

Revised Classification of Cancellina and Neoschwagerina, and Evolution of Sumatrininae and Neoschwagerininae

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Revised Classification of *Cancellina* and *Neoschwagerina*, and Evolution of Sumatrininae and Neoschwagerininae

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Introduction

The subfamily Neoschwagerininae of the family Fusulinidae was first introduced by DUNBAR and CONDRA (1928) to include *Cancellina* HAYDEN, *Neoschwagerina* YABE, *Yabeina* DEPRAT and *Sumatrina* VOLZ. Later *Lepidolina* and *Colania** by LEE (1933) and *Afghanella* by THOMPSON (1946) were added to the subfamily. In 1946, KAHLER and KAHLER set up the subfamily Sumatrininae to which they referred *Afghanella*, *Sumatrina* and *Lepidolina*. In 1954, THOMPSON showed a list containing all valid genera known up to that time, in which the above mentioned genera were grouped into two subfamilies, the one Neoschwagerininae including *Cancellina*, *Neoschwagerina* and *Yabeina*, and the other Sumatrininae *Afghanella*, *Sumatrina* and *Lepidolina*. However the systematic position of *Cancellina* and *Lepidolina* in their classifications seems to be inappropriate in regard to the phylogenetic evolution of those genera. Although the evolution of the neoschwagerininids has hitherto been discussed by many authors, there are still certain unsettled questions relating to several species of the doubtful generic affinity and to mutual relation among the genera *Cancellina*, *Neoschwagerina* and *Afghanella*.

I have studied the material collected from the Permian rocks of the Kuma massif of Kyushu in connection with my stratigraphical work and that obtained from the Akasaka, Taishaku and Akiyoshi limestones of western Japan. Furthermore, through the courtesy of Prof. T. KOBAYASHI of Tokyo University, I fortunately had an opportunity to study OZAWA's collection from the Akasaka and Akiyoshi limestones. As a result of the study I have noticed the need of a certain revision on the general classification of primitive neoschwagerininids, which would seem to be able to satisfactorily explain some unsettled questions on the evolution of the two subfamilies. In this paper I intend to discuss at length the classification of primitive neoschwagerininids with some necessary remarks on the taxonomic criteria. In connection with this matter, I will at this time give the following view on the evolution of the two subfamilies with a new proposal of classification.

* *Colania* has been regarded as a synonym of *Yabeina* or *Lepidolina* by many authors.

Cancellina and *Neoschwagerina*

I) *Previous diagnoses*

HAYDEN (1909) set up the subgenus *Cancellina*, with *Neoschwagerina primigena* (HAYDEN) as the type species and distinguished it from the subgenus *Neoschwagerina* in having no axial septula. OZAWA (1925 a, b) at first followed HAYDEN on the diagnosis of *Cancellina* that it has no axial septula. Later he (1927) employed it in a concept different from that defined by HAYDEN, to which, without giving any remark on axial septula, he assigned even a form [*Yabeina schellwieni* OZAWA", 1924; "*N. (C.) schellwieni* OZAWA", 1927], which is so much advanced as to have secondary transverse septula and now referred to *Afghanella* by THOMPSON (1948) and HANZAWA (1954). Furthermore he laid much stress on the thinness of spirotheca and septa as the distinctive feature of that subgenus. On that occasion he described two species of primitive neoschwagerinids, *Neoschwagerina* (s.s.) *simplex* and *N. (Cancellina) nipponica*.

THOMPSON published a magnificent monograph on all of fusulinid genera known in 1948 and gave detailed remarks on them. Indeed his work is comprehensive by which our knowledge has been much advanced, but in so far as the designation of the genus *Cancellina* and that of the primitive species of the genus *Neoschwagerina* are concerned, several questions still remain. In that paper he stated that the spirotheca of *Cancellina* has thick keriotheca. Besides the type species, he referred only one species, *N. simplex*, to *Cancellina*, but he put in doubt *C. nipponica* and *Doliolina neoschwagerinoides* DEPRAT to refer to *Cancellina* on account of their thin spirotheca. At that time he illustrated a form (pl. 18, figs. 6-9) assigned to *C. primigena* with a query from Persia, and his generic diagnosis (p. 62) on *Cancellina* seems to be based largely on the features of this form.

II) *A new proposal to the definition and classification of Cancellina and Neoschwagerina*

At any rate Hayden's classification of *Cancellina* and *Neoschwagerina* has been accepted by most of later workers to discriminate the primitive neoschwagerinids, although a certain revision was given by OZAWA on the diagnosis of *Cancellina*, and several species of both the genera were successively described or identified from various parts of the Tethys-sea region. However the previous diagnoses seem to me to be inappropriate to classify the primitive neoschwagerinids more naturally and to understand the evolution of the Neoschwagerininae and Sumatrininae more reasonably.

In my opinion, among the species referred to *Cancellina*, *Neoschwagerina* or *Doliolina* (= *Misellina*), the primitive species, whose generic assignment to *Neoschwagerina* or to *Cancellina* is not clear, can be classified into the following two

groups, based on the shell structures. The first group, namely the species which are considered to be assigned to *Cancellina*, besides the type species, are as follows:

Doliolina neoschwagerinoides DEPRAT, 1913

Neoschwagerina parva COLANI, 1924

Cancellina primigena (HAYDEN), DOUTKEVITCH and KHABAKOV, 1934

Cancellina schellwieni (DEPRAT), CHEN, 1934

Cancellina primigena (HAYDEN), HUZIMOTO, 1936

On the other hand the following forms seem better to be referred to *Neoschwagerina* (the type species and advanced forms of this genus are excluded here):

Neoschwagerina simplex OZAWA, 1927

Cancellina ? sp. LEE, 1933

Cancellina cf. *C. simplex* (OZAWA), DOUTKEVITCH and KHABAKOV, 1934

Cancellina kobayashii TORIYAMA, 1947

Cancellina tosayamensis TORIYAMA, 1947

Cancellina cf. *C. primigena* (HAYDEN), DUNBAR, 1947

Cancellina primigena (HAYDEN) ?, THOMPSON, 1948

The reason for this classification will be given in the following paragraphs, but it should be noticed that in all the forms of the first group, the spirotheca, septa and septula are thin in contrast to those of the forms of the second group which have thicker ones. The species of the second group have been mostly referred by many authors to *Cancellina*. For instance, *Neoschwagerina simplex* OZAWA, which was originally reported from Akasaka, was later included into *Cancellina* by DOUTKEVITCH and KHABAKOV (1934) and THOMPSON (1948). However this species is not similar to the type species of *Cancellina*, but is very close to that of *Neoschwagerina*. Here the confusion on the designation of *Cancellina* and *Neoschwagerina* arises.

