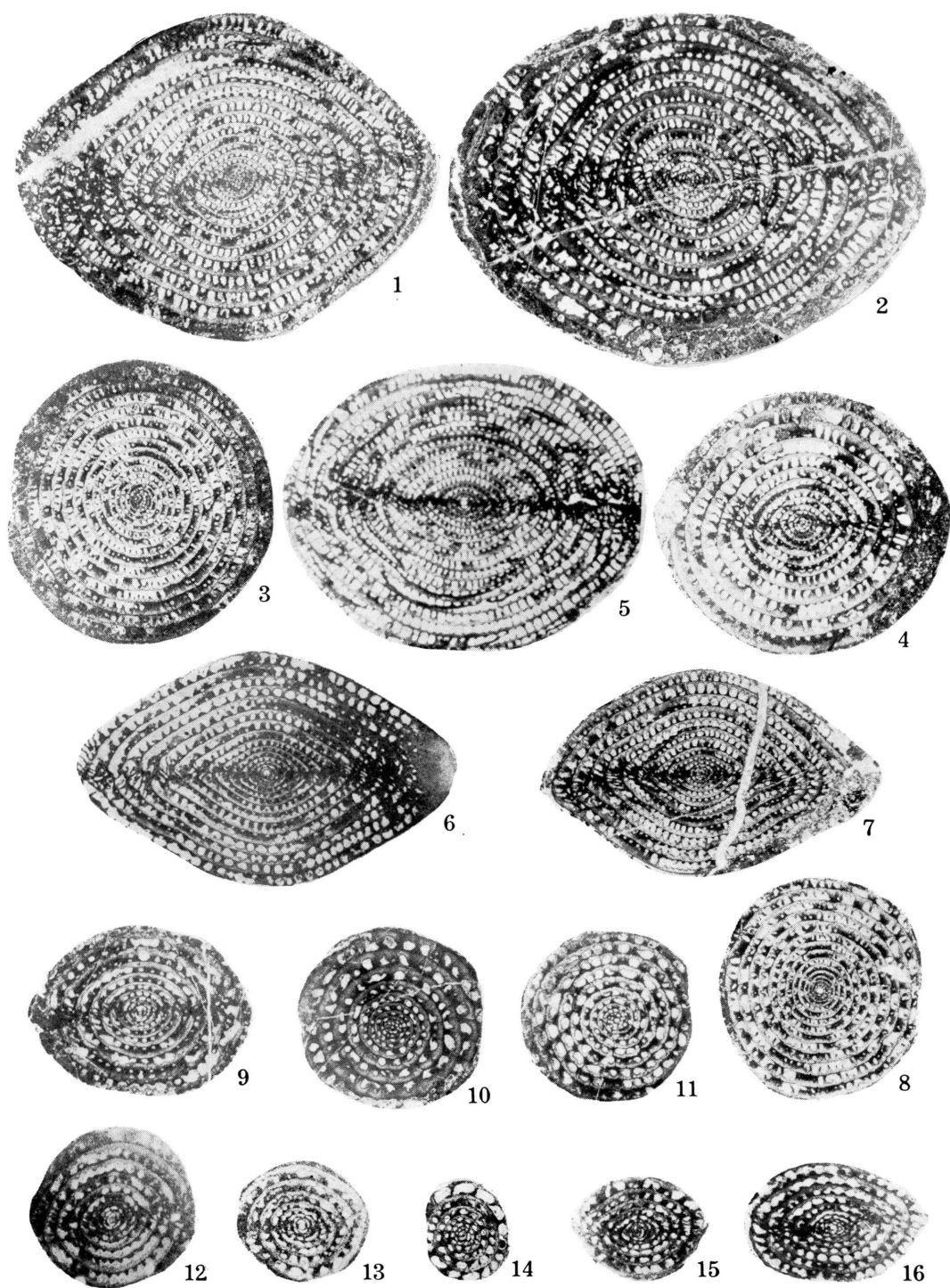
Type-species of *Maklaya*. 12, axial section of a microspheric specimen. 13, axial section of a megalospheric specimen. 12, 13, from the Rat Buri Limestone, Changwat Sara Buri, Thailand. (After KANMERA and TORIYAMA, 1968).

Figs. 14, 15. *Maklaya saraburiensis* KANMERA and TORIYAMA

14, sagittal section of a microspheric specimen. 15, axial section of a microspheric specimen. The same locality as Figs. 12 and 13. (After KANMERA and TORIYAMA, 1968).

