

EVOLUTION OF THE PSEUDOSTAFFELLIDAE IN THE BASHKIRIAN STAGE (MIDDLE CARBONIFEROUS)

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Abstract. The origin and evolution of the family Pseudostaffellidae is discussed, based on the study of foraminifers from the stratotype and reference sections of the Bashkirian stage of the Southern Urals. Primitive *Plectostaffella* gave rise to two lineages: one lineage produced *Semistaffella* – *Pseudostaffella*, whereas the other lineage produced more advanced *Plectostaffella* – *Varistaffella* gen. n. The species from the Southern Urals assigned to *Varistaffella* are here described.

Riassunto. Viene discussa l'origine e l'evoluzione della famiglia Pseudostaffellidae sulla base dei foraminiferi presenti nello strato-tipo e in altre sezioni di riferimento del Bashkiriano degli Urali meridionali. Le *Plectostaffella* primitive diedero origine a due linee evolutive: una si concretizzò con *Semistaffella* – *Pseudostaffella*, mentre l'altra produsse le più avanzate *Plectostaffella* – *Varistaffella* gen. n. Sono inoltre descritte le specie di *Varistaffella* provenienti dagli Urali meridionali.

Introduction

Middle Carboniferous stratigraphy is largely based on evolutionary sequences within the Fusulinoida. The family Pseudostaffellidae is particularly important in the biostratigraphy of the Bashkirian. The study of foraminifers from the Bashkirian of the Southern Urals revealed an evolutionary sequence in the development of the family Pseudostaffellidae. The collection of foraminifers studied is housed in the Geological Museum of Ufa (coll. nos. 640 and 592 by Z.A. Sinitsyna) and in the Institute of Geology of the Ufa Research Center, Russian Academy of Sciences (coll. no. 121 by E.I. Kulagina). The material studied comes from the type section and reference sections of the Bashkirian stage in the Southern Urals, which are described by Sinitsyna and Sinitsyn (1987) and Kulagina et al. (2001). The most important sections are Askyn, Zigan, Akavas, Bogdanovka and Bolshoi Kizil (Fig. 1). A Bashki-

rian stratigraphic scale, which includes four substages (Syuranian, Akavassian, Askynbashian and Arkhangelskian) and six horizons, was used (Fig. 2). The evolutionary sequence of the Pseudostaffellidae is revealed in the complete Bashkirian sections of the Southern Urals.

Previous studies on the evolution of the family Pseudostaffellidae

According to Reitlinger (1971), the appearance of the Pseudostaffellidae was preceded by the evolution of the Eostaffellidae in the Serpukhovian stage, when the test became sub-spherical due to a widening periphery and corresponding lengthening of the coiling axis. In the lineage *Eostaffella*–*Pseudostaffella* this evolutionary trend was first marked by the appearance of the short-lived genus *Eostaffellina*. At the beginning of the Bashkirian (Syuranian), selection pressure still favored an elongated axis, as indicated by the development of tests with skewed coiling, such as in the large *Plectostaffella*. In the Syuranian, the more progressive genus *Semistaffella* appeared. Originally, the *Pseudostaffella* (*Semistaffella*) *variabilis* group was described by Reitlinger (1961) (Fig. 3) as primitive *Pseudostaffella* that resemble *Pseudostaffella antiqua* (Dutkevich) and also *Eoschubertella* and *Eostaffellina*. Rauzer-Chernousova (1949) studied the ontogeny of the *Pseudostaffella* species and showed the evolutionary development of the lineage *Pseudostaffella antiqua* – *Neostaffella sphaeroidea* based on anaboly (Fig. 4). Rozovskaya (1975) regarded the subfamily Pseudostaffellinae as a separate lineage evolving from *Eostaffella*. Solovieva (1977) also indicated the stages in the evolutionary transformations of the morphological characters in the fusulinids, includ-

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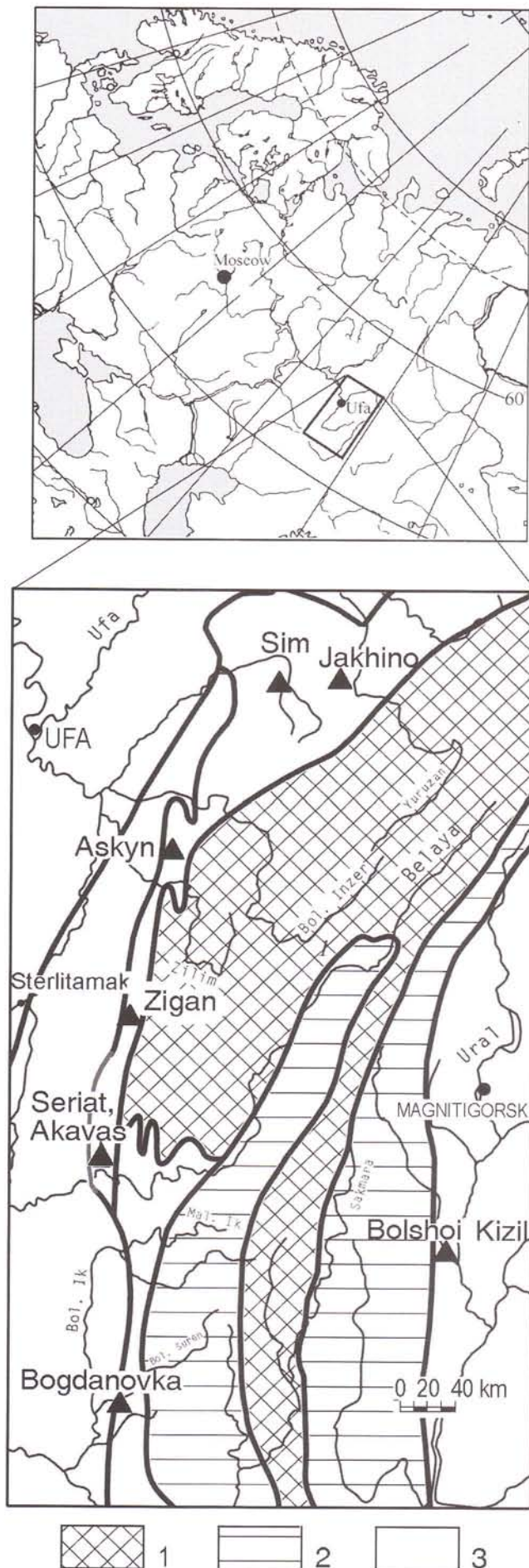


