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Dimensional Parameters of Columnar Stromatolites as a Result of Stromatolite Ecosystem Evolution

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Abstract—Columnar stromatolites representing more than a half of species described in Precambrian stromatolite assemblages reveal a regular trend of size variations during the Proterozoic and Early Paleozoic. Their dimensional parameters grew gradually during the Paleoproterozoic to attain peak values in the Early Riphean and to decline steadily afterward during the Middle–Late Riphean, Vendian, and Cambrian. Size variations are established based on statistically averaged maximum diameters of columns calculated for 230 taxa and on percentages of large, medium and small species occurring in successive units of stratigraphic scale. The units correspond to three Paleoproterozoic subdivisions (time span from 2.3 to 1.65 Ga) and to five subdivisions of the Riphean, Vendian and Early Paleozoic jointly spanning a comparable period of geologic time. The results of calculation depict a unimodal variation curve with one infliction point designating inversion of ascending and descending trends in the Early Riphean time. The inversion and cardinal changes in taxonomic composition of the entire stromatolite community across the Riphean lower boundary appear to be interrelated. Abiotic events, which certainly influenced diversity of all, especially columnar stromatolites, have no manifestation however in the size-variation curve lacking perceptible oscillations in both the ascending and descending branches. Consequently, dimension parameters of columnar stromatolites appear to be independent of direct influence of abiotic events.

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Key words: Paleoproterozoic, Riphean, Vendian, Early Paleozoic, columnar stromatolites. evolution, dimension parameters.

INTRODUCTION

When it was shown that stromatolites representing peculiar organogenic-sedimentary buildups were able and did evolve as ecosystems under influence of diverse factors (Semikhatov and Raaben, 1994, 1996), the relevant problems attracted attention of many specialists. The evolution of stromatolites is evident from their morphological and structural changes detectable in geological records. Based on distinctive features of the Late Precambrian and Early Paleozoic stromatolites, Korolyuk (1960, 1963) discriminated their paleotype and neotype buildups, and Riphean successions were established first for single stromatolite taxa (Keller et al., 1960) and soon afterward for taxonomic assemblages (Korolyuk et al., 1962; Krylov, 1962, 1963; Semikhatov, 1962; etc.). Researches were initially uncertain of evolutionary character of stromatolite successions, as it would be contradicting the conservative nature of stromatolite-forming microorganisms belonging to cyanophytes (cyanobacteria). Hesitations faded away, when representative data proved later on that mat-forming microorganisms and stromatolites were able to evolve as ecosystems.

Stromatolite buildups should be regarded as a peculiar category of algal-mat biolithites originated in ecosystems containing stromatolite-forming microorganisms. Inheritance, the notion introduced by Korolyuk (1960), is the most characteristic property of algal mats producing stromatolites. Each algal-bacterial film inherits morphostructure of the previous one thus producing fine lamination, the main and indispensable character of all the stromatolite taxa discriminating them from thrombolitites, the other category of biolithites attached to substratum. The progressing evolution of stromatolites is evident from their diversity dynamics (Semikhatov and Raaben, 1994, 1996) controlled by successive biotic and abiotic events interrelated or independent of each other.

Researchers who considered evolutionary trends of stromatolite buildups noted a series of concrete changes in their features indicative of their progressing development. These are transformation in laminae microstructures recorded in a higher proportion of biogenic component or in development of more complicated lamination rhythms (Korolyuk, 1960; Komar et al., 1965; Semikhatov, 1978; Xing et al., 1985; Cao, 1991), conversion of one-layer walls of columnar stromatolites into multilayer ones (Korolyuk, 1960), and complication (Krylov, 1963) or regulation (Raaben, 1969) of branching.

Examination of ministromatolites, the buildups having quasi-microscopic columns and representing separate category of stromatolites, showed a distinct trend of changes in dimensions of their columns during the Proterozoic (Raaben, 2005). This turned attention to the same parameter of common columnar stromatolites termed sometimes columnites (from Latin Columnithi) for convenience (Raaben and Sinha, 1989; Semikhatov and Raaben, 2000). Data on very numerous stromatolite taxa from this supergeneric grouping show that their dimensions also changed regularly with time obeying some specific factors considered below.

