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PARALLEL TENDENCIES IN THE EVOLUTION OF THE FUSULINIDS

(Pl. I)

Paralelne tendencije razvoja u fuzulinida

(Tabl. I)

Abstract: Some morphologic features, such as cuniculi, „rugosity” of the spirotheca, orimontary foramina and parachomata, the first transverse septula and the uncoiled last volution, were hitherto considered to be characteristic for single genera. Now it is clear that these characters occur in genera of different phylogenetic origins. Owing to parallel evolution, similar forms were produced. Therefore the view is expressed that some fusulinid „genera” represent assemblages of diverse genetic ancestry.

Recently many papers have been published on problems concerning the evolution of the Fusulinida. Especially important is the paper written by R a u z e r - C h e r n o u s o v a (1963). In the present account, a few points based predominantly on material from Yugoslavia are made.

It is known that in the foraminiferal order Fusulinida, some characteristics repeatedly occur in different evolutionary trends. Thus highly elongated cylindrical or fusiform tests are found in the genera of various families (for example, *Fusiella*, *Minojapanella*, *Quasifusulina*, *Wedekindellina*, *Parafusulina*, *Polydiexodina*, *Monodiexodina*, *Pseudodoliolina*, *Sumatrina*, etc.) especially as the final forms of single phylogenetical branches. Furthermore, the nautiloid form is repeated mostly in the primitive genera *Pseudoendothyra*, *Staffella*, *Kahlerina*, *Brevaxina*, *Pseudostaffella*, *Eostaffella*, the ellipsoidal form in *Schubertella*, *Leella*, *Zellia*, *Misellina*, *Neoschwagerina* and the spherical one in *Pseudoendothyra*, *Pseudostaffella*, *Sphaerulina*, *Verbeekina*, *Schubertella*, in different representatives of *Pseudoschwagerininae* and rarely in *Neoschwagerina*. The repeated occurrence of cylindrical and various inflated, fusiform shells is also known.

A. D. M i k l u k h o - M a k l a i (1959) wrote about homaeomorphical features of the outer forms in the fusulinid genera and drew attention to the fact that many recognized genera represent, in fact, collective units, possessing different juvenaria. He was inclined to consider deve-

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lopment of similar final stages as indicating the assumption of similar modes of life.

In as early as 1942, F. Kahler expressed the opinion that the spheroidal form of different species of *Pseudoschwagerina* (s.l.) is indicative of a planktonic way of life in the adult stage. However, it is doubtful that a planktonic mode of life can be assumed by all spheroidal species. Closely coiled volutions and elements of secondary skeletons, which frequently occur in spherical fusulinids, do not support such a conclusion.

Very distinctive are the so-called aberrant forms known as partially uncoiled shells. In the subfamily Boultoniinae, this feature is typical for *Codonofusiella*, *Paraboultonia* and *Paradoxiella*, for *Nipponitella* in the subfamily Schwagerininae, for *Reichelina* in the subfamily Ozawainellinae. Slightly evolute coils have been registered in *Millerella*, *Novella* and *Pseudoendothyra* forming the beginning of evolute whorls and are known also from the assymmetrically shaped shells of *Chenella* (Pasini, 1965, p. 100).

The unity of all the genera of the order Fusulinida is also evident in repetition of some features characteristic for most of the families, such as the tunnel, chomata and axial fillings as well as in the phylogenetic development of spirotheca, which represent a transition between a primitive layered wall and advanced spirothecal structure with keriotheca in some species (e.g. *Protriticites*).

Recently, some features have been found in greater numbers of genera than was previously assumed. Cuniculi, previously considered characteristic for *Parafusulina* and *Polydiexodina*, were recognized also in *Monodiexodina*, then in initial stages of development (outer whorls only) in the genus *Eoparafusulina* Skinner & Wilde, *Praeparafusulina* Tournanskaya and even more primitive in *Paratriticites* Kochansky-Devidé (1969). Furthermore, the present author succeeded in recognizing orimontary cuniculi in species of *Quasifusulina* occurring sporadically in the outer volutions only (Pl. I, Fig. 4). This observation was also made by F. Kahler, who independently recognized this feature in Alpine specimens. Cuniculi were found also in *Cuniculinella* Skinner et Wilde and in *Lantschichites* (= *Paraboultonia*?).