Fig. 1 - Locations of the strato-typestratotype and other Bashkirian reference sections in the Southern Urals. Key to symbols (1) - Pre-Paleozoic and metamorphic rock complex, (2) - Paleozoic Pre-Carboniferous rocks, (3) - Carboniferous and younger rocks.

ing the Pseudostaffellidae, which were used as a basis for a foraminiferal zonal scale for the Middle Carboniferous. Later, the hypothesis of the origin and early evolution of the Fusulinida was formulated by Groves (1988) and Groves et al. (1994). According to Groves's hypothesis, the Eostaffellidae root stock gave rise to the subfamily Pseudostaffellinae by the appearance of *Plectostaffella jakhensis*, which in turn gave rise to *Semistaffella variabilis*. Maslo & Vachard (1997) suggested that the genera *Semistaffella* and *Plectostaffella* evolved synchronously and gave rise to two lineages, the first leading to the genus *Pseudostaffella*, and the second to *Schubertella*.

The material studied in the present paper supports the presence of transitional taxa between the families Eostaffellidae and Pseudostaffellidae, allowing the recognition of the major evolutionary trends in the Pseudostaffellidae, which are used to substantiate the foraminiferal zonal scale of the Bashkirian.

Evolution of the Pseudostaffellidae

The evolution of this group in the Bashkirian passed through the following stages.

Syuranian substage

This substage is notable for the diversification of *Plectostaffella*, which gave rise to two separate lineage (Fig. 5). Small representatives of *Semistaffella* (*S. minuscularia* Reitlinger), closely similar to *Plectostaffella reitlingerae* Groves, with few volutions and a variable periphery, appear first. *Semistaffella variabilis* Reitlinger, in which the coiling axis is displaced at almost 90°, and *S. primitiva* Reitlinger with more symmetrical coiling, appear at the end of the Syuranian. *Semistaffella* is the ancestral genus of the rounded pseudostaffellides, and has a nautiloid or subspherical test, asymmetrical coiling, and variable chomata.

Akavassian substage

During the Akavassian time, a group of species with a three-layered wall, small chomata, a nautiloid test and strongly skewed coiling branched off from *Plectostaffella* (Pl.1, fig. 3-14, 16-18). This group (*Varistaffella*, gen. n.) was a blind lineage; it preserved the nautiloid shape and asymmetrical coiling throughout the Bashkirian and in the early Moscovian, when it disappeared. At the same time *Semistaffella* gave rise to the subspherical *Pseudostaffella* with distinct chomata, a three-layered wall, and planispiral

Standard Scale of Russia				Uralian horizon	Proposal Scale		Units of the Southern Urals	
Series	Stage	Sub-stage	Ammonoid Genozones		Substage	Horizon	Foraminiferal zones	
Middle Carboniferous	Bashkirian	Upper	<i>Diaboloceras - Axinolobus</i>	Asatausky	Arkhangelskian	Asatausky	<i>Tikhonovichiella tikhonovichi</i>	
			<i>Brammocereras - Gastrioceras</i>	Tashastinsky		Tashastinsky	<i>Ozawainella pararhomboidalis - Pseudostaffella gorskyi</i>	
			<i>Bilinguites-Cancelloceras</i>	Askynbashsky	Askynbashian	Askynbashsky	<i>Pseudostaffella praegorskyi - Staffellaeformes staffellaeformis</i>	
		Akavassky		Akavassian	Akavassky	<i>Ps. antiqua</i>	<i>Ps. grandis</i>	
							<i>Ps. posterior</i> <i>Ps. proozawai</i>	
							<i>Ps. antiqua</i> <i>V. ziganica</i>	
		<i>Reticuloceras - Bashkortoceras</i>	Syuransky	Syuranian	Kamennogorsky	<i>E. pseudotrivei</i>	<i>Semistaffella variabilis</i>	
		<i>Homoceras - Hudsonoceras</i>					Bogdanovsky	<i>Semistaffella minuscularia</i> <i>Pl. bogdanovkensis</i> <i>Pl. varvariensis</i>

Fig. 2 - Bashkirian stratigraphic scale (according to Kulagina et al. 2001).

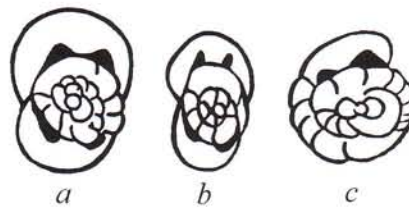


Fig. 3

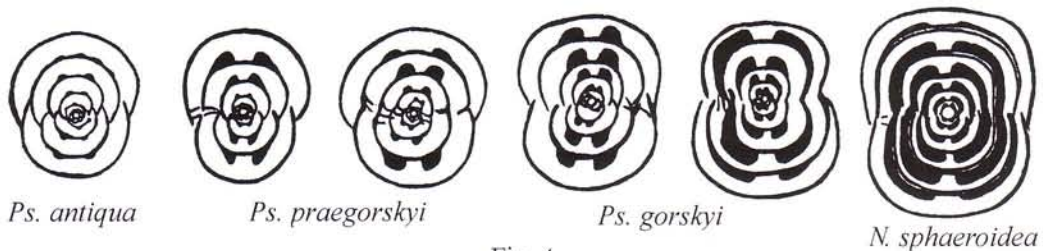


Fig. 4

- Fig. 3 - Schematic figures drawings of some species *Semistaffella* (from Reitlinger 1961, p. 240, fig. 2): a - *Semistaffella variabilis* (Reitlinger), b - *S. primitiva* (Reitlinger), c - *S. minor* (Rauzer).
- Fig. 4 - Ontogenies in the lineage *Pseudostaffella antiqua grandis* - *Ps. praegorskyi* - *Ps. gorskyi* - *Neostaffella sphaeroidea* showing development through anaboly (from Rauzer-Chernousova 1949, p. 146, fig. 4).