Fig. 16. *Maklaya sethaputi* KANMERA and TORIYAMA

Axial section of a megalospheric specimen. Loc. ditto. (After KANMERA and TORIYAMA, 1968).



## Plate 5

## Explanation of Plate 5

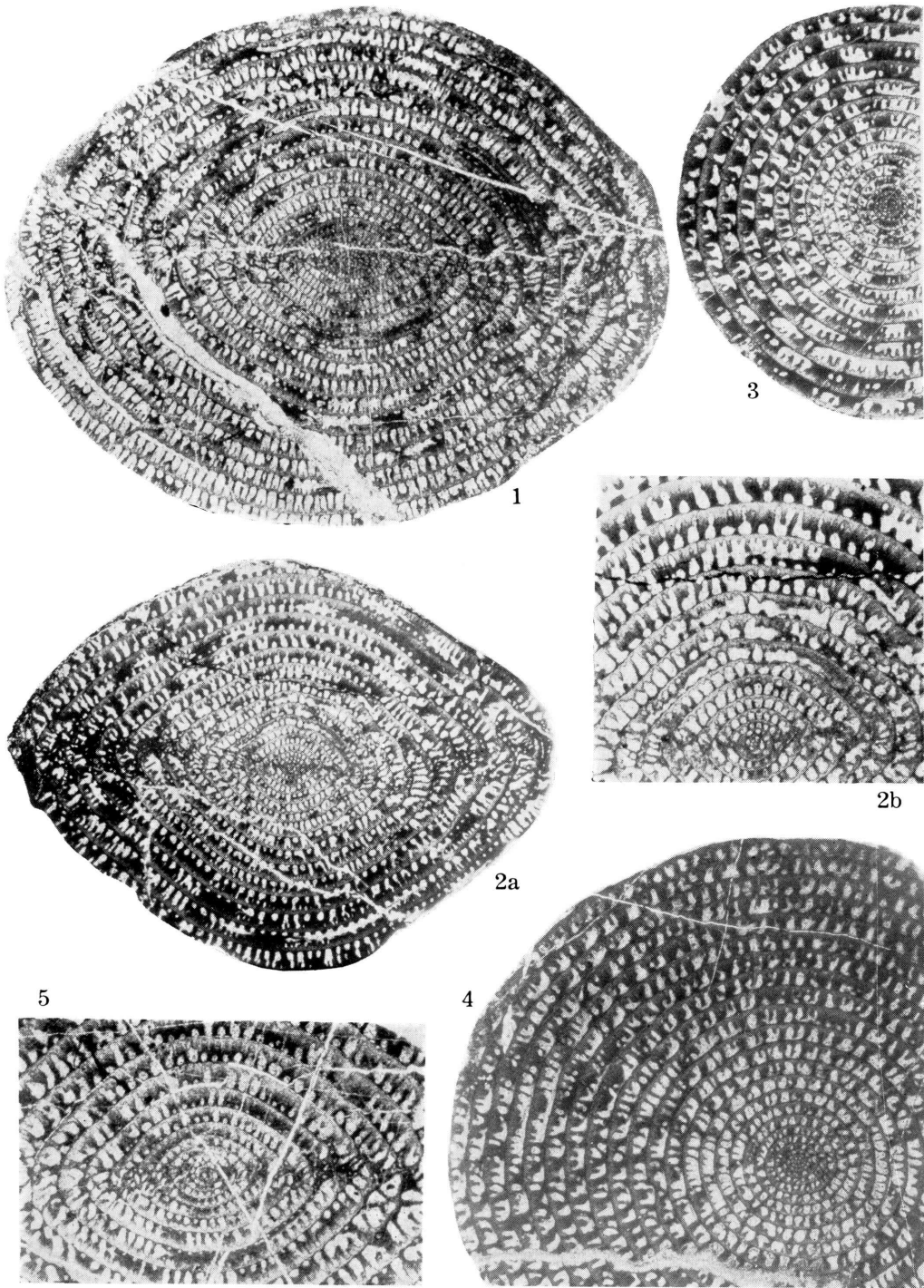
All figures are  $\times 10$ , except for Figs. 2b and 5 which are  $\times 20$

### Neoschwagerininae

Genus *Yabeina* DEPRAT, 1914

Figs. 1-5. *Yabeina globosa* (YABE)

1, axial section of a fully mature specimen. 2, axial section. 3, 4, sagittal sections. 2b, enlarged part of Fig. 2a showing inner volutions. 5, enlarged part of a specimen showing juvenile volutions and proloculus. (Figs. 2, 3, and 4 are Late Dr. OZAWA's collection). All from the Akasaka Limestone, Central Japan.