A big problem has appeared recently concerning the „rugosity” of the spirotheca. Small dimples in the tectum and unevenness of irregular spirotheca were at first considered to be characteristic for the genus *Rugosofusulina*, which also shows irregularities in septal fluting. Consequently axial sections have a „disordered” appearance. However, extreme rugosity was later recognized in *Rugosochusenella*, in some species (or specimens) of *Fusulina*, *Fusulinella* and *Triticites* and in juvenaria only in *Rugososchwagerina* and *Chusenella* (*Sosioella*). Problems of nomenclature became even more complicated when rugose spirotheca was found in *Pseudofusulina huecoensis* Dunbar & Skinner, the genoholotype, first by Thompson (after Skinner & Wilde 1965, p. 58) and later by Skinner & Wilde (1965, 1966). Then a number of American *Pseudofusulinae* with slight rugosity of the spirotheca were described. The present author established the subspecies *Pseudofusulina vulgaris rugosa* Kochansky 1968 before reading the papers of Skinner & Wilde. *P. vulgaris rugosa* is a small form with a minutely rugose tectum, derived from the group *P. vulgaris*. Thus the present author considers „rugosity” to be a subspecific feature of

a smooth species. In addition, it should also be noted that the classical *Rugosofusulina alpina* of elongated form and with thin, irregularly fluted septa, features typical for the genus *Rugosofusulina*, does not have rugose spirotheca at all finding places. P a s i n i (1963) found specimens of the subspecies *alpina antiqua* with smooth walls only and considered the subspecies to be not representative of the genus *Rugosofusulina*. In the Yugoslav Alps, specimens with smooth walls occur at some localities and those with rugose shells at the others (Pl. I, Figs. 1, 1a, 2, 2a). Some Schwagerinidae especially show differently folded and somewhat irregular spirotheca. Also in the primitive genera of this family (for examples *Biwaella*), undulated walls occur. Not only in the Schwagerinidae, but also in *Hidaella*, of the subfamily Fusulininae, which has a primitive spirotheca of *Fusulinella*-type, irregularly folded walls were found.

Consequently „rugosity” occurs mainly in several genera and species. However, this cannot be considered to be the only feature applicable in the determination of a genus or species.

Most fusulinologists pay little attention to septal count and morphology in sagittal section. Thus they pay no attention to the fact that some primitive genera of different families have scarce septa, remote one from another, as in *Biwaella* (Pl. I, Fig. 3), from the Schwagerinidae and in *Kahlerina* which, according to several authors, belongs to either the Verbeekinidae or the Staffellidae.

Most individuals of all species of the genus *Kahlerina*, and of the different species of *Sphaerulina*, as well as the most primitive species of *Eoverbeekina* and the genus *Chenia* have identical features, namely the first foramina and small orimentary parachomata. The progressive species of *Staffella* have only sporadically foramina. It is interesting to note the gradual appearance of the foramina and parachomata in different developmental stages of the progressive species of Staffellinae, *Chenia* and *Kahlerina*. They do not develop uniformly, either in different species of the same genus or in different individuals of the same species. This initial, but as yet unsettled, development in the Staffellinae, *Kahlerina* and *Chenia* is parallel with that of the Misellininae, Verbeekininae, Pseudodoliolininae and Neoschwagerinidae. Development reached a more advanced stage in the last four groups. Several observations of the initial foramina and parachomata were made on well preserved specimens from Velebit Mountain (K o c h a n s k y - D e v i d é 1966 b).