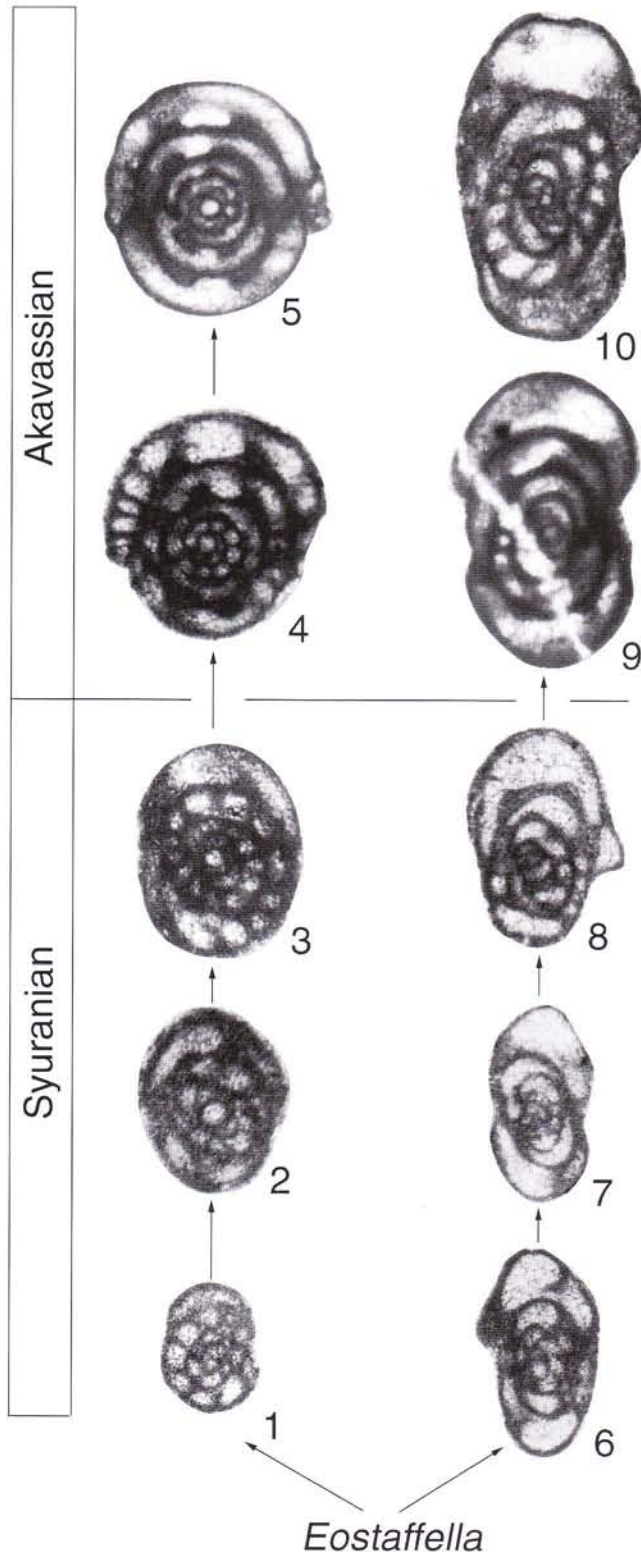


Fig. 5 - Evolutionary lineage of the Pseudostaffellidae. 1- *Plectostaffella reitlingeriae* Groves, 1994, Jakhino, x100, spl. 61/2; 2 - *Semistaffella minuscularia* Reitlinger, 1971, x100, Askyn, spl. 12/2; 3 - *Semistaffella variabilis* Reitlinger, 1961, x 80, Askyn, spl. 167; 4 - *Pseudostaffella antiqua* (Dutkevich, 1934), x 75, Askyn, spl. 171a; 5 - *Pseudostaffella antiqua posterior* Safonova, 1951, x 60, Askyn, spl. 185; 6, 7 - *Plectostaffella varvariensis* (Brazhnikova and Potievskaya, 1938), 6 - x 75, Muradymovo, spl. 77; 7 - x 85, Bogdanovka, spl. 3/25; 8 - *Plectostaffella jakhensis* Reitlinger, 1971, x 80, Askyn, spl. 12/2; 9, 10 - *Varistaffella ziganica* (Simitsyna, 1975), 9 - x 70, Askyn, spl. 279, 10 - x 85, Zigan, spl. 27zh.

coiling in the outer volutions. The Akavassian is marked by wide speciation within the genus *Pseudostaffella*, resulting in the emergence of the major trends towards increased size, larger chomata and differentiated wall. At this time many short-lived transient forms with variable chomata and periphery appeared.

The instability of species characters is indicated by the presence of taxa with different types of chomata (Pl.1, fig.19). During the Akavassian, *Ps. antiqua* increased in size and gave rise to a few varieties. The evolutionary transition *Ps. antiqua antiqua* - *Ps. antiqua posterior* - *Ps. grandis* occurred. In its ontogeny, the *Pseudostaffella antiqua* group passes through a stage resembling *Semistaffella variabilis* (double turn of the coiling axis at 90°).

Askynbashian substage

The Askynbashian substage shows a further development of *Pseudostaffella*. The genus gave rise to three lineages. The first, most progressive lineage, evolving towards the elongated coiling axis ($L/D > 1$) gave rise to the new genus *Staffellaformes* Solovieva, 1986. The second and third lineages exhibit more distinct symmetrical coiling and massive chomata. The second lineage is related to the appearance of a broadly nautiloid and subspherical test with a convex periphery and asymmetrical chomata (*Ps. proozawai* Kireeva group). The third lineage exhibits a spherical form with more or less flat periphery and high, short chomata (*Ps. praegorskyi* Rauzer and *Ps. krasnopolskyi* (Dutkevich)). All the lineages show a variable gray diaphanotheca in the wall structure.

Arkhangelskian (Upper Bashkirian) substage

In this substage the development of planispiral coiling, massive chomata and a four-layered wall continued. Taxa that later became widespread in the Moscovian, as well as taxa ancestral to the genus *Neostaffella* Mikluho-Maclay, 1959 appeared in this stage. These were *Ps. gorskyi* (Dutkevich) with subquadratic chomata, and *Ps. conspecta* Rauzer with asymmetrical chomata. In the Arkhangelskian, the transitional taxa *Pseudostaffella* - *Neostaffella* appeared. This time is also noteworthy for the diversification of the rhomboidal *Profusulinella* and the appearance of Aljutovellidae.

A gradual appearance of Pseudostaffellidae species may be observed in the strato type of the Bashkirian (Askyn section) and in the nearby Zigan section (Fig. 6, 7).