PECULIARITY OF COLUMNAR STROMATOLITES

Columnar stromatolites represented by more than 500 form species of valid identification have been long the favorite objects of research. They represent one of very important supergeneric morphologic groupings of diverse stromatolite buildups. Three groupings of columnar, nodular and stratiform stromatolites (Korolyuk, 1960) are acknowledged in practice nearly worldwide. One more grouping of microstromatolites distinguished later (Raaben, 1980) is studied partly so far, only with respect to minicolumellids (columnar microstromatolites) frequently regarded as "ministromatolites" (Hofmann and Jackson, 1987). All the groupings represent Stromatoliti Pia, the highest stromatolite taxon in traditional system of classification. As is shown (Semikhatov and Raaben, 2000), the system incorporated classification principles expounded in works of the 1960s to 1980s. I should mention here that classification of stromatolites has nothing in common with classifications of algae or bacteria. Like other paleontological classifications, it is hierarchical, using binary nomenclature introduced into practice since the earliest descriptions of stromatolites. As one of artificial systems, the stromatolite classification is based on observable morphological features used to discriminate all the taxa of highest rank and majority of form genera or "groups," as they are often termed. Form species ("forms") are distinguished commonly based on microstructure of laminae and partly on some morphological details.

Columnar, stratiform and nodular stromatolites used to be considered as taxa of one rank, although some researches define the latter two groupings as "non-columnar stromatolites" (Walter, 1972). According to practice of research, discrimination between them and columnar stromatolites has a sense and concerns directly the dimensional characteristics of buildups.

Dimensional parameters mean in essence the height and diameter of stromatolite buildups. As coefficient H/D (height to diameter ratio), both parameters are used in practical diagnosis of columnar, nodular and stratiform stromatolites: the ratio is greater than one for columnar stromatolites and lesser than one for other forms (Korolyuk, 1960). Empirical data on dimensions of stromatolites show that diameters of columnar buildups are two orders of magnitude lower at least (Raaben, 1980). As area of buildups is proportional to squared diameter, one can easily realize how significant is difference between columnar and non-columnar stromatolites.

Another important feature of columnar stromatolites discriminating them from non-columnar buildups is a limited range of diameters characteristic of the former. The maximum diameters vary from a few decimeters that is typical of most columnar species to a few meters in largest forms, being below a certain upper limit characteristic of particular taxon. In contrast, lateral extension of stratiform and nodular stromatolites varies without limitations, sometimes within several orders of magnitude for one taxon. Diameters of ministromatolites (columnar microstromatolites) range within very narrow limits: Proterozoic ministromatolites mostly have diameters of millimetric scale (Raaben, 1991, 1998, 2003), being below the upper limit of 20 mm suggested for these forms (Hofmann and Jackson, 1987).

Besides limitation of diameters, ministromatolites and common columnar forms have one more feature differing them from non-columnar stromatolites. This feature or "colonialism," as it has been termed improperly sometimes, means arrangement of columns in groups, their persistent plurality in buildups or sedimentological bodies (Orleanskii and Raaben, 1998). On the other hand, characteristic of non-columnar taxa are typical solitary buildups representing frequently the isolated stromatolitic bodies.

Provided limited dimensional parameters of all columnar stromatolites, we have an opportunity to calculate and compare their average values in rock complexes of different age. Their "colonialism" is an advantage for statistical processing of data characterizing dimensions of each taxon.

MATERIALS USED TO ANALYZE SIZE VARIATIONS

Monographs and other works published in the last century or later and devoted to stromatolites contain concrete information about dimensions of columns and buildups of the described taxa. The published data are variably informative: average diameters of columns are reported not always, but their lower and upper limits or maximum values are given regularly, except for a few publications. Vertical dimensions of columns are reported for a great number of species, but these parameters are hardly appropriate for comparative analysis. On the one hand, the height of columns and buildups, especially of the latter, is parameter dependent to a considerable extent on local sedimentation settings. On the other hand, it was measured frequently in hand specimens, where columns have no natural limitations. Consequently, the maximum diameters of columns, which are known for majority of form species, are the most convenient parameters for comparative analysis of

