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Morphological Variability of Testate Amoebae (Rhizopoda: Testacealobosea: Testaceafilosea) in Natural Populations

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Summary. Morphometric investigation of 24 species of testate amoebae (*Centropyxis sylvatica* (Deflandre) Thomas, *Cyclopyxis eurystoma* v. *parvula* Deflandre, *C. puteus* Thomas, *Hyalosphenia papilio* Leidy, *H. elegans* Leidy, *Schoenbornia humicola* (Schönborn) Decloitre, *Difflugia acuminata* Ehrenberg, *D. corona* Wallich, *D. gramen* Penard, *D. labiosa* Wailes, *D. lanceolata* Penard, *D. limnetica* (Levander) Penard, *D. lithophila* Penard, *D. lobostoma* Leidy, *D. oblonga* Ehrenberg, *D. parva* Ogden, *D. pyriformis* Perty, *D. urceolata* Carter, *Phryganella acropodia* (Hertwig et Lesser) Hopkinson, *Assulina muscorum* Greef, *Tracheleuglypha acolla* Bonnet, Thomas, *Trinema lineare* Penard, *Wailesella eboracensis* (Wailes) Deflandre, *Difflugiella oviformis* f. *fusca* (Penard) Bonnet et Thomas) is conducted. Variability of natural populations of testate amoebae is expressed either in the changes of the shell size (correlated), or in the changes of the size of separate parameters (non correlated), resulting in a significant broadening of phenotypic spectrum in populations. The size of shell aperture demonstrates the greatest variability. The character of variability (its amplitude and correlativity) differs not only in different species, but also in different populations of the same species. Three main types of size variability in testate amoebae populations are established. There are monomorphic populations, polymorphic populations with correlated characters and populations with a high phenotypic plasticity, non-correlated characters and the elements of discreteness. A scheme of the close related species analysis is proposed.

Key words: morphology, morphometry, Rhizopoda, testate amoebae.

INTRODUCTION

Testate amoebae are unicellular predominantly asexual organisms. At present only a minor part of testate amoebae is known to possess different forms of sexual reproduction (Schönborn 1966). In some species *(Trinema lineare, Corythion dubium, C. orbicularis, C. delamarei*) asexual binary fission is alternated with isogamic copulation of trophozoids during the life cycle (Sukhanova and Yudina 1990, Yudina and Sukhanova 2000). In a testate amoeba *Arcella vulgaris* meiotic stages in the reproduction cycle have been observed (Raikov *et al.* 1989, Mignot and Raikov 1992).

The applicability of the "biological species" concept for testate amoebae, as well as for the rest predominantly asexual protists, is questionable. Delimitation of panmyxic reproductively isolated systems turns out to be difficult. However, this does not mean that asexual organisms are "extraspecific forms of life". All living

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things in the recent biosphere are thought to be organized in species, but there are species of various types, differing from each other (Zavadsky 1968, Poljansky 1992). At present the species is defined not as a genetically closed, but as a genetically stable system. Thus, in asexual forms, a species may be considered as a system of close biotypes (groups of individuals phenotypically resembling each other), possessing closely related genotypes, inhabiting a common distribution area and bound by a common evolutionary fate (Yablokov and Yusufov 1998).

In the diagnoses of testate amoebae species morphological criteria traditionally predominate. Recently a "morphospecies" concept has been proposed as a basic one for protists (Finlay *et al.* 1996, Finlay 1998). However, in the case of testate amoebae as well as other protists (e.g. diatoms) the difficulty in the application of this concept lies in their great morphological variability, which forms continuous network, which is not clearly defined into taxonomic units.

Biometric analysis is the most important part of phenotypic analysis of testate amoebae, as organisms with few morphological characters. Testacean systematics as well as foraminiferan or radiolarian taxonomy is based on morphological features of external structures. Some protistologists (Couteaux 1976) consider this approach to be incorrect, postulating that systematics should be based on the morphology of cellular structures. However, this standpoint does not agree with the data on genetically controlled shell construction (Netzel 1972a, b, c; Ogden 1979a, b; Anderson and Cowling 1994; Anderson 1995). Protozoologists working in the fields of taxonomy, biology and ecology of testate amoebae consider shell morphology to be as important as the features of cellular structures (Anonymous 1977). Most of the subsequent descriptions of new species have been based on shell morphology only. Cytological analysis, as a rule, amounted to description of pseudopodia shape (Chardez 1990, 1991, 1994). Rarely it was used in differential diagnosis (Ogden and Meisterfeld 1989, Ogden 1991). The investigation of clones during describing new species or redescribing old ones is also difficult to carry out in practice.