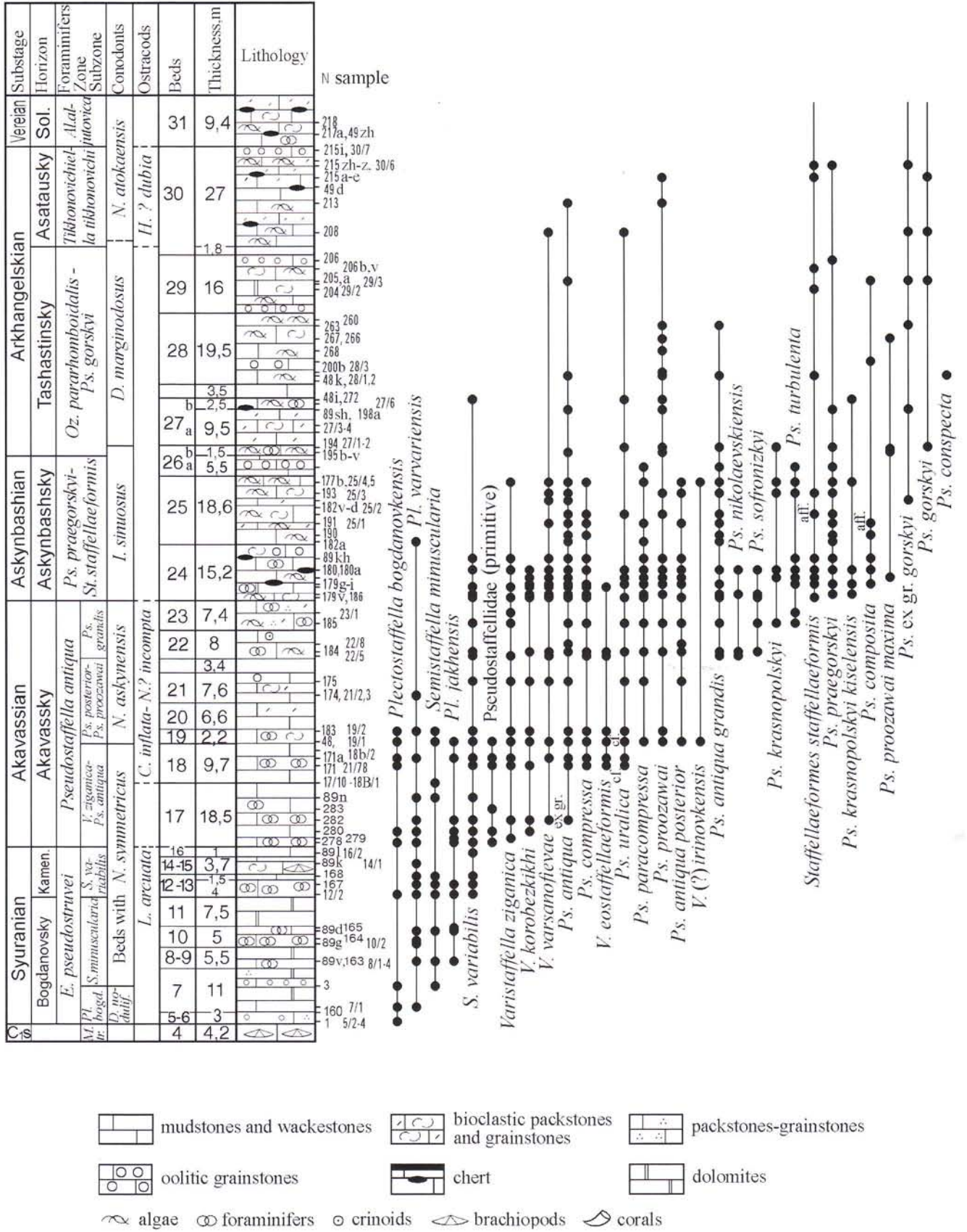


Fig. 6 - Distribution of the Pseudostaffellidae and related species in the Bashkirian deposits in the Askyn section. M.tr. = *Monotaxinoides transitorius* zone.