Table 1. Dimensional parameters of Paleoproterozoic columnar stromatolites

Taxa	D^{max}, cm	Age			Region
		PR_1^b	PR_1^c	PR_1^d	
Acaciella sp.	3			+	S. Australia
Baicalia ? *burra* Preiss	10			+++	″
Butinella borealis Makar.	4	+			N. Europe
Colonnella carelica Makar.	5	++			″
Columnacollenia rantama Kryl., Pert.	12	+++			″
Columnaefacta ? *composita* Zhu	4	+			N. China
conspicua Zhu et al.	4	+			″
oligoclada Zhu et al.	6	++			″
Confunda confuta Semikh.	5		++		Canada
″ ?	7	++			N. China
Conophyton biformatus Semikh.	8		++		Canada
garganicus Korol.	15		+++		Siberia
infernum Semikh.	17		+++		Canada
Discorsia discorsa Semikh.	7		++		″
wutaishanensis Zhu et al.	3	+			N. China
Dongyella dongyensis Zhu	4	+			″
Ephyaltes sp. Grey	16			+++	S. Australia
Externia externa Semikh.	6		++		Canada
″	6	++			N. China
yilgarnia (Preiss)	30			+++	S. Australia
Gemmifera ministolata Zhu	3	+			N. China
Gymnosolen ? *fallus* Zhu et al.	4	+			″
sinplex Zhu.	3	+			″
Jurusania grossovaginata Zhu et al.	4	+			″
rhythmica Zhu et al.	2	+			″
Kanpuria kanpura Raab.	4	+			India
Kussiella minor Zhu et al.	3	+			N. China
Kussoidella limata Semikh	5		++		Canada
planicolumnaris Zhu	2	+			N. China
yaoshinensis Zhu et al.	2	+			″
sp.	4		+		Canada
Mugurra nabberubia Grey.	5			++	S. Australia
Nanluella bulbosa Zhu et al.	3	+			N. China
Nordia laplandica Kryl., Pert.	8	++			N. Europe
cornostyla Zhu et al.	5	++			N. China
daguandelinensis Zhu et al.	2	+			″
dentifornis Zhu et al.	5	++			″
hebeiensis Zhu et al.	3	+			″
tienpenguaoensis Zhu et al.	3	+			″
Omachtenia kvartisimaa Kryl., Pert.	30	+++			N. Europe
sp.	4	+			″
teagiana Grey	5			++	S. Australia
Paraboxonia comnera Zhu et al.	8	++			N. China
laolifera Zhu et al.	8	++			″
Pilbaria perplexa Walt.	30			+++	S. Australia
″	8		++		Canada
deverella Grey	10			+++	S. Australia
beidaxiensis Zhu et al.	4	+			N. China
inzeriformis Bertr.-Sarf.	10	+++			″
minuscula Zhu et al.	7	++			″
Shugongsiella shugongsiensis Zhu et al.	6	++			″
Tielingella crassiformis Zhu et al.	30	+++			″
Tungussia ? *striolata* Zhu et al.	5	++			″
Vertexa termina Semikh.	10		+++		Canada
Windidda grumulosa Grey.	20			+++	S. Australia
Yandilla meekatharrensis Grey.	10			+++	″

Table 2. Dimensional parameters of Riphean columnar stromatolites from North Eurasia, non-branching forms (conophytonids)

Taxa	D^{max}, cm	Age					
		R_1	R_2^1	R_2^2	R_3^1	R_3^2	V
Colonnella complanata Golov.	50	+++					
cormosa Komar	100		++++	++++			
discreta Komar	200	++++					
frequens (Fent.)	–	–	–	–	–		
kyllachii Schap.	7		++				
laminata Komar	40	+++					
lineata Komar	40		+++				
plagulata Golov.	10	+++					
ulakia Komar	4			+	+		
Columnocollenia tigris Korol.	2						+
uluntuica Korol.	10			+++			
Conophyton anabaricus Golov.	20		+++				
baculus Kirich.	10				+++		
cadilnicus Korol.	20			+++			
circulus Korol.	7						++
cylindricus (Grab.)	40	+++	+++	+++	+++		
garganicus Korol.	150	++++	++++	++++			
" v. *nordicus* Komar	150				++++		
" v. *ikeni* Raab., Kom.	15				+++		
kotuikanicus Golov.	10	+++					
kurtunicus Korol.	–			–			
kuzha Komar.	15		+++				
lituus Masl.	40	+++	+++	+++	+++		
metula Kirich.	70		++++	++++			
miloradovici Raab.	15					+++	
" v. *krylovi* Raab.	18					+++	
" v. *murchisonicus* Gol.	100					++++	
punctatas Komar	30	+++					
reticulatus Komar	25			+++	+++		
Conusella irregularis Golov.	15	+++					
regularis Golov.	35	+++					
Ephyaltes gorgonotus Vlas.	10	+++					
microcranus Vlas.	40	+++					
ermakovi Vlas.	10				+++		

dimensional variations characterizing columnar stromatolites.