The analysis of morphological variability of testate amoebae began in the first quarter of the XXth century with the studies of morphological variability of *Difflugia corona* clones (Jennings 1916), longtime modifications and variability of testaceans from the genus *Arcella* (Hegner 1919, Reynolds 1923, Jollos 1924) and *Centropyxis* (Root 1918). Concurrently biometric approach to the analysis of variability of testacean natural populations was developing (Bassine 1929, Zinger 1935, Hoogenraad and de Groot 1937). Later, the relations between morphological features of testate amoebae and environmental parameters were established (Schönborn 1962, 1983; Heal 1963; Chardez and Leclercq 1963). Biometric approach has been extensively applied in the last two decades. It yielded detailed information on the variability of natural populations and laboratory cultures of some testacean species (Schönborn *et al.* 1983, 1987; Lüftenegger *et al.* 1988; Schönborn and Peschke 1988, 1990; Wanner 1988, 1991, 1994a, b, 1995; Schönborn 1990, 1992; Lüftenegger and Foissner 1991; Wanner and Meisterfeld 1994; Wanner *et al.* 1994). In some cases it was used for comparative geographical analysis (Bobrov *et al.* 1995) and redescription of closely related species (Foissner and Korganova 1995, 2000).

Recently Wanner (1999) reviewed the data on variability in testate amoebae and the influence of environmental conditions upon their morphology. It was emphasized that for understanding the phenomena in question a detailed biometric analysis of variability of natural populations is necessary, as well as laboratory experiments on clones. All this makes possible to reveal different aspects of adaptive mechanisms of testate amoebae, including their reaction to environmental factors and their combinations.

The aim of the present study was to perform a detailed analysis of intra- and interpopulation variability in natural populations of 24 testacean species inhabiting different biotopes (soils, sphagnum bogs and freshwater habitats) on the basis of original and literature data.

MATERIALS AND METHODS

Morphological investigation of 24 testate amoebae species has been conducted.

The samples containing testate amoebae were taken in different geographical areas of Russia and from different biotopes: freshwater, soil and bogs: *Centropyxis sylvatica* (Deflandre) Thomas - Central Forest Biosphere Nature Reserve, Tverskaja province, mixed spruce forest, podzolic brown soil. *Cyclopyxis eurystoma* v. *parvula* Deflandre - Central Forest Biosphere Nature Reserve, Tverskaja province, mixed spruce forest, podzolic brown soil. *Cyclopyxis puteus* Thomas - Primorsky kray, Sikhote-Alin reserve, *Pinus sibirica* and larch forest with *Ledum*, dark colored skeleton soil. *Hyalosphenia elegans* Leidy - Malozemelskaia shrub tundra (Pechora River basin), microcommunity *Sphagnum angustifolium. Hyalopshenia papilio* Leidy Population 1 - Malozemelskaia shrub tundra (Pechora River basin), peat, depth 330-335 cm. *Hyalopshenia papilio* Leidy Population 2 - Malozemelskaia shrub tundra (Pechora River basin), peat,