Between the two genera grouped above there are several marked morphological differences with regard to the shell structures. Now the type specimens of *C. primigena* have thin spirotheca and septa. Nevertheless, as seen in the above listed species, most authors, except OZAWA, did not pay deep attention to the thickness of spirotheca of those species. In laying much stress on the thinness of spirotheca and septa as an important feature of *Cancellina* I hold with OZAWA's view (1927). As to the development of septula, most authors have currently accepted HAYDEN's classification. While, as already mentioned, OZAWA assigned to *Cancellina* even the species now referred to *Afghanella* which has secondary transverse septula. In this respect I have reached a conclusion that differs from the current opinions. I am of the opinion that the development of axial and transverse septula is in parallel in *Cancellina* and *Neoschwagerina*. In other words, both the genera can not be discriminated each other in the development of septula.

In primitive species of both the genera the transverse septula are poorly developed, reaching the parachomata immediately adjacent to the septa, and the axial ones are not present. The respective examples are visible in *Cancellina primigena* and "*Doliolina neoschwagerinoides*", and *Neoschwagerina simplex* and the species assigned by THOMPSON (1948, pl. 18, figs. 6-9) to *C. primigena* with a query. The former twos, of which the second species should also be referred to *Cancellina*, have thin spirotheca and septa. While the latter twos, and, in addition, *Cancellina kobayashii* TORIYAMA, *C. tosayamensis* T. and the species referred by LEE (1933, pl. 4, figs. 4, 4 a) to *Cancellina* with a query, exhibit a number of characteristics in common which appear to set them aside as a closely related group. In having no axial septula they coincide with the diagnosis of *Cancellina* defined by HAYDEN. However they are closely allied to the type species of *Neoschwagerina* than to that of *Cancellina* in a number of characteristics mentioned below, especially in having thick spirotheca and septa. I believe they should be referred to the most primitive forms of *Neoschwagerina*. *Cancellina nipponica* which is similar to *C. primigena* in possession of thin spirotheca and septa has rather poorly developed transverse septula but one axial septulum occurs between the septa even in inner volutions.

In morphologically more advanced forms of both the genera the axial septula occur in inner volutions, and increase in number to two in outer volutions. Such representative of *Cancellina* is the species described by CHEN (1934) as *C. schellwieni* from the Chihshia limestone, and those of *Neoschwagerina* are some subspecies of *N. craticulifera*, such as *haydeni* DOUTKEVITCH and KHABAKOV and *rotunda* DEPRAT.

Thus we can recognize the nearly parallel and progressive development of septula in morphologically primitive and slightly evolved forms of both the genera. However, noteworthy to say, no species of *Cancellina* has yet been known which has axial septula as many as three to five between the septa, as in *N. margaritae*, *N. megaspherica* and other advanced species.

Highly advanced forms of *Cancellina* are the species assigned by DUNBAR (1947, pl. 1, figs. 12-14) to *C. schellwieni* from Yunnan and *C. parva* (COLANI) which was originally referred to *Neoschwagerina*. They are, however, rather intermediate in the shell structures between *Cancellina* and *Afghanella*, and they become to have sometimes the secondary transverse septula in outermost volutions. Thus *Cancellina* has probably a more limited range than *Neoschwagerina* in the morphological development of shell and also in the geologic occurrence as will be mentioned later.

In short there is no reason to distinguish *Cancellina* from *Neoschwagerina* in that the former has no axial septula. As already mentioned, one of the significant distinction of both the genera thus revised is the extreme thinness of spirotheca in *Cancellina*.

The other important criteria for distinction between both the genera, in the revised sense, also are in the structure of septa, septula and parachomata. The septa of

Cancellina are exceedingly thin in contrast to those of *Neoschwagerina*. In *Cancellina* the keriothecae on both sides of the septa are essentially very thin and extend about one-half or a little more the distance down the septa, while those of *Neoschwagerina*, except its advanced forms, are thick, extending about three-fourths or more of the distance down the septa. The distinction in thickness is remarkable especially in their upper part: The keriothecae on both sides of the septa become much more thicker towards the upper part in *Neoschwagerina* than in *Cancellina*. In addition the transverse and axial septula are also thinner and shorter in *Cancellina* than in *Neoschwagerina*.

Parachomata in *Neoschwagerina* are broad but comparatively low, while those of *Cancellina* are narrow but relatively high and are joined by the primary transverse septula at a higher position than in *Neoschwagerina*. This feature is most marked in *C. neoschwagerinoides* and *C. parva*. Furthermore it should be noticed that this character is inherited from *Cancellina* to *Afghanella*, which has narrow but conspicuously high parachomata.

The shape of the shell of *Cancellina* is little differ from that of *Neoschwagerina*, but the species of the former mostly are much smaller in size than those of the latter.

It is a matter of course that the comparison of such structures between the two genera as the thickness of spirotheca and septa, the height of parachomata and the size of shell should be examined between the forms of nearly the same degree in evolutionary development.

Thus the species of *Cancellina* are distinguishable from *Neoschwagerina* in possessing relatively thinner spirotheca and septa, thinner and shorter septula, and narrower but higher parachomata. It is my opinion that *Cancellina* should not be confined to neoschwagerininids which have no axial septula, but should be assigned to the forms having the above mentioned features.

On the Phylogeny of Sumatrininae and Neoschwagerininae

The phylogenetic evolution and classification of the neoschwagerinids have hitherto been discussed by DEPRAT (1912, '13, '14), COLANI (1924), OZAWA (1925 a, b, '27), DUNBAR and CONDRA (1928), LEE (1933), GUBLER (1935), DUNBAR (1940), DUNBAR and HENBEST (1942), KAHLER and KAHLER (1946), THOMPSON (1946, '48, '54), YABE (1948) and HANZAWA (1954) and others. Based on the knowledges introduced by these workers and on the data obtained by myself, I here discuss the mutual relation of genera in question and their evolution.

1) *Progressive morphic development in Cancellina, Afghanella and Sumatrina*

The generic concept of *Cancellina* revised above reveals clearly a connecting

link with *Afghanella*. There are several species of *Cancellina* and *Afghanella* which seem to be phylogenetically closely related one another in successive order in the development of the shell.

In primitive species of *Cancellina*, such as *C. primigena* and *C. neoschwagerinoides*, the shell is small and ellipsoidal in shape, the transverse septula are short and are joined by parachomata at about two-thirds the height of the chambers, leaving rather large lateral openings in the center of the chambers. The axial septula are absent. The parachomata are triangular in cross-section and relatively high. The shell structure similar to the above mentioned species is seen in inner volutions of the species assigned by DUNBAR (1947, pl. 1, figs. 12-14) to *C. schellwieni* from the Chiench'uan district of Yunnan, and of *Afghanella ozawai* HANZAWA and *A. schencki* THOMPSON. In addition these species become to have secondary transverse septula between the primary ones in outer volutions: In DUNBAR's species the transverse septula occur at a rudimentary state in outer few volutions. This species is seemingly not referable to *A. schellwieni* and is either intermediate in structure between *Cancellina* and *Afghanella* or the most primitive form of the latter genus. In *A. ozawai*, which is a primitive form of *Afghanella*, according to HANZAWA, the secondary transverse septula first occur in the eighth volution and only a single septulum is present between the primary ones even in the mature stage. Axial septula first appear in the sixth volution and two to three occur in mature volutions. In *A. schencki*, which is a moderately evolved form of *Afghanella*, the secondary transverse septula first appear in the fourth to fifth volution and sometimes two occur in outer volutions. One axial septulum appears in the third volution and the number increases to four in outer volutions of mature specimens.