Preliminary data showed that average dimensional parameters of columnar stromatolites changed during the Proterozoic (Raaben, 2002). The presumption is checked in this work by means of processing database for 230 forms (species and varieties) of Proterozoic and Early Paleozoic columnar stromatolites with known maximum diameters of their columns. Their chronological levels are established based on stratigraphic scale divided into units two times lesser than Riphean subdivisions used by analysis of diversity dynamics of Proterozoic stromatolites (Semikhatov and Raaben, 1994, 1996; Raaben and Semikhatov, 1996). The processed data characterize all branching and non-branching columnar stromatolites (with a few exceptions)

Table 3. Dimensional parameters of Riphean and Vendian columnar stromatolites from North Eurasia (kussiellids)

Taxa	D^{max}, cm	Age					
		R_1	R_2^1	R_2^2	R_3^1	R_3^2	V
Aldania sibirica Kryl	3						+
Gornostachia longa Schap.	3				+		
Iliella kotuikanica Kryl.	10	+++					
Jurusania aldanica Schenf.	3						+
chineulica Schenf.	3						+
cylindrica Kryl.	4				+		
judomica Kom., Semikh.	40						+++
nizvensis Raab.	3				+		
sibirica (Yakovl.)	3						+
tumuldurica Kryl.	7						++
tuructachica Schenf.	3						+
Kurtunia uluntuica Schenf.	3			+	+		
Kussiella aequessa Golov.	30	+++					
enigmatica Raab.	5					++	
kussiensis (Masl.)	40	+++	+++				
taeniata Golov.	22	+++					
timanica Raab.	10					+++	
vittata Komar	6	++					
Omachtenia givunensis Nuzh.	5	++					
omachtcnsis Nuzh.	4	+					
utschurica Nuzh.	8	++					
Schancharia schancharia Korol.	5						++

known from Paleoproterozoic of different regions (Table 1). These forms are distributed in three divisions of that era (PR_1^b, PR_1^c, PR_1^d), which correspond to chronometric intervals of 2.3–2.0, 2.0–1.8, and 1.8–1.65 Ga. Dimensional variations in subsequent units are established based on majority of species and varieties of columnar stromatolites known from the Riphean, Vendian, and Lower Paleozoic deposits of North Eurasia, where their position in the Riphean scale of high resolution is determined without serious problems. All the data are summarized in Tables 2–6, where species are grouped in accord with their affiliation to taxa of supergeneric rank that visually demonstrates to what extent the general morphological diversity of Riphean columnar stromatolites is taken into consideration. Principal characteristics of supergeneric taxa are known from a series of publication (Raaben, 1964, 1969, 1986; Raaben and Zabrodin, 1972; Konyushkov, 1978; Bertrand-Sarfati, 1972; Raaben and Sinha, 1989), and, as such, the taxa are broadly acknowledged in stratigraphic practice.

Subjected to processing are only data on well-documented forms, 230 in total (Tables 1–6). Besides, some species are transit, occurring in two, less frequently in three or four stratigraphic divisions, and total set of points used in calculations is therefore over 250. Judging from commonly accepted criteria, database of this volume seems satisfactory; for this study in particular, it is representative as including all principal supergeneric groupings of columnar stromatolites.

Omitted from consideration and not included in the tables are stromatolites with atypical columns (horizontal off-lap in *Conophyton gaubitza*) and occurring in heterogeneous (*Jacutophyton, Gaardakia*) or plank-shaped buildups (*Parallelophyton, Platella*). The last four genera include not more than ten species. Ten forms, which are lacking data on column diameters (D^{max}) and useless therefore for calculations, are included in the tables to complete only the lists of species belonging to relevant genera.

Data used by compiling the tables are from the following set of works: Vlasov, 1977; Golovanov, 1966, 1967, 1970, 1972, 1981; Dol'nik, 1978, 2000; Dol'nik and Vorontsova, 1974; Kirichenko, 1961; Komar, 1964, 1966, 1973, 1978; Komar et al., 1964, 1965, 1970, 1973; Korolyuk, 1956, 1960, 1963; Korolyuk and Sidorov, 1971; Krylov, 1963, 1967, 1969, 1975; Krylov

Table 4. Dimensional parameters of Riphean and Vendian columnar stromatolites from North Eurasia (tungussids)

Taxa	D^{max}, cm	Age					
		R_1	R_2^1	R_2^2	R_3^1	R_3^2	V
1	2	3	4	5	6	7	8
Anabaria camenensis Schenf.	2				+		
divergens Komar.	5		++				
glebosata Golov.	5		++				
massulata Golov.	7				++		
radialis Komar	4		+				
visenda Doln.	15			+++	+++		
Appia topicalis Schap.	8			++			
Baicalia aborigena Schap.	10		+++				
aimica Nuzhn.	5			++			
ampla Semikh.	15				+++		
baicalica (Masl.)	12			+++	+++		
bulbuchtensis Doln.	10			+++	+++		
buriatica (Masl.)	6					++	
filaris Doln.	12			+++	+++		
hirta Doln.	5			++	++		
impexa Doln.	7		++				
ingilensis Nuzhn.	8				++		
inventa Schap.	10			+++			
kirgisica Kryl.	–		–	–			
lacera Semikh.	12				+++		
maica Nuzhn.	4				+		
maculata Schenf.	7					++	
mariinica Doln.	3			+	+		
minuta Komar	6		++				
nitchatica Doln.	–			–	–		
nova Kryl. et Schap.	20		+++				
ondoka Doln.	–			–	–		
polita Doln.	5			++	++		
prima Semikh.	4			+	+		
ex gr. prima	14				+++		
prisca Doln.	8		++				
rara Semikh.	4			+	+		
reticulata Doln.	3		+	+	+		
schrenica Schenf.	4						
tcharica Doln.	3				+		
trautfetrica Golov.	8	++					
unca Semikh.	3			+	+		
valuchtensis Doln.	3			+	+		
sp. 1 Schapov.	10			+++			
Linella avis Kryl.	8						++
akkaniella Bertr.	6					++	
simica Kryl.	8					++	
trollina Bertr.	10					+++	
ukka Kryl.	12					+++	
zhuica Schenf.	6						++