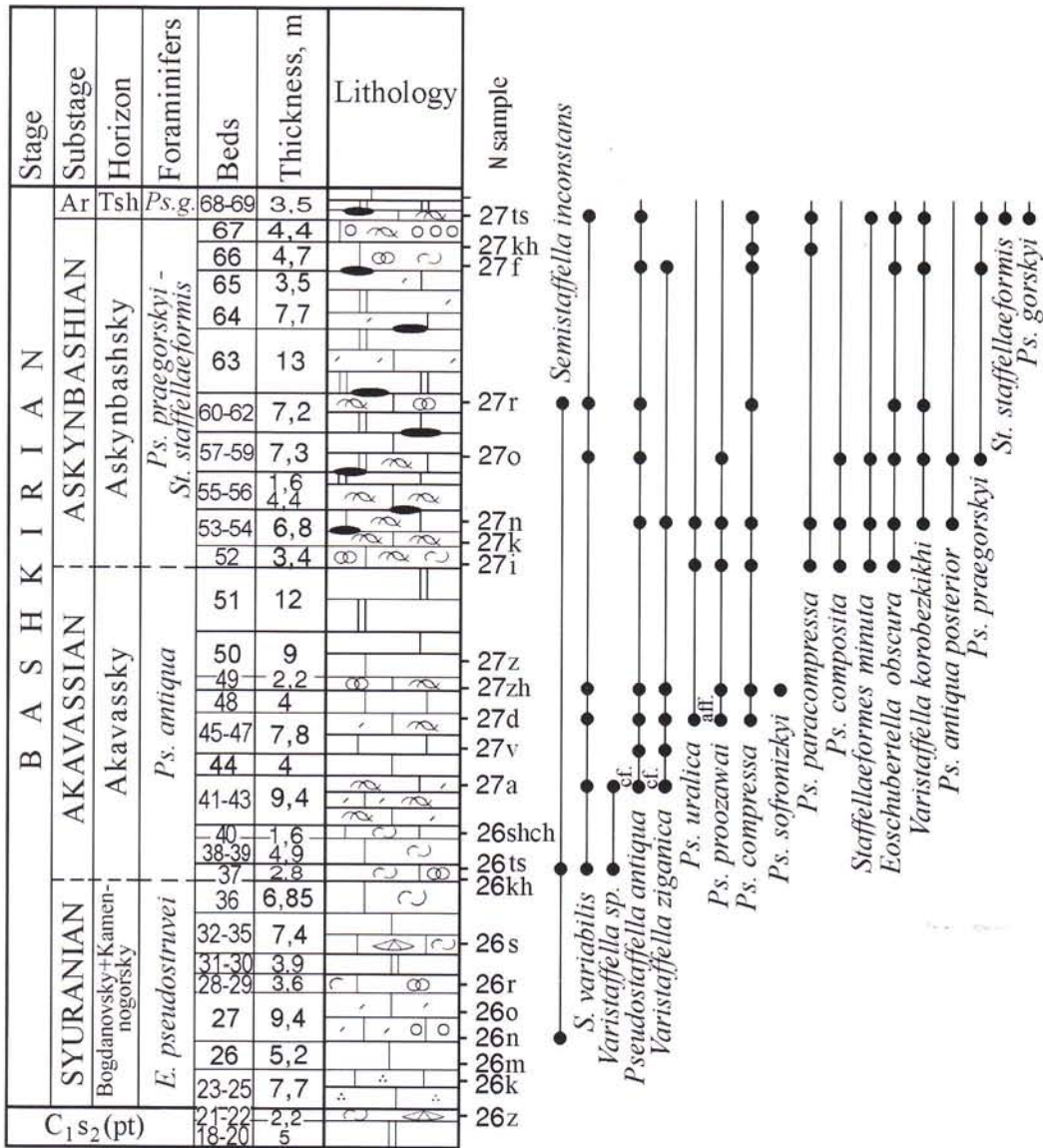


Fig. 7 - Distribution of the Pseudostaffellidae and related species in during the Bashkirian in the Zigan section. (For legend see the Fig. 6).

Systematic Paleontology

The fusulinid taxonomy used in the present paper was published in the Reference Book on the systematics of Paleozoic foraminifera (Rauzer-Chernousova et al. 1996).

Family Pseudostaffellidae Putrja, 1956
(nom. transl. ex Pseudostaffellinae Putrja,
1956 by Solovieva and Reitlinger
in Rauzer-Chernousova et al. 1996)

Genus *Varistaffella* Kulagina and Sinitsyna gen. nov.

- 1951 *Pseudostaffella* Thompson, 1942 – Rauzer-Chernousova et al. (partim), p. 101-102, pl. 5, fig. 15-18, 19-20(?), 22 (?).
1970 *Pseudostaffella* Thompson, 1942 – Rumyanzeva (partim), pl. 12,

fig. 3-4, 9, 11-13, pl. 13, fig. 9.

- 1973 *Semistaffella* (?) Reitlinger, 1971 – Popova & Reitlinger, p. 71, pl. 12, fig. 11-12.
1975 *Pseudostaffella* Thompson, 1942 – Sinitsyna in Grozdilova et al., p. 45, pl. 7, fig. 18.
1987 *Pseudostaffella* Thompson, 1942 – Sinitsyna & Sinitsyn (partim), pl. 7, fig. 16-17, 19, 21, pl. 9, fig. 12.
2000 *Plectostaffella* (*Eoplectostaffella*) Postojalko, 1990 – Ivanova, p. 42, pl. 1, fig. 10.
2001 *Pseudostaffella* Thompson, 1942 – Kulagina et al. (partim), pl. 3, fig. 6-10.

Etymology. From the Latin *varians* (variable).

Type species. *Pseudostaffella ziganica* Sinitsyna, 1975 in Grozdilova et al. 1975, p. 45, pl. 7, fig. 18, Akavassian, Southern Urals, Zigan River, Gumerovo Village.

Diagnosis. Small-sized Pseudostaffellidae with broadly lenticular or nautiloid test, skewed coiling, three-layered wall, distinct small chomata.

Description. The test is small, broadly lenticular or nautiloid in shape throughout all growth stages. The periphery is broadly-rounded or rounded-subacute. The coiling is usually strongly skewed throughout or becomes nearly planispiral and partly evolute in the last 1-1.5 volutions. The L/D ratio is 0.5-0.8. The first volutions are more tightly coiled. The height of the subsequent volutions gradually increases as the test grows. The wall is three-layered (inner and outer tectoria and tectum) from the third volution, while in the early volutions it is usually undifferentiated. Chomata distinct, small, tuberculate.

Remarks. The genus *Varistaffella* includes species previously assigned mostly to the genus *Pseudostaffella* Thompson, 1942. These two genera are similar in having the three-layered wall. The new genus is distinguished from *Pseudostaffella* in the more compressed test shape, the coiling pattern and small, tuberculate chomata. The L/D ratio in *Varistaffella* ranges from 0.5 to 0.8, whereas in *Pseudostaffella* it is 0.8 to 1.0. The coiling in *Varistaffella* is very similar to that in *Plectostaffella* Reitlinger, 1971, from which it is apparently evolved through the differentiation of the wall and development of the chomata. This is supported by the presence of transitional forms, which in some parts of their test show the tectum.

Species composition: *Varistaffella ziganica* (Sinitsyna), *V. varsanofievae* (Rauzer-Chernousova), *V. korobezkikhi* (Rauzer-Chernousova & Safonova), *V. eastaffellaeformis* (Rumyanzeva), *V. libera* (R. Ivanova), *V. irinovkensis* (Rauzer-Chernousova).

Occurrence. Bashkirian, Akavassian up to the lower part of the Moscovian. Most widespread in the Akavassian and Askynbashian.

Varistaffella ziganica (Sinitsyna, 1975)

Pl. 1, fig. 3-6

- 1975 *Pseudostaffella ziganica* Sinitsyna in Grozdilova et al., p. 45, pl. 7, fig. 18.
 1987 *Pseudostaffella ziganica* – Sinitsyna & Sinitsyn, pl. 7, figs. 16-17.
 1997 *Pseudostaffella ziganica* – Kulagina & Sinitsyna, pl. 1, fig. 23.
 2001 *Pseudostaffella ziganica* – Kulagina et al., pl. 3, fig. 8-10.

Neotype. Pl. 1, fig. 3, Geological Museum, Ufa, no. 592/7, Southern Urals, Zigan River, Gumerovo Village.

Material. Twenty-six axial sections from the Askyn, Zigan, Jakhino, and Sim sections (Fig. 1).

Description. The test is broadly lenticular, with a narrowly rounded or rounded-subacute periphery, 4.5-5 volutions. The last half-volution is often semi-evolute and is increased in height. The coiling is constantly skewed. The test wall is differentiated, three-layered in the outer 2-3 volutions. The chomata are rounded tubercles. The test wall is 0.018-0.020 mm thick. The aperture is moderately wide.

Dimensions.