There are species of another group which probably belong genetically to the same link. I have obtained an undescribed primitive *Cancellina* from stratigraphically a little lower horizon than *C. nipponica* in the Akasaka limestone. It seems to be genetically closely related to the latter species but is distinguishable as a subspecies in having a smaller shell with less numerous volutions, a discoidal juvenarium, and in later appearance of transverse and axial septula. In this subspecies the transverse septula first appear at the end of the third volution, and a single axial septulum occurs between the septa in outer several volutions (see pl. 19, figs. 6, 7). The parachomata are slender but high, and are joined by the transverse septula, leaving rather large lateral openings. Now there is a form morphologically very similar to *C. nipponica* and its subspecies mentioned above. It is the species described as *C. schellwieni* by CHEN (1934, pl. 15, figs. 5-12) from the upper part of the Chihhsia limestone of China. It has very thin spirotheca and septa, thin and short septula and slender but high parachomata. So far as seen in the photographs of that species, the secondary transverse septula appear to occur in a short rudimentary state in outer one or two volutions. Two axial septula occur between the septa in

outer volutions. This species seems to be an intermediate form between *Cancellina* and *Afghanella*, and not referable to *A. schellwieni*. The shell structure of this species strongly suggests that it is closely related to *C. nipponica*, but is more advanced than the latter. Unfortunately we have not yet known more evolved forms of *Afghanella* of this group. It is obvious that these forms constitute a branch different from the above mentioned one of *C. primigena* in the stock of *Cancellina*—*Afghanella*.

Furthermore I have obtained a primitive *Cancellina* which seems to be genetically closely allied to *A. schellwieni* in essential shell structures (see pl. 19, fig. 3).

In short we can recognize a progressive development of shell from *Cancellina* to *Afghanella* and some intermediate forms between both the genera. Generally speaking the shells of primitive and moderately advanced forms of *Afghanella* are quite similar in structure to those of the primitive species of *Cancellina* in their younger stage, and the shells of more advanced forms of *Afghanella* have a close resemblance to those of the advanced forms of *Cancellina* and to the middle-aged shells of primitive forms of *Afghanella* in their younger stage. Thus *Afghanella* must be a derivative from *Cancellina* and has no direct connection with *Neoschwagerina*.

Furthermore the shells of highly advanced forms of *Afghanella*, such as *A. pesuliensis* (OZAWA and TOBLER) and *A. sumatrinaeformis* (GUBLER), are entirely similar to those of *Sumatrina* in their later stage: In those species the spirotheca and septula are very thin and the parachomata are slender and very high. The secondary transverse septula first appear in the third volution and frequently twos occur in outer volutions. Two to four axial septula are present between the septa.

In *Afghanella* the secondary transverse septula and axial septula in inner volutions, even in outer volutions in primitive species, are of short rudimentary extensions of the keriotheca of the spirotheca, and are a little thick in their upper parts but are tapered towards their lower margins. However those of the mature stage become generally pendant club-shaped in cross-section, exceedingly thin, especially at their upper margins, and essentially uniform in length. These features are seen in the shells of *Sumatrina* in which the secondary transverse and axial septula are uniform in length, distinctly pendant-shaped throughout all volutions except in inner one or two volutions.

Cancellina, *Afghanella* and *Sumatrina* show successive gradual changes in the structure of the spirotheca and septa, the development of the septula and the structure of the parachomata, and in the shape and size of the shell. The spirotheca gradually reduces the relative thickness of the keriotheca from *Cancellina* through *Afghanella* to *Sumatrina*, corresponding to the increase in number of septula and to thin consolidation from the first to the third genus. The spirotheca of *Afghanella* is provided with the structure similar to that of *Cancellina* in its inner volutions

and with nearly the same feature as that of inner volutions of *Sumatrina* in outer volutions of advanced forms where it has extremely thin keriotheca.

The shape of the parachomata also stands in close relation among those genera. For example, the parachomata of *Afghanella schencki* closely resemble not only those of *Cancellina*, such as *C. primigena* and *C. neoschwagerinoides*, in its younger stage, but also those of *Sumatrina annae* in its later stage. Generally speaking the parachomata of the primitive forms of *Afghanella* are close to those of *Cancellina*, and those of the moderately and highly advanced forms are similar to those of *Sumatrina*. They become gradually and successively more slender but higher in shape from *Cancellina* through *Afghanella* to *Sumatrina*. The parachomata of these three genera are joined by the primary transverse septula at a comparatively higher position than in the respectively corresponding genera *Neoschwagerina*, *Yabeina* and *Lepidolina* in evolutionary development, that is, they are about two-thirds to three-fourths the height of the chambers and frequently are dilated thickly beneath the junction with the primary transverse septula.

The shape of the septa, which is observed in sagittal section, is common to those genera and is different from that of *Neoschwagerina*—*Yabeina*—*Lepidolina* series which will be mentioned later. The distinction in the shape of the septa between *Cancellina* and *Neoschwagerina*, both in the revised sense, was already mentioned. The septa of *Afghanella* and *Sumatrina* are extremely thin at their upper margins but their main parts are thickly coated with the dense calcite which are the same in nature as parachomata, and their lower ends are sharply tapered and extended forwardly at large angles from normal to the spirotheca. They are markedly longer than the axial septula and distinctly discernible from the latter. However, in *Yabeina* and *Lepidolina* the septa are generally bar-like in cross-section, not so thickly coated with the dense calcite as in *Afghanella* and *Sumatrina*, although being slightly thickened at their lower margins. In *Yabeina* the septa are generally thicker at their upper margins than at the lower parts, and in *Lepidolina* they are thin and have almost the same thickness throughout the distance. Furthermore, as the axial septula are irregular in length, mostly not pendant-shaped, and sometimes distinctly long so as to attain about two-thirds the height of the chambers, it is frequently difficult to discriminate the septa from the septula. In short the septa are reduced in the thickness and extension of the keriotheca from *Cancellina* through *Afghanella* to *Sumatrina*, but become to be coated with the dense calcite comparatively more largely.