Table 4. (Contd.)

1	2	3	4	5	6	7	8
Litia diformis Schapov.	10		+++				
Parmites concrescens Raab.	3					+	
meridionalis Raab.	3					+	
nubilosus	3					+	
Patomella kelleri Raab.	3					+	
Patomia ambigua Doln.	3						+
ossica Kryl.	3						+
Poludia mutabilis Raab. et Kom.	20					+++	
polymorpha Raab.	11					+++	
russa Raab.	20					+++	
torta Raab.	4				+		
Ramulus sociabilis Raab.	3					+	
Svetliella avzianica Komar.	4		+				
svetlica Schap.	4		+				
tottuica Kom. et Semikh.	–			–			
venusta Schap.	3		+				
Telemsina sp.	–			–			
Tenupalusella bracteata Golov.	3			+			
Tungussia bassa Kryl.	12					+++	
colcimi Raab.	12				+++		
conrusa Semikh.	7				++		
enpiggeni Raab.	8				++		
golovanovi Raab.	4					+	
(=*Eleonora*) *laponica* Bertr.	12					+++	
laquesa Golov.	–				–		
nodosa Semikh.	15				+++		
nuzhnovi Raab.	4				+		
parmensis Raab.	6					++	
perforata Raab.	7					++	
Turukhania arbora Semikh.	7				++		

and Pertunen, 1978; Krylov and Shapovalova, 1970; Lyubtsov, 1979; Makarikhin, 1978; Makarikhin and Kononova, 1980; Nuzhnov, 1967; Raaben, 1964, 1969, 1981; Raaben and Zabrodin, 1969; 1972; Raaben and Komar, 1982; Raaben and Oparenkova, 1997; Raaben and Tevari, 1978; Semikhatov, 1962, 1978, Semikhatov et al., 1970; Sidorov, 1960; Khomentovskii et al., 1972; Shapovalova, 1968, 1974; Shenfil', 1978, 1991; Yakovlev, 1934; Bertrand-Sarfati, 1972; Bertrand-Sarfati and Eriksson, 1977; Bertrand-Sarfati and Siedlezka, 1980; Cloude and Semikhatov, 1970; Donaldson, 1963; Grey, 1984, 1994; Hofmann, 1969, 1976, 1981; Liang et al., 1984, 1985; Preiss, 1972, 1974; Walter, 1972; Xing et al., 1985; Zhu et al., 1987). Stratigraphic position of forms is determined using the other series of works (Raaben, 1975; Semikhatov and Raaben, 1994, 1996; Semikhatov and Serebryakov, 1983; Semikhatov et al., 1999; *The Riphean Stratotype*..., 1983; Shpunt and Shapovalova, 1979; Raaben et al., 1980; Hofmann, 2000; Preiss, 2000, etc.).

SIZE VARIATIONS OF COLUMNAR STROMATOLITES

Procedure used to reveal secular size-variations of stromatolites in the database under consideration included (a) statistical estimation of average maximum diameters of columns for all taxa occurring in each stratigraphic division and (b) parallel calculation of percentages for forms different in size occurring in the same division. The value of average maximum diameter is quotient of maximum diameters (D^{max}) sum divided by number of taxa counted in the given strati-

Table 5. Dimensional parameters of Riphean and Vendian columnar stromatolites from North Eurasia (gymnosolinids)