depth 340-345 cm. *Hyalopshenia papilio* Leidy Population 3 - Malozemelskaia shrub tundra (Pechora River basin), microcommunity *Sphagnum balticum*. *Hyalopshenia papilio* Leidy Population 4 - Tomskaya oblast', fen, microcommunity *Sphagnum capillifolium*. *Hyalopshenia papilio* Leidy Population 5 - Malozemelskaia shrub tundra (Pechora River basin), microcommunity *Sphagnum angustifolium*. *Schoenbornia humicola* (Schönborn) Decloitre Population 1 - Khabarovsky kray, coast of Okhotsk Sea, spruce forest, brown soil. *Schoenbornia humicola* (Schönborn) Decloitre Population 2 - Khabarovsky kray, coast of Okhotsk Sea, spruce forest with *Hylocomium*, *Dicranum*, *Rhytidiadelphus*, brown soil. *Schoenbornia humicola* (Schönborn) Decloitre Population 3 - Novgorodskaya oblast', pine forest, podzol soil. *Schoenbornia humicola* (Schönborn) Decloitre Population 4 - Karelia, pine forest, podzol soil. *Difflugiella oviformis* f. *fusca* (Penard) Bonnet et Thomas - Kirovskaia province, mesotrophic-oligotrophic swamp, microcommunity *Sphagnum girgensonii*. *Phryganella acropodia* (Hertwig et Lesser) Hopkinson - archipelago Komandor Islands, Bering Island, dry shrub rich in herbs with heath tundra, brown skeleton soil. *Wailesella eboracensis* (Wailes) Deflandre Population 1 - Malozemelskaia shrub tundra (Pechora River basin), microcommunity *Sphagnum flexuosum*. *Wailesella eboracensis* (Wailes) Deflandre Population 2 - Malozemelskaia shrub tundra (Pechora River basin), microcommunity *Sphagnum balticum*. *Assulina muscorum* Greef - Malozemelskaia shrub tundra (Pechora River basin), microcommunity *Sphagnum nemorum*. *Tracheleuglypha acolla* Bonnet et Thomas - Central Forest Biosphere Nature Reserve, Tverskaja province, mesotrophic swamp. *Trinema lineare* Penard - archipelago Komandor Islands, Bering Island, dry shrub rich in herbs with heath tundra, brown skeleton soil. *Difflugia pyriformis* Perty - Penza region, pond, debris. *Difflugia oblonga* Ehrenberg - Penza region, boggy lake. *Difflugia acuminata* Ehrenberg - Penza region, pond, debris. *Difflugia parva* Ogden - Penza region, boggy lake. *Difflugia labiosa* Wailes - Penza region, Sura River, debris. *Difflugia lanceolata* Penard - Penza region, pond, debris. *Difflugia lithophila* Penard - Penza region, Sura River, sandy sediments. *Difflugia urceolata* Carter - Penza region, Sura River, sandy sediments. *Difflugia limnetica* (Levander) Penard - Penza region, pond, debris. *Difflugia corona* Wallich - Penza region, Sura River, sandy sediments. *Difflugia gramen* Penard - Penza region, Sura River, sandy sediment. *Difflugia lobostoma* Leidy - Penza region, pond, debris.

Morphometrical measurements were conducted by means of a light microscope under the magnification of 400×. Statistical analysis was performed with the help of STATISTICA 5.5A Software.

RESULTS

Analysis of variation coefficients provides general information on the degree of variability of characters in populations (Table 1). It appears to vary for different characters in different populations. Some species (*Hyalosphenia elegans, Wailesella eboracensis, Difflugia lithopohila, D. oblonga, Cyclopyxis puteus, Difflugiella oviformis)* are characterized by a minor degree of variability. Others (*Difflugia acuminata, D. labiosa, D. lanceolata, D. urceolata, Schoenbornia humicola, Trinema lineare*), on the contrary, are characterized by great morphometrical variability. The greatest variation coefficients are revealed for shell aperture diameter, lesser ones - for the shell length.

On the basis of our own results and literature data (Schönborn *et al*. 1983; Wanner and Funke 1986; Schönborn *et al*. 1987; Balik 1988; Lüftenegger *et al*. 1988; Schönborn and Peschke 1988, 1990; Wanner 1988; Schönborn 1990, 1992; Lüftenegger and Foissner 1991; Dekhtyar 1993, 1994; Bobrov *et al*. 1995) variation coefficients of morphometrical parameters in 75 testacean species from 133 populations have been analysed. Results, represented in Fig. 5, show that in some populations variation coefficients may reach 40 %. However, in an overwhelming majority of cases coefficients do not exceed 20 % (for aperture size) and 15 % (for length, breadth and depth of the shell). In general, the size of the pseudostome is characterized by greatest variability.