Thus we can observe a progressive development in the shell structures from *Cancellina* through *Afghanella* to *Sumatrina*. It is no doubt that *Afghanella* is of intermediate between *Cancellina* in the revised sense and *Sumatrina* in the evolutionary development. This development not only within a genus but also among genera under consideration is not a simple upward replacement, but is displayed stratigraphically

by an additional appearance of more advanced forms. The structure of spirotheca, the arrangement of septula and the nature of parachomata and the general structure of those genera are markedly different from those of *Neoschwagerina*, *Yabeina* and *Lepidolina*.

II) *Progressive morphic development in Neoschwagerina, Yabeina and Lepidolina*

In all the species of *Neoschwagerina* revised above the spirotheca, septa and septula are thick respectively in contrast to those of *Cancellina*. In primitive species of *Neoschwagerina* which include *N. simplex* and the species assigned by THOMPSON (1948) to *C. primigena* with a query, the axial septula are absent, and the transverse septula are broad and short, reaching the parachomata only immediately adjacent to the septa. But in somewhat and moderately advanced forms, such as *N. craticulifera haydeni*, *N. craticulifera rotunda* DEPRAT, *N. craticulifera* and *N. colaniae* OZAWA the transverse septula extend to the tops of the parachomata, leaving small lateral openings immediately behind or in front of the septa. In those forms there are one to three axial septula between the septa in outer volutions, whereas three to five axial septula occur in outer volutions of the highly advanced forms, such as *N. margaritae* and *N. megaspherica* DEPRAT. In such highly advanced forms the primary transverse septula become relatively slender and rather longer, and a single secondary septulum is sometimes intercalated between the primary septula in outer one or two volutions. All the structural features in advanced stage of *Neoschwagerina* show a close resemblance to those seen in inner and middle-aged several volutions of *Yabeina*.

Parachomata are broad in primitive forms but become relatively slender in advanced forms.

As mentioned in the foregoing chapter, septa of *Neoschwagerina* are very thick, especially at their upper parts, in contrast to those of *Cancellina*, and are tapered sharply towards the lower margins. Keriothecae on both sides of the septa extend about two-thirds the distance down the septa. However they become rather thinner in highly advanced forms.

In primitive species of *Yabeina*, such as *Y. inouyei* DEPRAT, *Y. katoi* OZAWA, *Y. kaizensis* HUZIMOTO and *Y. cascadiensis* (ANDERSON), the spirotheca is still rather thick and the secondary transverse septula first appear in the sixth to eighth volution. There is a single secondary transverse septulum between the primary ones in most volutions, but occasionally two in outer one or two volutions. However, in advanced forms of *Yabeina*, such as *Y. elongata* (GUBLER), *Y. gubleri* KANMERA, *Y. yasubaensis* TORIYAMA and *Y. minuta* THOMPSON, WHEELER and DANNER, the keriotheca of the spirotheca is very thin in inner volutions. Especially it is so thin in outer volutions that it is hard to observe a layer of the keriotheca at a low magnification. In those advanced forms the septula are also thin and

the secondary transverse septula appear in the first to third volution, increasing in number to two, occasionally to three, in the fifth or sixth volution to maturity. These septula still do have fine but distinct keriothecal structure in their upper parts, but they are fairly consolidated in their lower parts.

The shell structure in outer volutions of highly advanced forms of *Yabeina* bears a close resemblance to that of the inner volutions of *Lepidolina*. As SKINNER and WILDE (1954, p. 450) emphasized, the differences between *Lepidolina* and *Yabeina* are in degree of the evolutionary development of the shell and not in kind. So far as I have been known, there are five species of *Lepidolina*, that is, *L. multiseptata* (DEPRAT), *L. kwangsiana* (LEE), *L. toriyamai* KANMERA, *L. kumaensis* KANMERA and *L. (?) gigantea* TORIYAMA. In those species the spirotheca and septula are exceedingly thin, being almost consolidated as dark thin plates, although fine vestiges of the keriotheca remain at the upper parts of the septula. In *L. toriyamai* and *L. kumaensis*, which I reported from the Kuma massif of Kyushu, an exceedingly thin layer of the keriotheca is seen in inner two to three volutions, but its fine vestiges remain in only the upper portion of the septula in outer volutions.

The derivation of *Lepidolina* from *Yabeina* can be fairly elucidated also with reference to the other shell structures. It is not doubt that *Lepidolina* is a phylogenetically extreme descendant of the series of *Neoschwagerina* and *Yabeina*. Thus we can observe progressive changes of the shell structure from *Neoschwagerina* through *Yabeina* to *Lepidolina*.

III) *Revision of classification of the Neoschwagerininae and Sumatrininae*

Several evolutionary trends of the fusulinids have been already elucidated with assurance by many authors. Especially OZAWA, LEE and THOMPSON discussed in detail as to those of the neoschwagerinids. However, by grasping the generic concept of *Cancellina* and *Neoschwagerina* as mentioned above and by designating them as respective forerunners of the above mentioned two series, some common evolutionary trends between the two series are clearly recognized as progressive developments of the shell structures. The distinct trends are as follows:

- 1) the shell became larger and increased in number of volution: 2) the shell changed in shape from subspherical or ellipsoidal to elongate subcylindrical: 3) the spirotheca and septa became relatively thinner: 4) the septa and septula were consolidated gradually from their lower margins to their upper parts and became thinner especially at their upper margins: 5) the septula including the secondary transverse septula increase in number, and the axial and secondary transverse septula appeared in earlier stage as shell evolved: 6) the parachomata became relatively slender.

These evolutionary developments had taken place in parallel between the two groups but independently within the respective group.

Being combined the developments in the shell structures mentioned above, *Cancellina* evolved to *Afghanella*, and *Afghanella* to *Sumatrina*, while *Neoschwagerina*

developed to *Yabeina*, and *Yabeina* to *Lepidolina*. Of course, their stratigraphical occurrence is introduced into this phylogenetic considerations, as far as the available material is concerned. These evolution, however, are not a simple upward replacement, but more evolved genus branched out in the middle or later stage of the immediately preceeding one. Those two groups respectively belong to the entirely different link in their phylogenetic developments, and run the nearly parallel course in shell development. Namely *Cancellina* corresponds to *Neoschwagerina* in evolutionary stage, *Afghanella* to *Yabeina*, and *Sumatrana* to *Lepidolina*, but there is no direct connection between the analogous genera, respectively. In addition, as will be mentioned later, *Afghanella* appeared geologically more earlier than *Yabeina*, and *Sumatrana* than *Lepidolina*.

KAHLER and KAHLER (1946) and THOMPSON (1954) classified the neoschwagerinid genera into two subfamilies, as stated before. However their classification seems to be quite artificial from the phylogenetical point of view.

As already mentioned, *Lepidolina* superficially resembles *Afghanella* and *Sumatrana*, but it has no direct connection with them. The apparent similarity shows that the analogous genera are only of the same stage in development. So it is inappropriate to include *Lepidolina* in the same subfamily with the latter two genera. Family or subfamily should include genera which genetically belong to the same stock. Such being the case, I am of the opinion that those genera should be classified into two subfamilies as shown in the following table.