Specimen no.	D mm	L mm	L/D ratio	d mm	D 1 mm	D 2 mm	D 3 mm	D 4 mm	D 5 mm	n
Neotype 592/7	0.5	0.3	0.6	0.029	0.06	0.11	0.20	0.31	0.5	5
640/54	0.52	0.29	0.55	0.031	0.075	0.12	0.20	0.31	0.53	5
592/8	0.42	0.23	0.55	0.029	0.087	0.12	0.28	0.42		4
121/980	0.5	0.26	0.52	0.017	0.006	0.087	0.18	0.32	0.5	5

D - diameter, L - width, d - diameter of proloculus, D 1 - D 5 - diameters of the volutions (from first to finished last), n - number of volutions.

Remarks. Since the holotype is lost, a neotype is proposed in the present paper (Pl. 1, fig. 3). Sinitsyna & Sinitsyn (1987, pl. 7, figs. 16-17) and Kulagina & Sinitsyna (1997, pl. 1, fig. 23) indicated erroneously that the specimens shown in their papers came from the Askyn section, whereas, in fact, they were recovered from the Zigan section. This species is very similar to *Plectostaffella jakhensis* Reitlinger (1971, p. 14, pl. 1, figs. 1-5) differing in the larger test, semi-evolute last volution and three-layered wall. Reitlinger (1971) indicated that in the genus *Plectostaffella* the wall is thin, undifferentiated, and sometimes the tectum may be seen. We studied foraminifers from the same section Jakhino (along the Berdyash River), type locality for *Plectostaffella jakhensis* and traced a successive appearance in the section of the tests with an undifferentiated wall and a three-layered wall (Pl. 1, fig. 2, 4). Our study suggests that the specimens with a tectum are transitional from *Plectostaffella jakhensis* to *Varistaffella ziganica*.

Occurrence. Bashkirian (Akavassian and Askynbashian) of the Southern Urals.

Varistaffella korobezkikhi

(Rauzer-Chernousova & Safonova, 1951)

Pl. 1, fig. 7-9, 11

- 1951 *Pseudostaffella korobezkikhi* Rauzer-Chernousova & Safonova in Rauzer-Chernousova et al., p. 101, pl. 5, fig. 15-16.
 1967 *Pseudostaffella varsanofievae* Rauzer-Chernousova – Brazhnikova et al., pl. 21, fig. 21.
 1969 *Pseudostaffella varsanofievae* Rauzer-Chernousova – Manukalova et al., p. 51, pl. 14, fig. 9.
 1970 *Pseudostaffella korobezkikhi* Rauzer-Chernousova & Safonova – Rumyanzeva, pl. 12, fig. 3-4.
 1976 *Pseudostaffella irinovkensis* Leontovich – Ektova, pl. 1, fig. 23-24.
 1979 *Pseudostaffella varsanofievae* Rauzer-Chernousova – Dzhenchuraeva, pl. 3, fig. 17-18.
 1987 *Pseudostaffella korobezkikhi* Rauzer-Chernousova & Safonova – Sinitsyna & Sinitsyn, pl. 7, fig. 19, pl. 9, fig. 11.
 1991 *Semistaffella korobezkikhi* (Rauzer-Chernousova and Safonova) – Marfenkova, pl. 19, fig. 11.
 1999 *Pseudostaffella korobezkikhi* Rauzer-Chernousova & Safonova – Ivanova, pl. 1, fig. 7.

Material. Twenty-two axial sections from the Askyn, Zigan, Seriat, Akavas, and Bolshoi Kizil sections.

Description. The test is subnautiloid, laterally compressed, with umbilici. The test wall is differentiated in the outer 1.5-2 volutions. The chomata are narrow triangular or rounded tubercles. The test wall is 0.018 - 0.020 mm thick. The aperture is moderately wide.

Dimensions.

Specimen no.	D mm	L mm	L/D	d mm	D 1 mm	D 2 mm	D 3 mm	D 4 mm	D 5 mm	n vol.
Holotype GIN 3287 129	0.46	0.31	0.67		0.09	0.13	0.22	0.38		4.5
640/46	0.53	0.38	0.71	0.03	0.07	0.12	0.17	0.27	0.53	5
640/47	0.46	0.36	0.78	0.04	0.08	0.15	0.21	0.32	0.46	5
640/49	0.42	0.29	0.69		0.052	0.1	0.17	0.26	0.42	5
121/983	0.50	0.32	0.63	0.04	0.064	0.13	0.25	0.40		4.5

Comparison. This species differs from other species of the genus in the presence of the distinct umbilici.

Occurrence. Bashkirian (from Akavassian) and Moscovian (lower part) of the Urals, East European Platform, Dniepr-Donetz Basin; lower Bashkirian of the Tien-Shan and Kazakhstan.

Varistaffella varsanofievae (Rauzer-Chernousova, 1951)

Pl. 1, fig. 12-14

- 1951 *Pseudostaffella varsanofievae* Rauzer-Chernousova in Rauzer-Chernousova et al., p. 101-102, pl. 5, fig. 17-18.
 1956 *Pseudostaffella varsanofievae* Rauzer-Chernousova - Putrja, p. 396-397, pl. 5, fig. 8.
 1973 *Semistaffella* (?) *varsanofievae* Rauzer-Chernousova - Popova & Reitlinger, p. 71, pl. 12, fig. 11-12.
 1970 *Pseudostaffella varsanofievae* Rauzer-Chernousova - Rumyanzeva, pl. 12, fig. 9.
 1970 *Pseudostaffella* sp. - Rumyanzeva, pl. 13, fig. 9.
 1987 *Pseudostaffella ziganica* Sinitzyna - Sinitzyna & Sinitzyn, pl. 9, fig. 12.
 1997 *Pseudostaffella varsanofieva* Rauzer-Chernousova - Kulagina & Sinitzyna, pl. 1, fig. 24.