Taxa	D^{max}, cm	Age			
		R_2^2	R_3^1	R_3^2	V
Dabania chopichica Schenf.	10		+++		
Gymnosolen altus Semikh.	2		+		
asymmetricus Raab.	6			++	
(=*Inzeria*) *confragosus* Semjkh.	3		+		
furcatus Komar	4		+		
giganteus Raab.	10			+++	
irregularis Schenf.	2	+			
levis Kryl.	2			+	
ramsayi Steinm	5			++	
tungusicus Schenf.	3		+		
Inzeria chunbergica Golov.	4			+	
djejimi Raab.	2.5			+	
gigantea Doln.	6			++	
kolymica Golov.	6		++		
macula Golov	5		++		
nyfryslandica Raab,	4			+	
sinopivarra Bertr.-Sarf.	8			++	
sovinica Golov.	–		–		
tjomusi Kryl.	10		+++		
toctogulica Kryl.	5				++
variusata Golov.	6		++		
Katavia karatavica Kryl.	2.5		–	+	
lenaica Schenf.	3			+	
borlogella Doln.	5	++			
Lenia jacutica Doln	3			+	
Minjaria buguldeica Schenf.	4	+			
calciolata Korol.	8		++	++	
nimbifera Semikh.	10		+++		
procera Semikh.	5		++		
saharica Komar et al.	–	–			
tana Bertr.-Sarf.	6			++	
uralica Kryl.	20		+++	+++	

graphic unit. According to performed assessment, these values grew during the Paleoproterozoic from 6.1 cm in the interval of 2.3–2.0 Ga up to 9.5 and 13.9 cm in two subsequent intervals and reached the maximum (31.9 cm) in the Early Riphean. Afterward, they declined steadily down to 26.5 and 19.5 cm in the Middle Riphean, 11.6 and 9.7 cm in the Late Riphean, 6.8 cm in the Vendian, and 3.8 cm in the Early Paleozoic (upper diagram in the figure). When stromatolites are divided into three size categories of large (D^{max} 10 cm or greater), medium (D^{max} 5–10 cm), and small taxa (D^{max} less that 5 cm), distribution of larger and smaller forms against stratigraphic scale is of the same character (ministromatolites with maximum column diameters less than 20 mm are discarded). As one can see in the figure (lower diagram), proportion of larger forms increased beginning from the first unit of Paleoproterozoic (2.3–2.0 Ga) up to the Early Riphean maximum and then decreased down to the minimum in the Vendian–Early Paleozoic. Share of medium and small forms taken together varied in the other way. Proportions of small forms changed most significantly: their abundance declined from 55 to 10% during the Paleoproterozoic to be less than 5% in the Early Riph-

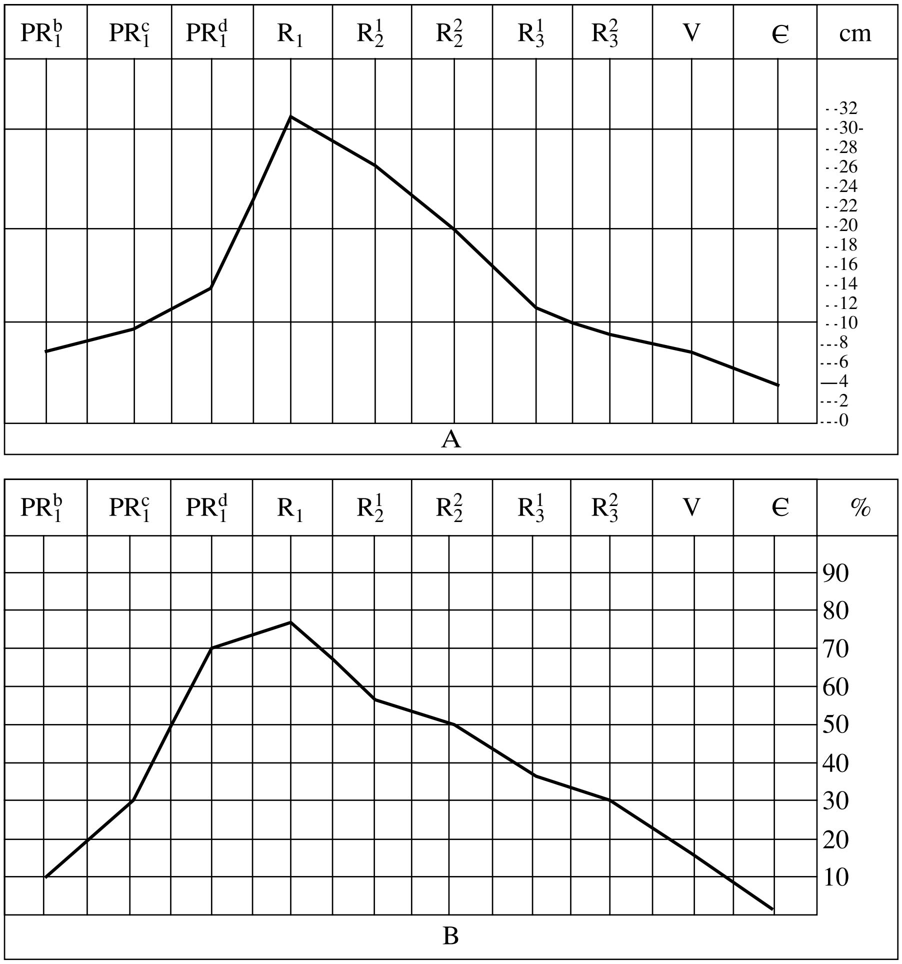
Table 6. Dimensional parameters of Riphean, Vendian and Cambrian columnar stromatolites from North Eurasia (Alternellaceae)