Subfamily Neoschwagerininae DUNBAR & CONDRA

Neoschwagerina YABE

Yabeina DEPRAT

Lepidolina LEE

Subfamily Sumatrininae KAHLER & KAHLER

Cancellina HAYDEN

Afghanella THOMPSON

Sumatrana VOLZ

I should like to adopt the subfamily Sumatrininae because it reveals a distinct branch of "Neoschwagerinidae" DUNBAR since the early Middle Permian.

As to the ancestry of *Cancellina*, it has hitherto been considered by many authors that it might have been derived from *Misellina*, and that *Cancellina* evolved to *Neoschwagerina*. However the available material suggests that both of *Cancellina* and *Neoschwagerina* in the revised sense developed in parallel and almost contemporaneously from *Misellina* in the early Middle Permian. The most primitive forms of both the genera have a staffelloid shell in their juvenile stage, as seen in the undescribed subspecies (pl. 19, fig. 6) of *C. nipponica* obtained from the Akasaka limestone and in a *Neoschwagerina* which was assigned originally to *Cancellina primigena* with a query by THOMPSON (1948). Their staffelloid juvenile structure agrees closely with

that of the genus *Misellina* in having only parachomata but no transverse septula.

As will be mentioned later, *Misellina* appeared geologically earlier than *Cancellina* and *Neoschwagerina*, and some species of *Misellina* were ranging up at least into

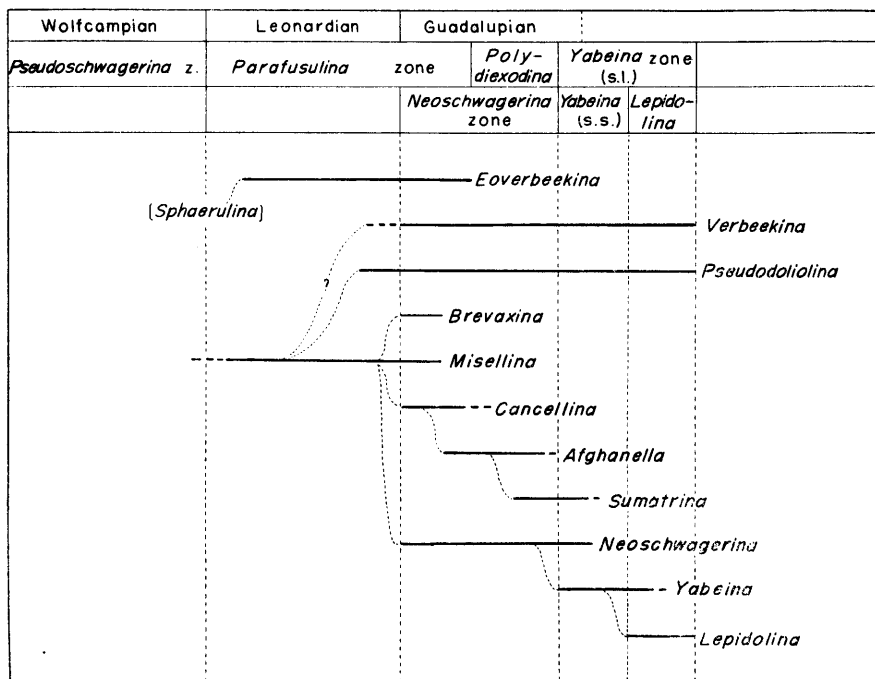


Figure 1. Phylogeny and stratigraphic zonation of Verbeekinae, Sumatrininae and Neoschwagerininae

the lower subzone of the *Neoschwagerina* zone. Primitive forms of *Cancellina* and *Neoschwagerina* must certainly be branched out from earlier members of *Misellina*. The presumed lines of descent among the neoschwagerinid and sumatrinid genera are drawn in the text-figure I.

Geologic Distribution

So far as now known, most of the species of *Misellina* are recorded from the "*Pseudofusulina* zone" which seems to be nearly equivalent in age to the lower part of the *Parafusulina* zone in North America. DEPRAT (1913-'15) described six species of *Misellina*, *ovalis*, *parvicostata*, *termieri*, *minor*, *subelliptica* and *aliciae* from Indo-China and Yunnan. Although their respective coexisted species are not listed here, most of them occur with the characteristic species of the "*Pseudofusulina* zone," such as *P. ambigua* (DEPRAT) and *Schwagerina japonica* (GÜMBEL), but noteworthy to say, not accompanied by any species of *Neoschwagerina*. In China *M. claudiae* was recorded from the Swine limestone which is intercalated between the underlying

Chuanshan limestone (*Pseudoschwagerina* zone) and the overlying Chihsia limestone (*Parafusulina* zone-Lower *Neoschwagerina* zone).

M. claudiae described by OZAWA from the Akiyoshi limestone is associated with *Nagatoella orientis* (OZAWA). Recently TORIYAMA and I clarified that it occurs from the horizon a little lower than *Parafusulina kaerimizensis* subzone of TORIYAMA (1954) at Kaerimizu of Akiyoshi, where the horizon is clearly lower than that of *N. craticulifera haydeni*.

HUZIMOTO (1936) reported *M. claudiae*, *M. minor* and *M. spp.* with the following accompanied species in the Kanto massif:

M. claudiae ... (at Katsubo-yama) *M. minor*, *M. sp.*, *Fusulinella* sp.; [at Asakaido (Asamido)]
N. craticulifera, *P. ambigua*, *S. japonica*

M. minor (at Katsubo-yama) above tabulated; (at Shomaru-pass) *N. minoensis* DEPRAT
em. OZAWA, *Yabeina shiraiwensis* OZAWA, *S. japonica* var. *hayasakai* (LEE)

However these associations of fusulinids seem to be abnormal. In fact the limestone specimens from Asakaido (MORIKAWA, 1954, p. 56, Loc. no. 31), which were sent to me by Dr. Morikawa of Saitama University, contain the species of *Misellina*, *Neoschwagerina*, *Triticites* and *Fusulinella*, but they are distinctly limestone conglomerates, and fusulinids are found only in the pebbles. Such being the case, the fusulinid assemblages previously known from those localities should be reexamined in detail.

TORIYAMA (1947) described *M. iisakai*, *M. tosayamensis* and *M. ? sp.* from the Tosayama limestone of Shikoku. They are associated with *N. tosayamensis* (TORIYAMA), *N. kobayashii* (T.), *N. staffelloides* T., *N. iisakai* T., *Verbeekina katoi* and *V. katoi ? **. *N. tosayamensis* and *N. kobayashii* were originally described as *Cancellina*, but, in my view, they should be included in the primitive group of *Neoschwagerina*, together with *N. staffelloides* and *N. iisakai*. Their morphological characters and stratigraphic position show that they are comparable with the *Neoschwagerina simplex-Cancellina nipponica* fauna defined by OZAWA (1927) in the Akasaka limestone.