## Plate 6



## Explanation of Plate 6

All figures are  $\times 10$ , unless otherwise stated

### Sumatrininae

Genus *Presumatrina* TUMANSKAYA, 1950

Figs. 1, 2. *Presumatrina schellwieni* (DEPRAT)

Type-species of *Presumatrina*. 1 and 2, axial section of a specimen in different magnification ( $\times 10$  and  $\times 20$ , respectively) from Dond-hoi Province, Vietnam. (After DEPRAT, 1913).

Figs. 3-5. *Presumatrina neoschwagerinoides* (DEPRAT)

Axial sections,  $\times 11$ . 3 and 4, from Ban-na-mat, Laos. (After DEPRAT, 1913); 5, from the Kuberganda Horizon, Pamir. (After LEVEN, 1967).

Genus *Afghanella* THOMPSON, 1946

Figs. 6, 7. *Afghanella ozawai* HANZAWA

6, axial section. 7, sagittal section. Akiyoshi Limestone, Southwest Japan. (After KANMERA, 1957).

Figs. 8, 9. *Afghanella robbinsae* SKINNER and WILDE

8, sagittal section. 9, axial section. In the Bar Soltane Well, Tunisia. (After SKINNER and WILDE, 1967).

Figs. 10, 11. *Afghanella sumatrinaeformis* (GUBLER)

10, sagittal section. 11, axial section. Pong Ova, Laos. (After GUBLER, 1935).

Genus *Sumatrina* VOLZ, 1904.

Fig. 12. *Sumatrina annae* VOLZ

Axial section from Khao Imot, Rat Buri Limestone, Sara Buri area, Thailand. The type-species of *Sumatrina*.

Figs. 13, 14. *Sumatrina longissima* DEPRAT

13, sagittal section. 14, axial section. Loc. ditto.

### Lepidolininae

Genus *Cancellina* HAYDEN, 1909.

Figs. 15, 16. *Cancellina* ? sp. nov.

15, axial section. 16, sagittal section. 15 and 16,  $\times 20$ . Nariki Formation, Kwantō Mountains, Central Japan.

Fig. 17. *Cancellina danneri* SKINNER and WILDE

Axial section from the Twin Lakes area, northwestern Washington, U.S.A. (After SKINNER and WILDE, 1966).

Figs. 18, 19. *Cancellina nipponica* OZAWA

18, sagittal section. 19, axial section. Akasaka Limestone, Central Japan. (After OZAWA, 1927).