Is it possible that the parallelism may be so well developed that, as a result of homaeomorphy, we cannot distinguish various forms which have followed different evolutionary trends. In the opinion of the present author, in such simple organisms as Foraminifera, it is possible that some, such as Fusulinida, have more complicated tests. The author has proposed a diphyletic development for the genus *Reichelina*. One of the oldest species *R. serbica* K o c h a n s k y - D e v i d é — from the Troglkofel limestone — is the largest representative of the genus, its size not being in accordance with its age. The material of its spirotheca is to a considerable degree replaced by secondary mineralization, as is the case of *Nankinella*, and its inner volutions are nautiloidal, that is more rounded.

The older species of the genus *Reichelina* have nautiloidal inner volutions, like *Reichelina* (?) *kiluensis* S a u r i n (the author has already

emphasized the presence of inner volutions similar to these in *Nankinella*), and *R. slovenica* Kochanský-Devidé, which also has secondary mineralized walls. It is debatable whether the true representatives of *Reichelina* have developed from *Ozawainella*, whereas „*Reichelina*” *serbica*, „*R*”. *slovenica* and „*R*”. *kiluensis* are derived from an unknown genus of the family Staffellidae similar to *Nankinella*. It should be noticed, however that *Nankinella* proper appears somewhat later than the „*Reichelina*” species of the Trogkofel limestone. In another paper, the author indicated (Kochanský-Devidé 1966, a, pp. 43—44) arguments against parallel development of the forms similar to *Reichelina*. However, the possibility of parallel trends still exists and seems to be now more probable.

The genus *Darvasites* is from *Triticites* hardly distinguishable. Many authors consider the former to be a subgenus. *Darvasites* appeared some time after the development of the true representatives of the genus *Triticites*. In southern Europe, the true *Triticites* end in the Gshel-beds, while *Darvasites* is especially numerous in the Trogkofel limestone. In Central Asia *Darvasites* is most common in Darvas beds, while in the older Karatschatyr beds, neither *Triticites* nor *Darvasites* are recorded (Miklukho-Maklai 1963, pp. 58—61). It is unclear whether *Darvasites* is a *Triticites*, or developed from an unknown form of the Schwagerininae, which lived for relatively short time at the beginning of the Permian.

The examples of *Reichelina* and *Darvasites* give rise to skepticism with regard to the interpretation of some fusulinid genera. It is possible that a genus represents only a group of forms. This is probable especially with long-lasting genera, rich in species. Then, parallel trends in different evolutionary lines can produce test of similar shapes being — if very simple — even undistinguishable.

Differences in the interpretation of genera are clearly seen in the case of *Staffella/Pseudostaffella*. Dunbar (1963, p. 26) takes them to be one genus only. Most others, however place importance upon differences in the development of chomata, juvenaria, etc., as well as in age of the genera (*Pseudostaffella* is of the Middle Carboniferous, *Staffella* of the Permian).

The author has found an especially good example confirming that even distantly related groups show some parallelism, and proving that the Fusulinida constitute a genetically homogenous group. This is especially clear in the development of the transverse septula of *Pseudoschwagerina*: though they are regularly developed in the family Neoschwagerinidae only, they were found also in *Pseudoschwagerina* cf. *turbida* Kahler & Kahler, from the „Grenzlandbänke” (Sakmarian) of the Karawanken (Pl. I, Fig. 5).

Some relations between *Pseudoschwagerina* and *Verbeekina* have been mentioned already by Kahler & Kahler (1941, p. 76) describing *P. glomerosa* (Schwager) and by Ciry (1943, p. 33) in *P. subrotunda* Ciry. These authors report minute parachomata in the outer volutions. According to Ciry, these are only convergent features. The present author could not find any parachomata in *P. subrotunda*.

Thus the skeletal elements of Fusulinida are extremely variable. The present author thinks that they are the effects not only of adaptation, but also of a common genetic inclination to create in different families

genera, species and individuals similar features in parallel morphogenetic trends.