MORIKAWA (1955) reported *M. claudiae* from Terazawa, Arakawa-mura, Chichibugun, Kanto massif, where it occurs with several species of *Pseudofusulina*, *Schwagerina* and *Nagatoella*.

I have obtained abundant specimens of *M. minor* and *M. claudiae* from the Kozaki formation of the Kuma massif. The former was found in the limestone pebble in a conglomerate of the formation, associated with *P. ambigua*, *P. parumvoluta* (DEPRAT), *Schwagerina* spp., *Scubertella irumensis* (HUJIMOTO) and *Ozawainella* cf. *O. kueichihensis* LEE. The latter, *M. claudiae*, is associated with *Sphaerulina crassispira* LEE and *S. japonica*, and occurs in the limestone lenses which are stratigraphically slightly lower than those containing the faunas common to the *N. simplex-C. nipponica* zone of Akasaka.

* This species was originally described as *Pseudoschwagerina* sp., but later KONISHI (1955) corrected it as *Verbeekina*. (Jour. Geol. Soc. Japan, vol. 59, p. 435)

As mentioned above, with the possible exception of the doubtful long-ranging occurrence in the Kanto massif, *Misellina* seems to have a rather short geologic range*, namely, in Japan it appeared in the upper part of the *Pseudoschwagerina* zone, flourished in the lower half of the *Parafusulina* zone, and ranged up into the *N. simplex*—*C. nipponica* subzone (=Upper *Parafusulina* zone), the lowest part of the *Neoschwagerina* zone.

Cancellina is almost contemporary with *Neoschwagerina* in its appearance but it seems to have a shorter geologic range than the latter. Such a situation seems to correspond to the fact that *Cancellina* has a more limited range than *Neoschwagerina* in morphological development: No species of *Cancellina* has been found, which is corresponding to the advanced forms of *Neoschwagerina*, providing with as much as three to five axial septula. In connection with this matter, *Afghanella* also appeared geologically earlier than *Yabeina*, and *Sumatrina* than *Lepidolina*, which respectively correspond to each other in evolutionary development.

Cancellina previously described from Japan is *C. nipponica* by OZAWA from Akasaka and *C. primigena* by HUZIMOTO from the Kanto massif. The former occurs in association with the followings:

N. simplex, *Verbeekina* "sphaera" OZAWA, *Pseudodoliolina ozawai* YABE and HANZAWA, *S. japonica*, "Parafusulina" *granum-avenae* (ROEMER), *Neofusulinella compressa* (OZAWA), *N. giraudi* DEPRAT, *N. phairaiensis* COLANI

OZAWA (1927) illustrated only one parallel section of *N. (C.) schellwieni* DEPRAT from *C. nipponica* zone of Akasaka without any description. Reexamining myself the OZAWA's original sections**, however, the specimen is clearly referable to *C. nipponica*. *C. primigena* from Kanto appears to be intermediate in shell development between *Misellina* and *Cancellina*, and it is associated with the species assigned to *P. ambigua* with a query. *C. nipponica* was also recorded from Funafuse of central Japan and from Shikoku, and *C. primigena* from Shikoku, but their associated species are unknown.

I have found a primitive species of *Cancellina*, which seems to be the ancestry of *A. schellwieni* (DEPRAT) and *C. neoschwagerinoides*, from the Kozaki formation of the Kuma massif, which are accompanied by *N. simplex*, *V. "sphaera"*, *Pseudodoliolina ozawai*, *Parafusulina yabei* HANZAWA, *P. tchussovensis* RAUSER-CHERNOUSSOVA, *P. spp.*, *Yangchienia iniqua* LEE and CHEN, *Neofusulinella phairaiensis* and *Schubertella irumensis*. These faunas are largely common to those of the *N.*

* THOMPSON (1948) and YABE (1948) had referred *Schwagerina lepida* SCHWAGER to *Misellina*. Although it is omitted here to state my opinion, however, I consider it is more likely referable to *Pseudodoliolina*.

** HANZAWA (1954) stated that he could not find *A. ozawai* in the Akasaka limestone even though he reexamined OZAWA's original collection from Akasaka and made extensive collections from the same locality. I also made numerous sections myself from the *Cancellina nipponica* zone, but I failed to find it.

simplex—*C. nipponica* zone of Akasaka, being most probably equivalent in age.

As mentioned above, *Cancellina* in Japan is accompanied by *Misellina*, primitive forms of *Neoschwagerina*, *Verbeekina* and *Pseudodoliolina* and several species of *Parafusulina*, but is not associated with the advanced forms of *Neoschwagerina*.

Afghanella was reported from only western Japan. HANZAWA (1954) established *A. ozawai* based on the specimens from the Akiyoshi and Taishaku limestones, to which he identified OZAWA's *Yabeina schellwieni* [= *N. (C.) schellwieni*, 1927] from Akiyoshi*. He stated that it was found in the *Neoschwagerina* zone, but he did not show the accompanied species.

Afghanella schencki THOMPSON and *A. sp.* reported by TORIYAMA from the *P. kaerimizensis* and *N. craticulifera* subzones in the Akiyoshi limestone are associated with the following forms:

N. craticulifera, *N. craticulifera haydeni*, *N. spp.*, *Pseudodoliolina ozawai*, *P. pseudolepida*, *Pseudofusulina gigantea* (DEPRAT), *P. edoensis* (OZAWA), *P. kaerimizensis* (OZAWA)

Thus *Afghanella* in Japan has been known to occur with more advanced species of neoschwagerinids and schwagerinids than those associated with *Cancellina*.

The *Neoschwagerina* zone characterized by moderately and highly advanced forms of *Neoschwagerina* in Japan are designated as the *N. craticulifera* and *N. margaritae* subzones in ascending order. The zones are typically developed in the Akasaka limestone and were clearly elucidated by OZAWA. The *Neoschwagerina* zone is widely distributed in various separated areas in Japan and was distinctly defined by many authors, although the two subzones cited above is hardly distinguished as in Akasaka. The faunas of the two subzones include *N. craticulifera* and its several subspecies, *N. margaritae*, and *N. colaniae* OZAWA. In addition, almost always *Verbeekina verbeeki* and sometimes *Pseudodoliolina pseudolepida* are associated with them.

The occurrence of *Sumatrina* is restricted in western Japan as far as known, and *S. annae* VOLZ and *S. sp.* had been reported from Akiyoshi, Taishaku, Atetsu, Koyama and Akasaka. However the generic affinities of forms of *Sumatrina* formerly reported from the latter four localities without any illustration and description can not be determined, since *Sumatrina* formerly included forms now referred to *Afghanella*.