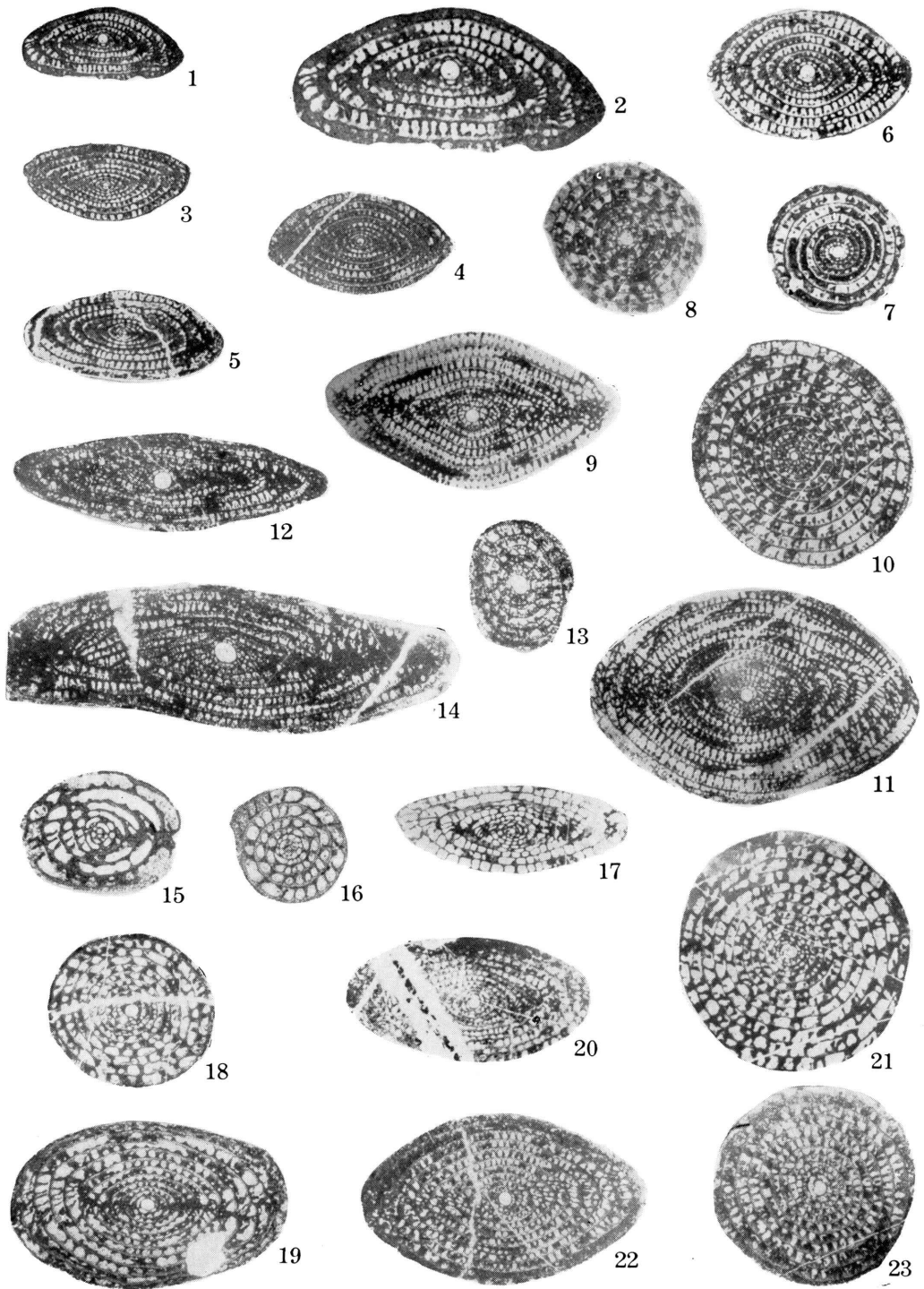
Genus *Colania* LEE, 1933

Figs. 20, 21. *Colania amicula* (HONJO)

20, axial section of the holotype. 21, sagittal section. Akasaka Limestone, Japan. (After HONJO, 1959).

Figs. 22, 23. *Colania* sp.

22, axial section. 23, sagittal section. Khao Imot, Rat Buri Limestone, Sara Buri area, Thailand.



## Plate 7

## Explanation of Plate 7

All figures are  $\times 10$

### Lepidolininae

Genus *Lepidolina* LEE, 1933

Figs. 1, 2. *Lepidolina multiseptata shiraiwensis* (OZAWA)

1, axial section of a megalospheric specimen. 2, sagittal section of a megalospheric specimen. Irimi, Akiyoshi Limestone, Southwest Japan. (ISHIBASHI's collection).

Genus *Colania* LEE, 1933

Figs. 3, 4. *Colania kwangsiana* LEE.