Taxa	$D^{\max}$, cm	Age				
		R_2	R_3^1	R_3^2	V	Є
Alternella bianca Raab.	3			+		
hyperboreica Raab.	4			+		
(=*Aldania*) *sibirica* (Yakovl.)	4				+	
Boxonia allahjunica Komar, Semikh	3				+	
divertata Sidor…	3					+
gracilis Korol.	6				++	
grumulosa Komar.	10				+++	
ingilica Komar, Semikh.	15				+++	
juedensis Schenf.	6					++
knjasevi Doln., Vorontz.	4				+	
krasivica Golov.	6			++		
lissa Komar	5		++			
togoica Golov.	15		+++			
tolbotchanica Doln.	3					+
zharcovi Doln.	5				++	
Columnaefacta elongata Korol.	3					+
erica Kryl.	7					++
ilica Kryl.	2					+
schancharia (Korol.)	5					++
usatica Schenf	3					+
vulgaris Sidor.	2					+
Tunicata nochtuica Sidor.	4					+

ean and increased afterward up to 50% in the Vendian and to 70% in the Early Paleozoic. The increase was of persistent character without meaningful fluctuations. Percentages of medium forms, which noticeably fluctuated in the Paleoproterozoic, remained within narrow limits during the Riphean ranging from 25 to 35% in divisions of the latter. Thus, secular size-variations depended mostly on relative proportions of large- and small-sized species. It is remarkable that small forms, which represented a negligible part of columnar stromatolite species in the Early Riphean, look like supplanting large forms up to the moment, when columnar stromatolites dwindled to nothing. "Giant forms" with columns 0.5 m and more in diameter practically disappear in the Vendian and are unknown from the Cambrian, when percentage of small forms was at the maximum.

It would be incorrect to insist on the absolute rank of calculated average diameters and percentages of different stromatolite categories. The calculated values are of relative precision, because we operate by calculations with initially rounded values. Besides, amounts of species are not identical in different stratigraphic units, and accuracy is lower, when stromatolite assemblage is relatively impoverished. On the other hand, it is logical to expect changes in the used values after discovery of new species and varieties or in response to additional data on dimensions of considered taxa and on verified stratigraphic ranges of stromatolite-bearing formations. All these factors can change of course the concrete values, but they can hardly transform the general trend of secular size variations of columnar stromatolites that is established using the available database. In terms of statistics, the database is large enough, comprising all principal morphological categories of columnar stromatolites, in particular, more than 90% of species occurring in North Eurasia and about a half of all forms known worldwide. Difference between parameters characterizing adjacent units of stratigraphic scale is obviously meaningful, and tendency of secular variations is distinct, depicting not disordered fluctuations, but the regular trend. Both variants of calculations used in this work depict identical trends of secular variations in size of the Proterozoic to Early Paleozoic columnar stromatolites (diagrams A and B in the figure).

The size-variation curves are unimodal, having one maximum of significant magnitude against the Early Riphean. Ascending and descending branches of both



Secular size variations of Proterozoic to Early Paleozoic columnar stromatolites inferable from statistically average maximum diameters of their columns (A) and percentages of large forms in assemblages (B).

curves are lacking meaningful inflection points. Especially smooth is the descending branch characterizing the greater interval of the Riphean and extending to the Early Paleozoic. The Early Riphean maximum marks the point of turning from the trend of steadily growing dimensional parameters of columnar stromatolites to the opposite one. This inversion of trends was obviously interrelated with biotic and/or abiotic events that controlled development of stromatolite communities.