According to OZAWA (1927), *S. annae* from Akasaka was a doubtful fragment from the Daiiri limestone where it occurred with *Yabeina globosa* (YABE) (= *Y. inouyei* DEPRAT) and *Y. katoi* (OZAWA). However *S. annae* from Akiyoshi was reported by him (1925) without any associated species.

* I am inclined to regard OZAWA's "*Y. schellwieni*" as a different species from *A. ozawai*, in which the secondary transverse septula appear earlier than in the latter and sometimes twos occur in outer volutions.

HUZIMOTO (1944) listed *S. annae* from several localities in the Taishaku limestone. In most of those localities it was found in the limestone breccias which are interpreted to be of reworked origin, being associated with the Carboniferous and Lower Permian fusulinids and the highly advanced neoschwagerinids. Accordingly the accompanied species of *S. annae* is not known. In one locality where the rocks do not contain reworked rocks the following species were reported in association with it:

N. craticulifera, *N. margaritae*, *N. douvillei* OZAWA, *N. sp.*, *Yabeina sp.*, *Sumatrina sp.*, *Schwagerina sp.*

HANZAWA (1954) described *S. annae* on the basis of the specimens from many localities, and illustrated the specimen collected from Iwakurayama, Hinaga, Ominé City, Yamaguchi Pref. He did not list any associated species in other localities except in the south entrance of the Onigasako tunnel, Kushiromura, Hiba-gun, Hiroshima Pref., where, according to him, it was found in association with *A. ozawai* in the *Neoschwagerina*-limestone blocks entombed in schalstein of the Cretaceous Nochi formation. However, as the blocks are of apparently derivative, it is doubtful whether they were found in the same one pebble. Furthermore he stated *Sumatrina* is accompanied by *Cancellina*, although he did not show its specific name and its locality. However the coexistence of *Sumatrina* with *Cancellina* and primitive species of *Afghanella* such as *A. ozawai* seems to me unlikely.

TORIYAMA (1954) listed *S. annae*, *S. annae* var. *stricta* DEPRAT and *S. annae*, var. nov., from several limestone lenses of the Tsunemori group which is distributed in the western adjacent area of the Akiyoshi limestone. According to him, those limestone are of all limestone conglomerates consisting of pebbles, cobbles and huge boulders of limestone which are prolific in fusulinids from the *Fusulinella* zone to the *Yabeina* zone. The limestone at Iwakurayama, Hinaga, whence *S. annae* was illustrated by HANZAWA (1954) and SKINNER and WILDE (1954), is one of the limestone conglomerates. Such being the case, associated species of *S. annae* have not yet been known clearly.

I have examined numerous sections obtained from the Taishaku limestone at Ichirizuka, Tojo-town, Hiroshima Prefecture. Abundant specimens of *S. annae* are found in association with *N. margaritae*, *Pseudodoliolina pseudolepida*, *Schubertella* sp. and *Reichellina* sp. However *Yabeina* has not been found at all.

At any rate, in our present knowledge we are still far from leading a confirmative conclusion on the stratigraphic horizon of *S. annae*. However it is certain that it occurs in the *Neoschwagerina* zone and it may range up into the lower *Yabeina* zone containing primitive *Yabeina*, such as *Y. inouyei* (= *Y. globosa*) and *Y. katoi* and several species of *Neoschwagerina*, but not into the upper *Yabeina* or *Lepidolina* zone.

HUZIMOTO (1936) added *S. japonica* from the Shomaru-pass of the Kanto massif to

this genus. It is superficially similar to *Sumatrina*. HANZAWA (1954) and I (1952, 1954) independently pointed out it is probably referable to *Yabeina* or *Lepidolina*.

Sumatrina longissima DEPRAT was found only from the Akiyoshi limestone by TORIYAMA (1954), where it is associated with *Y. shiraiwensis* OZAWA and *Y. sp.* As inferred not only from the morphological characters but also from the faunal assemblage, it seems to appear in the upper horizon than *S. annae* does. At any rate the stratigraphic distribution of *S. longissima* has not yet been confirmed in Japan.

As I (1952) already pointed out, the so-called *Yabeina* zone in Japan is separable into two subzones based on the faunal assemblage and on the rock unit, the lower *Yabeina globosa* zone and the upper *Lepidolina* zone. The fauna of the *Y. globosa* zone is always associated with several advanced species of *Neoschwagerina*, such as *N. margaritae*, *N. douvillei* and *N. megaspherica*, while that of the *Lepidolina* zone in Japan is characterized by *L. toriyamai* and *L. kumaensis*, containing highly advanced species of *Yabeina*, such as *Y. gubleri* KANMERA, *Y. shiraiwensis* OZAWA and *Y. yashubaensis* TORIYAMA, but is lacking *Neoschwagerina*. In the latter *Sumatrina* has not yet been found anywhere. As mentioned in the foregoing chapter, *Sumatrina* is in parallel with *Lepidolina* in the stage of the evolutionary development of the shell, but, so far as known, the former appeared earlier than the latter.

Acknowledgements

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K. KANMERA

Revised Classification of *Cancellina* and *Neoschwagerina*, and Evolution
of Sumatrininae and Neoschwagerininae

Plates

Plate 19

Sumatrininae and Neoschwagerininae

Figure

Genus *Cancellina* HAYDEN, 1909

- 1, 2—*Cancellina primigena* (HAYDEN). Genotype. 1, axial section of the holotype, 2, sagittal section of a paratype; $\times 10$. (After HAYDEN, 1909).
3—*Cancellina* sp., Axial section; $\times 10$. Kozaki formation, Kuma massif. This species seems to be a genetically closely related species to *Afghanella schellwieni* (DEPRAT).
4, 5—*Cancellina neoschwagerinoides* (DEPRAT). 4, sagittal section, $\times 24$; 5, axial section, $\times 10$. (After DEPRAT, 1913).
6, 7—*Cancellina nipponica*, new subspecies A. 6, axial section, 7, sagittal section; $\times 10$. The most primitive form of *Cancellina* from the lower part of the *Cancellina nipponica* subzone of the Akasaka limestone.
8-11—*Cancellina nipponica* (OZAWA). 8, axial section, 9, sagittal section, $\times 10$; 10, 11, enlarged sagittal sections showing structure of spirotheca and septa (10, outer volutions; 11, inner volutions), $\times 50$. Akasaka limestone.

Genus *Afghanella* THOMPSON, 1946

- 12, 13—*Afghanella ozawai* HANZAWA. 12, axial section, 13, sagittal section; $\times 10$. Primitive form of *Afghanella*. Akiyoshi limestone.
14, 15—cf. *Afghanella schencki* THOMPSON. 14, axial section, 15, sagittal section; $\times 10$. Moderately advanced form of *Afghanella*. Kaerimizu, Akiyoshi limestone.
16, 17—*Afghanella sumatrinaeformis* (GUBLER). 16, axial section, 17, sagittal section; $\times 10$. Highly advanced form of *Afghanella*. (After GUBLER, 1935).