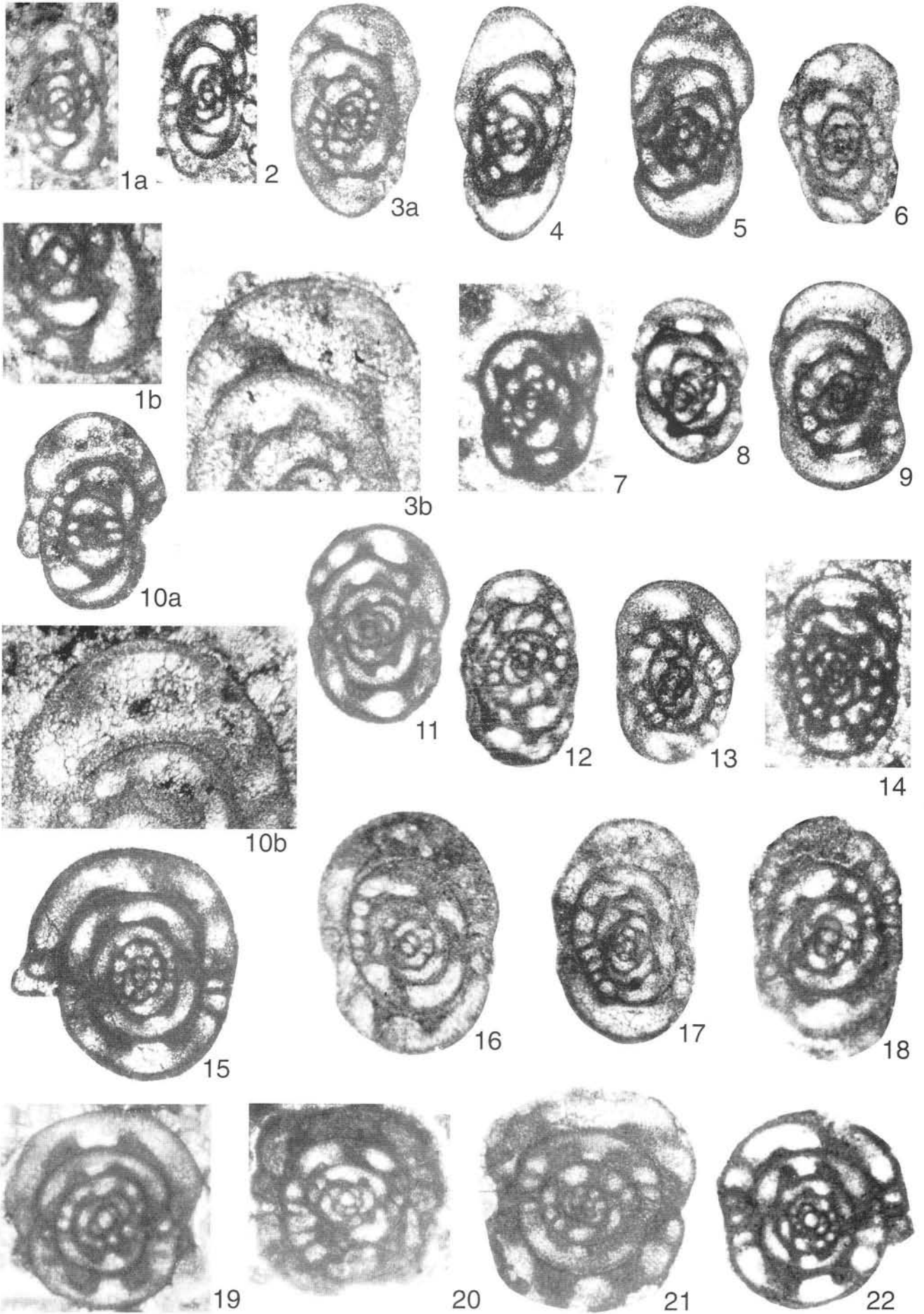
Material. Twelve axial and 3 sagittal sections from the Askyn and Bolshoi Kizil sections.

Description. The test is subnautiloid, with a broadly rounded periphery and flattened or weakly convex flanks. The volutions are very tightly spaced, regularly coiled; the last 1-1.5 volutions are turned at 90° relative to the inner volutions and possess 15 to 20 chambers. The wall in the outer 2-3 volutions is differentiated. The chomata are small rounded tubercles.

PLATE 1

All specimens are from the Southern Urals, x 80, except as noted.

- Figs. 1-2 - *Plectostaffella jakhensis* Reitlinger, 1971. Holotype GIN 4002/1 (originally pl.1, fig.1). 1b - x 150, enlarged part of 1a, showing the undifferentiated wall. 2 - axial section, IG 121/982, Jakhino (Berdyash River), sample 61/2, Bogdanovsky.
 Figs. 3-6 - *Varistaffella ziganica* (Sinitzyna, 1975). 3 - 5 - axial sections, 6 - subaxial section. 3 - Neotype, GM 592/7, Zigan section 27, sample 27n, Askynbashian, 3b - x 160, enlarged part of 3a, showing the structure of the wall with tectum; 4 - IG 121/980, Jakhino, sample 62/16, Akavassian; 5 - GM 640/54, Askyn, sample 282, Akavassian. 6 - GM 592/8, Zigan section 27, sample 27zh, Akavassian.
 Figs. 7-9, 11 - *Varistaffella korobezkikhi* (Rauzer-Chernousova & Safonova, 1951). 7 - Holotype GIN 3287/129 (originally pl. 5, fig.15). 8 - GM 640/49, 11 - x 100, GM 640/47, both from Askyn, sample 186, Askynbashian; 9 - IG 121/983, Bolshoi Kizil, sample 121v, Akavassian.
 Fig. 10 - *Varistaffella* sp., oblique tangential section, GM 592/9, Zigan, sample 26 ts, Akavassian. 10b - x 160, enlarged part of 10a, showing the structure of the three three-layered wall with tectum.
 Figs. 12-14 - *Varistaffella varsanofievae* (Rauzer-Chernousova, 1951). 12 - x 70, GM 640/55, Askyn, sample 180a, Askynbashian. 13 - IG 121/977, Bolshoi Kizil, sample 121v, Akavassian. 14 - holotype GIN 3287/131 (originally pl. 5, fig 18).
 Fig. 15 - *Pseudostaffella antiqua posterior* Safonova, 1951, subaxial section, GM 592/ 10, Zigan, sample 27n, Askynbashian.
 Figs. 16-18 - *Varistaffella eostaffellaeformis* (Rumyanzeva, 1970). 16, 17 - axial section, 18 - obliqua section. 16 - GM 640/18, Askyn, sample 171, 17 - GM 592/5, Askyn, sample 48, 18 - GM 592/11, Zigan, sample 27d. All are from the Akavassian.
 Fig. 19 - *Pseudostaffella antiqua* (Dutkevich, 1934) - *Ps. praegorskyi* Rauzer-Chernousova, 1949 transition forma, axial section, GM 640/56, Askyn, sample 185, late Akavassian.
 Figs. 20-22 - *Pseudostaffella praegorskyi* Rauzer-Chernousova, 1949. 20 - holotype, GIN 118 (originally pl. 1, fig. 8.) 21 - x70, nearly axial section, GM 640/31, Askyn, sample 186, Askynbashian. 22 - x 60, axial section, GM 640/30, Askyn, sample 180, same age.