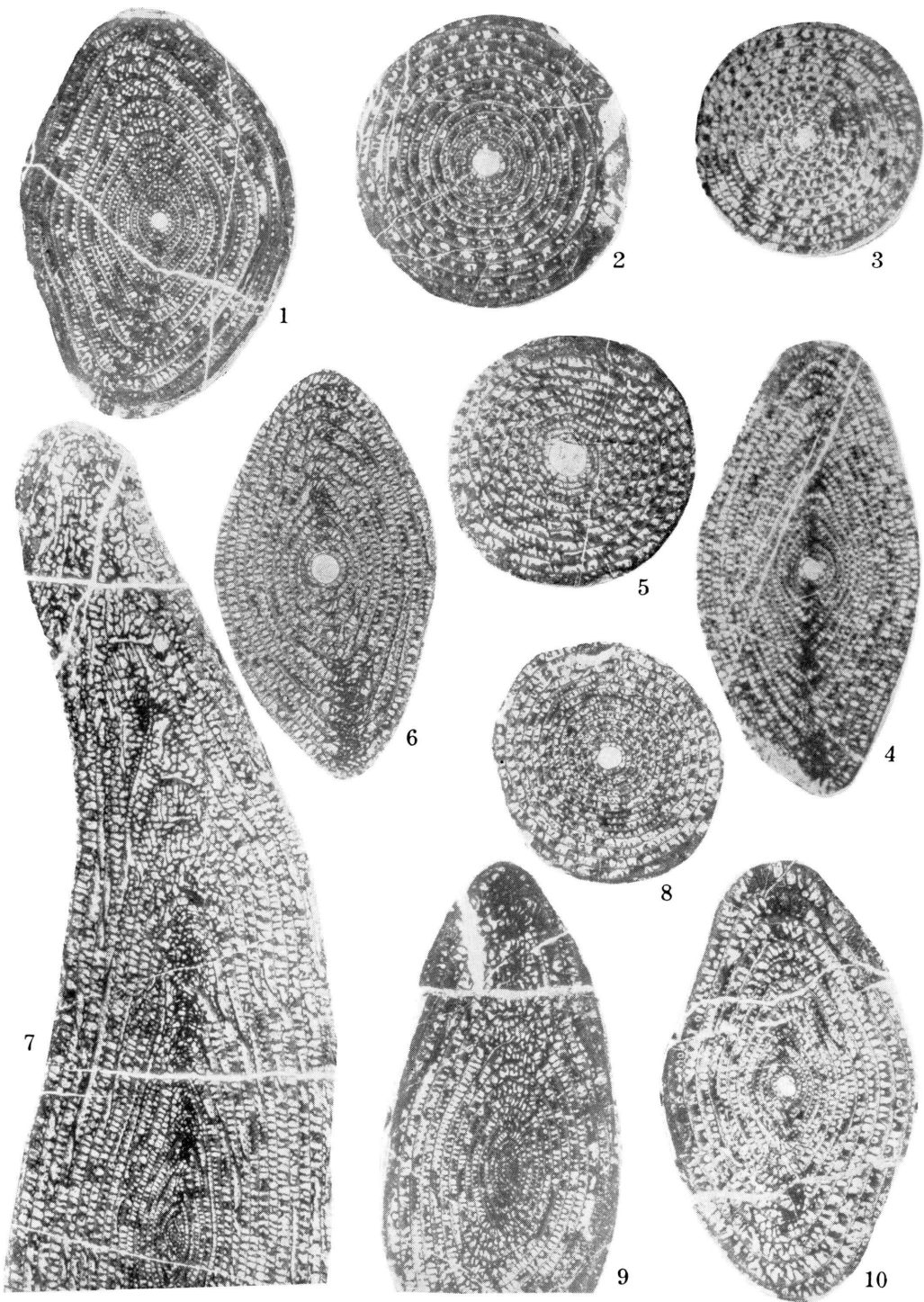
Type-species of *Colania*. 3, sagittal section of a megalospheric specimen. 4, axial section of a megalospheric specimen. 3 and 4, from the Maokou Limestone, South China. (After SHENG, 1963).

Figs. 5-7. *Colania* sp. nov.

5, sagittal section of a megalospheric specimen. 6, axial section of a megalospheric specimen. 7, axial section of a microspheric specimen. All specimens are from Khao Imot, Rat Buri Limestone, Sara Buri area, Thailand.

Figs. 8-10. *Colania douvillei* (OZAWA)

8, sagittal section of a megalospheric specimen. 9, axial section of a microspheric specimen. 10, axial section of a megalospheric specimen. All specimens from Hagiwara, Akiyoshi Limestone, Southwest Japan.



## Plate 8

## Explanation of Plate 8

All figures are  $\times 10$

### Lepidolininae

Genus *Lepidolina* LEE, 1933

Figs. 1–8. *Lepidolina multiseptata multiseptata* (DEPRAT).

Type-species of *Lepidolina*.

1 and 2, axial sections of megalospheric specimens. 3 and 4, axial sections of immature megalospheric specimens. 5, axial section of a microspheric specimen. 6 and 8, sagittal sections of megalospheric specimens. 7, sagittal sections of a polyvalent individual.

All specimens are from the Futamatao Formation, Kwanto Mountains, Central Japan, except for Fig. 2 which came from Phnom Bak, Sisophon, Cambodia. (ISHII and NOGAMI's collection).





## Plate 9

## Explanation of Plate 9

All figures are  $\times 10$ , except for Fig. 5 which is  $\times 20$

### Lepidolininae

Genus *Lepidolina* LEE, 1933

Fig. 1. *Lepidolina kumaensis* KANMERA

Axial section of a megalospheric specimen from the Otani Conglomerate, Hida Massif, Central Japan. (After HASEGAWA, 1965).

Figs. 2-5. *Lepidolina multiseptata multiseptata* (DEPRAT)

2, axial section of a megalospheric specimen. 3, sagittal section of a megalospheric specimen. 5, enlarged part of an axial section of a microspheric specimen, showing juvenile volutions. 2, 3 and 5, from the Upper Permian Futamatao Formation, Kwanto Mountains, Central Japan; 4, axial section of a microspheric specimen from the Phnom Komping Phui, Battambang, Cambodia. (After GUBLER, 1935).