Genus *Sumatrina* VOLZ, 1904

- 18, 19—*Sumatrina annae* VOLZ. 18, axial section, 19, sagittal section; $\times 10$. Ichirizuka, Tojo-town, Hiroshima Pref., Taishaku limestone.

Genus *Neoschwagerina* YABE, 1903

- 20, 21—*Neoschwagerina* sp. 20, axial section, $\times 10$; 21, enlarged sagittal section showing structure of spirotheca and septa; $\times 50$. The most primitive form of *Neoschwagerina*. [After THOMPSON, 1948, *Cancellina primigena* (HAYDEN)?, THOMPSON].
22, 23—*Neoschwagerina simplex* OZAWA. 22, sagittal section, 23, axial section; $\times 10$. Primitive form of *Neoschwagerina*. (After OZAWA, 1927) Akasaka limestone.
24—*Neoschwagerina craticulifera haydeni* DOUTKEVITCH and KHABAKOV. axial section; $\times 10$. Slightly advanced form of *Neoschwagerina*. (After THOMPSON, 1948) Bamian limestone.
25—*Neoschwagerina* sp. Sagittal section; $\times 10$. Slightly advanced form of *Neoschwagerina*. Akasaka limestone.

Photos by KANMERA

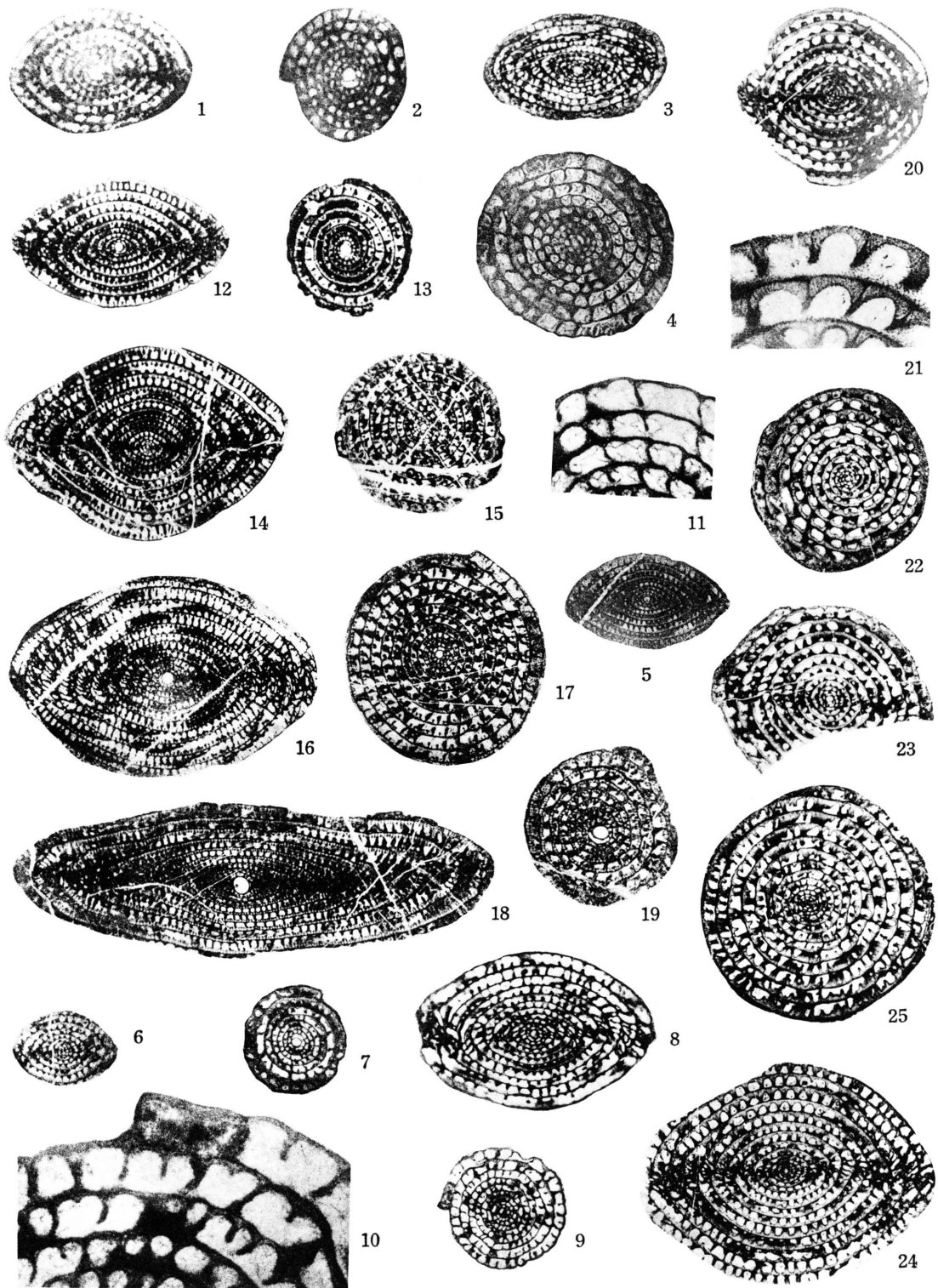


Plate 20

Neoschwagerininae

Figure

Genus *Neoschwagerina* YABE, 1903

- 1—*Neoschwagerina* sp. cf. *N. simplex* OZAWA. Sagittal section; $\times 10$. The most primitive form of *Neoschwagerina*. Kozaki formation, Kuma massif.
- 2—*Neoschwagerina kobayashii* TORIYAMA. Axial section; $\times 10$. The most primitive form of *Neoschwagerina*, which seems to be an intimately related form to *N. craticulifera* (SCHWAGER). Yoshiwo formation, Kuma massif.
- 3, 4—*Neoschwagerina margaritae* DEPRAT. 3, axial section, 4, sagittal section; $\times 10$. Advanced form of *Neoschwagerina*. Akasaka limestone (*Nm* subzone of OZAWA).
- 5, 6—*Yabeina globosa* YABE (= *Y. inouyei* DEPRAT). 5, axial section 6, parallel section; $\times 10$. Primitive form of *Yabeina*. Yonagu formation, Kuma massif.
- 7-9—*Yabeina gubleri* KANMERA. 7, axial section of the holotype, 8, sagittal section of a paratype; $\times 10$. Highly advanced form of *Yabeina*. 9, enlarged part of axial section showing structure of spirotheca and transverse septula. Kuma formation, Kuma massif.
- 10-13—*Lepidolina toriyamai* KANMERA. 10, axial section of the holotype, 11, 12, sagittal section of paratypes, $\times 10$, 13, enlarged tangential section of a paratype showing structure of spirotheca and transverse septula, $\times 100$. Kuma formation, Kuma massif.

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