Dimensions.

Specimen no.	D mm	L mm	L/D	d mm	D 1 mm	D 2 mm	D 3 mm	D 4 mm	D 5 mm	n vol.
Holotype GIN 3287 131	0.49	0.36	0.74	0.028	0.08	0.16	0.27	0.4		4.5
640/52	0.52	0.38	0.73	0.030	0.07	0.12	0.17	0.27	0.53	5
640/55	0.54	0.31	0.57	0.020	0.06	0.10	0.17	0.28	0.44	5.5
121/977	0.44	0.30	0.67		0.075	0.13	0.20	0.29	0.44	5

Comparison. This species differs by the peculiar coiling in which the axes of the last 1-1.5 volutions are almost at a right angle with the preceding ones.

Occurrence. Bashkirian (from Akavassian) of the Southern Urals, Central Tien-Shan and Donetz Basin; Bashkirian and Moscovian (Vereian) of the East European Platform.

Varistaffella eostaffellaformis

(Rumyanzeva, 1970)

Pl. 1, fig. 16-18

- 1970 *Pseudostaffella eostaffellaformis* Rumyanzeva, p. 172-173, pl. 12, fig. 11-13.
 1974 *Pseudostaffella korobezkikhi* Rauzer & Safonova – Potievskaya, pl. 7, fig. 25-27.
 2001 *Pseudostaffella eostaffellaformis* Rumyanzeva – Kulagina et al., pl. 3, figs. 6-7.

Material. Eight axial sections from Askyn and Zigan sections.

Description. The test is nautiloid, with a broadly rounded periphery, convex flanks, weak, wide umbilici, three-layered wall. The chomata are low, asymmetrical. The wall is 0.018 – 0.020 mm thick. The aperture is moderately wide.

Dimensions.

Specimen no.	D mm	L mm	L/D	d mm	D 1 mm	D 2 mm	D 3 mm	D 4 mm	D 5 mm	n vol.
592/5	0.59	0.36	0.61		0.1	0.15	0.23	0.37	0.59	5
640/18	0.58	0.42	0.72		0.075	0.12	0.23	0.36	0.57	5

Comparison. The specimens from the Southern Urals are similar to those described by Rumyanzeva (1970), but are distinguished by their larger size.

Occurrence. Bashkirian (Akavassian and Askyn-bashian) of the Southern Urals; lower Bashkirian of the Central Tien-Shan and Donetz Basin.

Genus *Pseudostaffella* Thompson, 1942***Pseudostaffella praegorskyi***

Rauzer-Chernousova, 1949

Pl. 1, fig. 20-22

- 1949 *Pseudostaffella praegorskyi* Rauzer-Chernousova, p. 352, pl. 1, fig. 8-10.

- 1951 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Rauzer-Chernousova et al., p. 107, pl. 6, fig. 5.
 1960 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Grozdilova & Lebedeva, p. 127, pl. 15, fig. 7-8.
 1964 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Potievskaya, p. 53-54, pl. 4, fig. 5-7 (non fig. 8).
 1967 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Brazhnikova et al., pl. 22, fig. 15.
 1973 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Popova & Reitlinger, p. 71, pl. 12, fig. 16-17, pl. 13, fig. 4.
 1975 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Grozdilova et al., p. 45, pl. 7, fig. 16.
 1976 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Ektova, pl. 3, fig. 17-18, pl. 6, fig. 15-16.
 1979 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Dzhenchurava, pl. 4, fig. 4-6.
 1979a *Pseudostaffella praegorskyi* Rauzer-Chernousova – Kireeva in Semikhatova et al., pl. 15, fig. 17-18.
 1979b *Pseudostaffella praegorskyi* Rauzer-Chernousova – Potievskaya in Semikhatova et al., pl. 19, fig. 27.
 1980 *Pseudostaffella gorskyi* (Dutkevich) – Malakhova, pl. 7, fig. 2-3 (only).
 1987 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Sinitsyna & Sinitsyn, pl. 9, fig. 17-18, pl. 12, fig. 12.
 1991 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Vachard & Beckary, pl. 337, pl. 5, fig. 25-26.
 2001 *Pseudostaffella praegorskyi* Rauzer-Chernousova – Kulagina et al., pl. 4, fig. 5-7.

Material. Twenty-two axial and near axial sections from the Askyn, Zigan, Seriat, Bolshoi Kizil sections.

Description. The test is subspherical, with asymmetrically coiled early volutions and more symmetrical coiling in the outer volutions. The coiling is slowly and regularly expanding. The chomata in the early stages are small tubercles as in *Pseudostaffella antiqua* (Dutkevich), later they become asymmetrical and in the last volutions they are high and narrow or subquadratic.

Dimensions.

Specimen no.	D mm	L mm	L/D	d mm	D 1 mm	D 2 mm	D 3 mm	D 4 mm	D 5 mm	n
Holotype GIN - 118	0.65	0.62	0.96	0.057	0.07	0.21	0.32	0.52	0.65	5
640/29	0.5	0.45	0.92	0.026	0.69	0.11	0.16	0.29	0.5	5
640/30	0.63	0.6	0.95	0.052	0.085	0.18	0.31	0.48	0.63	5
640/31	0.52	0.48	0.9		0.063	0.1	0.2	0.34	0.52	5

Comparison. The specimens from the Southern Urals are similar to those described by Rauzer-Chernousova (1949), but are distinguished by their smaller size.

Occurrence. Bashkirian and Moscovian (lower part) of the Urals, East European Platform, Donetz Basin, Tien-Shan, Cantabrian Cordillera.

Conclusions

The evolutionary sequence of the Pseudostaffellidae forms a basis for the subdivision of the Bashkirian. The

Syuranian is marked by the appearance of *Semistaffella*. The base of the Akavassian is marked by the appearance of *Varistaffella* and *Pseudostaffella*. *Varistaffella* occurs in the lower part of the Akavassian in the Southern Urals considerably more frequently than the rounded *Pseudostaffella* and it is often used as a marker for the lower boundary of the Akavassian, since in some sections (Zigan, Sim, Jakhino) *Varistaffella* appears earlier than the typical *Pseudostaffella antiqua*. The lower boundary of the Askynbashian is defined by the appearance of *Pseu-*

dostaffella praegorskyi and *Staffellaeformes*. The base of the Arkhangelskian is defined by the evolution of the species *Ps. gorskyi* from *Ps. praegorskyi*.

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