The results of the comparison of variation coefficients in different taxonomical testaceen groups are shown in Table 2. It turned out that filose amoebae are more variable in size than lobose ones (Mann-Whitney U test: $p<0.001$). On the other hand, there are no differences in terms of degree of morphometrical variability between freshwater, bog and soil testate amoebae as well as between different life forms (simple acrostomia, compressed acrostomia, centrostomia, plagiostomia).

Characteristics, reflecting correlation between all morphological parameters, are more significant in morphometrical analysis. Pearson correlation coefficients between the main morphometrical characters of testate amoebas are represented in Table 3. It shows that there are species with highly correlated characters. However, there are species that possess non-correlated characters. For some species low values of correlation coefficients between the length and the breadth of the shell were noted. Pseudostome diameter is very often weakly correlated with the rest of the parameters. Low values of correlation coefficients suggest that some of the shell characteristics (size of the aperture, for instance) change independently of others. These characters appear to serve as tools of adaptation to variable environmental constraints. In other words, adaptation to environmental conditions is realized rather through a wider phenotypic spectrum than through a simple proportional decrease or increasing in the size of the shell. Such tendencies are pronounced in a greater or lesser degree in different species.

Table 1. Biometric characterisation of the investigated testacean species. Numbers designate features as described in Figs 1-4. Measurements in μm. $\bar{x}$ - arithmetic mean; M - median; SD - standard deviation; SE - standard error of mean; CV - coefficient of variation in %; Min - minimum; Max - maximum; n - number of specimens investigated.

Character	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Centropyxis sylvatica								
1	115.2	119.5	10.14	1.43	8.8	78.0	128.0	50
2	124.6	128.0	10.70	1.51	8.6	90.0	136.0	50
3	68.8	70.0	7.77	1.10	11.3	48.0	95.0	50
1:2	1.1	1.1	0.10	0.01	8.9	1.0	1.7	50
Cyclopyxis eurystoma v. *parvula*								
1	35.3	33.0	8.26	0.99	23.4	25.0	67.0	70
2	15.0	14.0	5.30	0.63	35.3	8.0	47.0	70
3	13.8	13.0	4.82	0.58	34.9	7.2	22.0	70
1:2	0.4	0.4	0.05	0.01	12.5	0.3	0.7	70
Cyclopyxis puteus								
1	148.1	142.0	12.74	1.88	8.6	130.0	180.0	46
2	124.2	124.0	2.95	0.48	2.4	120.0	132.0	38
3	39.8	40.0	2.63	0.39	6.6	34.0	46.0	46
1:2	0.8	0.9	0.07	0.01	8.3	0.7	1.0	38
Difflugia acuminata								
1	204.9	198.0	33.32	4.97	16.3	150.0	294.0	43
2	79.8	77.5	13.89	2.07	17.4	58.5	126.0	44
3	43.7	42.7	8.62	1.30	19.7	33.0	75.0	44
1:2	0.4	0.4	0.06	0.01	15.9	0.3	0.6	43
Difflugia lanceolata								
1	152.8	155.0	16.30	1.77	10.7	87.5	189.5	85
2	65.7	65.0	9.86	1.08	15.0	40.5	84.5	84
3	36.1	35.5	7.47	0.82	20.7	21.0	54.0	82
1:2	0.4	0.5	0.07	0.01	15.5	0.31	0.5	84
Difflugia corona								
1	166.1	165.0	12.54	1.58	7.5	141.0	210.0	63
2	159.9	159.1	9.83	1.24	6.1	132.5	184.5	63
3	67.9	69.5	12.90	2.28	19.0	8.5	86.1	32
1:2	1.0	1.0	0.06	0.01	6.1	0.8	1.1	62
Difflugia labiosa								
1	206.9	202.0	24.92	3.72	12.1	155.5	260.5	45
2	130.4	133.5	15.05	2.24	11.5	96.0	159.6	45
3	59.8	59.6	9.73	1.67	16.3	40.5	76.5	34
1:2	0.6	0.64	0.07	0.01	10.5	0.5	0.8	45
Difflugia limnetica								
1	104.2	102.7	9.29	1.03	8.9	84	130.5	82
2	85.3	84.5	10.82	1.19	12.7	60.5	11.5	82
3	33.4	32.5	6.14	0.94	18.4	23.5	51.5	43
1:2	0.8	0.8	0.08	0.01	9.6	0.7	1.0	82
Difflugia lobostoma								
1	159.0	162.5	15.81	3.10	9.9	124.5	185.5	26
2	138.3	139.1	15.50	3.04	11.2	110.5	163.5	26
3	45.9	46.5	6.60	1.41	14.4	35.5	57.5	22
1:2	0.9	0.86	0.07	0.01	8.4	0.7	1.0	26
Difflugia gramen								
1	68.8	69.0	6.92	1.09	10.1	57.0	85.5	40
2	51.5	49.9	8.58	1.36	16.7	39.5	77.5	40
3	23.3	2.5	5.40	1.08	23.2	15.9	36.0	25
1:2	0.8	0.7	0.08	0.01	10.9	0.6	0.9	40
Difflugia lithophila								
1	116.3	114.5	7.23	1.75	6.2	100.5	132.5	17
2	93.7	93.5	5.01	1.21	5.4	86.5	108.0	17
3	43.3	42.5	3.84	0.99	8.9	35.5	48.5	15
1:2	0.8	0.8	0.06	0.01	7.0	0.7	0.9	17