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SAŽETAK

Sinopsis. Neke morfološke značajke, smatrane svojstvenima za određene rodove, nalaze se sve češće i u fusulinidnih rodova različitog porijekla: npr. kunkuli, „rugoznost“ spiroteke, orimentarni foramina i parahome, prvi transverzalni septuli, odvijeni posljednji zavoj i dr. Zbog ovako paralelnih razvoja, koji mogu dovesti do sličnih oblika, naglašeno je, da su možda neki „rodovi“ zbirne grupe.

U raznim razvojnim granama fuzulinida dolazi često do jednakih oblika, kao i do ponavljanja pojedinih morfoloških značajki. Kod ponavljanja vanjskog oblika osobito su zanimljive aberantne forme: na svršetku različitih filogenetskih grana odvijaju se posljednji zavoji kućica. Moguće je, da jedan od takvih rodova, *Reichelina*, predstavlja zbirnu skupinu oblika, koji su se oblici razvili s jedne strane od roda *Ozawainella*, a s druge od forme nalik rodu *Nankinella*, ali starije. To mišljenje podupire opažanje, da postoji nešto različiti juvenarij i kristalasta stijenska starijih vrsta označenih u ovom radu kao „*Reichelina*”.

U filogenetski udaljenih fuzulinida mogu se ponavljati pojedina svojstva, ali samo kod nekih rodova. Npr. kunikuli, prolazi među susjednim komoricama ispod dubokih nabora sepata, u novije vrijeme se nalaze kod sve primitivnijih rodova, dok ih se prije smatralo svojstvom visoko razvijenih 2—3 rodova. Borana, tzv. rugozna spiroteka, najprije smatrana kao svojstvena rodu *Rugosofusulina*, poznata je sada već kod 8 rodova. To je svojstvo, koje ne može imati uvijek generičku važnost, pa čak ni specifičku nego subspecifičku ili infraspecifičku, kao što pokazuju i primjeri iz jugoslavenskih Alpa.

Kao daljnja paralelno razvijena svojstva raznih razvojnih grana prikazuje se i ističe razmaknutost sepata, orimentarni foramina i parahome familije Staffellidae i rodova *Kahlerina* i *Chenia* te počeci parahoma i transverzalnih septula u roda *Pseudoschwagerina*.

Kako je moguće, da se paralelnim razvojem više svojstava postigne veoma sličan oblik, upozoruje se, da vjerojatno postoje oblici međusobno veoma slični, a ne moraju biti uže srodni (npr. *Triticites* i *Darvasites*, a otprije poznati *Pseudostaffella* i *Staffella*).

Zaključno je istaknuto, da osim prilagodbenih značajki, koje s vremenom mogu postati genetski fiksirane, postoje izvjesne zajedničke, genetski uvjetovane sklonosti. Ove mogu odjednom doći do izražaja u paralelnim tendencijama u razvoju raznih taksona pa i pojedinih individua.

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EXPLANATION OF PLATE

Plate I

- Fig. 1. *Rugosofusulina alpina antiqua* (Schellwien). 681. $\times 10$. Specimen with rugose spirotheca. Karavanke Mountains, Savske jame
Fig. 1a. Detail of the same specimen. $\times 60$
Fig. 2. *Rugosofusulina alpina* cf. *communis* (Schellwien). 351/1. $\times 10$. Specimen with smooth spirotheca. Mt Košuta, Karavanke Mountains.
Fig. 2a. Detail of the same specimen. $\times 40$
Fig. 3. *Biwaella inopinata* (Kochansky-Devidé). 570. $\times 30$
Sagittal section with far remoted septa. Velebit, Medački kuk
Fig. 4. *Quasifusulina* cf. *longissima* (Moeller). J 457. $\times 40$ Cuniculi. Karavanke Mountains, ENE of Mojstrana
Fig. 5. *Pseudoschwagerina* cf. *turbida* Kahler & Kahler. J 186. $\times 70$. Orimentary transverse septula. Karavanke Mountains, Robe, Kranjska gora