Close in time to the above inversion are cardinal changes in taxonomic composition of different stromatolite grouping, which are detected by analysis of their diversification with time. In the corresponding curves of secular variations, these are the deep diversity minimum of columnar stromatolites and peak diversities of stratiform and ministromatolites. These changes in diversities are interpreted as related to early development stages of epi-Karelian platforms, and subsequent diversity variations have been explained by abiotic events, which took place in corresponding times (Semikhatov and Raaben, 1996). However, neither the diversification epochs of columnar and other stromatolites, nor changes in distribution of stromatolite-bearing strata have manifestation in the regular trend characterizing unidirectional decrease of dimensional parameters of columnar stromatolites during the Middle–Late Riphean, Vendian, and Cambrian. Especially remarkable is absence of the trend inflection in the Late Riphean, when diversity of stromatolites was extraordinary high. Consequently, abiotic events and/or associated reorganizations in biosphere, which certainly influenced morphology of Riphean columnar stromatolites and significantly diversified taxonomic composition of their assemblages (Semikhatov and Raaben, 1996), had no impacts on secular variations of their dimensional parameters.

With due consideration of current views on evolution of microbiotas (Sergeev, 2003), it is possible to assume that beginning of decline in size parameters of columnar stromatolites coincided in time with commencement of stasis in the world microorganisms, and that the descending trend of size-variation curve is indicative of "Neoproterozoic revolution." As these remarkable events had no impacts on the gradual character of trend, it seems interesting that inversion point of the curve coincided in time with the other biotic event, namely with cryptic incorporation of eucaryotes into communities of prokaryotic microorganisms. Like the aforementioned cardinal changes in taxonomic composition and morphology of stromatolites, this event is correlative with first development stages of epi-Karelian carbonate platforms (Sergeev, 2003).

As is evident form comparison of data on columnar stromatolites and Proterozoic ministromatolites, trends of size variations in both groupings do not coincide in time, and dynamics of their diversification is sharply different. The presumption that stromatolite-forming microbiotas of two groupings were different seems admissible therefore, suggesting dissimilar ways of evolution of corresponding ecosystems. Nevertheless, decline in dimensional parameters antedated dwindling of both groupings and their subsequent disappearance from geological records. Inversion of size-variation trends characteristic of columnites and striking disappearance of Proterozoic ministromatolites took place after incorporation of eucaryotes into cyanobacterial prokaryotic ecosystems that is recorded across the Paleoproterozoic–Riphean boundary (Sergeev, 2003). It is possible, therefore, that this early invasion of eukaryotic organisms into stromatolite-forming communities was the main factor that completely changed taxonomic composition of columnar stromatolites and cause inversion of their size-variation trends. Finally, this invasion caused extinction of columnar stromatolites.

CONCLUSION

Regular trend of changes in dimensional parameters of most numerous columnar stromatolites, representing the most widespread of supergeneric groupings, was a characteristic feature of their evolution. An important dimensional parameter of their species forming columns-stromatoids is diameter of the latter.

Each species of columnar stromatolites is characterized by column diameters, which do not exceed a certain value and are limited by the relatively narrow interval of dimensions. Maximum column diameters known for majority of columnar stromatolite species from their descriptions are most convenient parameters for the comparative analysis.

The analysis of database characterizing 230 columnar stromatolite forms revealed regular trends of secular changes in their size parameters. The statistically average maximum diameters of their columns grew steadily with time since the 2.3–2.0 Ga ago up to the peak value attained in the Early Riphean. Afterward, this parameter gradually declined in the Middle–Late Riphean, Vendian, and Early Paleozoic.

The same trend is established for percentages of large forms in stromatolite assemblages: their share increased in the Paleoproterozoic to reach maximum in the Early Riphean and then decreased in the Middle–Late Riphean, Vendian, and Cambrian. Proportions of small forms changed in opposite manner, and their abundance in the Early Paleozoic antedated final dwindling of columnar stromatolites.

Size variations estimated using two means of data processing depict the unimodal curve with the Early Riphean maximum. The ascending branch of the curve takes origin in the Paleoproterozoic interval of 2.3 to 1.65 Ga and ends in the Early Riphean. The descending branch spanning interval of the Middle–Late Riphean, Vendian, and Cambrian is very smooth, lacking any inflection points. The maximum amplitude means that average column diameters are getting first several times greater and then smaller to the same extent. The same mode of behavior is typical of parameters characterizing percentage of large forms in assemblages of columnar stromatolites.

The Early Riphean maximum separates distinct trend of increasing dimensional parameters from the opposite one. The inversion of trends is close in time to the early development stage of epi-Karelian carbonate platforms and appears to be interrelated somehow with this event. It is unlikely that inversion depended directly on paleogeographic and other reorganizations of that time, because other abiotic events of similar kind had no impacts on secular size variations.

On the other hand, the inversion is close in time to cardinal changes in taxonomic composition of stromatolite communities, and both biotic events seem tightly interrelated. As abiotic factors, which influenced perceptibly the diversity and abundance of columnar stromatolites, are not manifested in trends of their size variations, dimensional parameters of stromatolite columns can be regarded as independent of abiotic events.

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