Table 1 (contd.)

Difflugia urceolata								
1	248.8	245.5	28.43	3.22	11.4	189.0	341.1	78
2	192.4	192.1	38.06	4.31	19.8	100.5	275.5	78
3	114.8	114.0	18.11	2.15	15.8	77.5	148.5	71
1:2	0.8	0.78	0.11	0.01	13.7	0.4	1.0	78
Difflugia oblonga								
1	238.2	236.5	14.82	2.00	6.2	207.0	287.5	55
2	118.3	118.5	7.87	1.06	6.7	97.5	140.5	55
3	48.1	46.5	7.32	1.07	15.2	36.0	65.5	47
1:2	0.5	0.5	0.03	0.00	6.8	0.4	0.6	55
Difflugia pyriformis								
1	274.3	272.6	21.95	4.48	8.0	239.5	334.5	24
2	148.7	148.5	19.28	3.86	13.0	114.5	187.5	25
3	51.5	49.1	9.80	2.04	19.0	33.5	70.5	23
1:2	0.6	0.6	0.07	0.01	12.7	0.4	0.8	25
Difflugia parva								
1	155.3	155.5	12.51	2.25	8.1	128.5	177.5	31
2	72.4	70.5	10.12	1.82	14.0	51.5	90.0	31
3	28.2	27.0	4.94	0.89	17.5	18.5	39.5	31
1:2	0.5	0.36	0.07	0.01	14.3	0.4	0.6	31
Hyalosphenia elegans								
1	98.8	100.0	4.14	0.59	4.2	85.0	105.0	50
2	50.0	50.0	2.58	0.37	5.2	44.0	56.0	50
3	19.9	20.0	1.13	0.16	5.7	17.0	23.0	50
1:2	0.5	0.5	0.03	0.00	5.2	0.4	0.6	50
Hyalosphenia papilio Population 1								
1	124.9	125.0	5.93	0.84	4.7	115.0	140.0	50
2	83.1	84.0	5.51	0.78	6.6	65.0	97.0	50
3	37.0	38.0	1.77	0.25	4.7	33.0	40.0	50
1:2	0.7	0.7	0.05	0.01	7.1	0.5	0.8	50
Hyalosphenia papilio Population 2								
1	124.1	125.0	5.07	0.72	4.1	113.0	138.0	50
2	85.8	86.5	4.48	0.63	5.2	75.0	94.0	50
3	37.5	38.0	2.39	0.34	6.4	33.0	43.0	50
1:2	0.7	0.7	0.04	0.01	5.7	0.6	0.8	50
Hyalosphenia papilio Population 3								
1	103.5	102.0	7.34	1.04	7.1	88.0	122.0	50
2	67.9	67.0	5.14	0.73	7.6	58.0	80.0	50
3	29.7	23.0	5.19	0.74	9.8	23.0	37.0	50
1:2	0.7	0.7	0.04	0.01	5.7	0.6	0.7	50
Hyalosphenia papilio Population 4								
1	99.2	98.0	4.09	0.58	4.1	91.0	115.0	50
2	65.6	65.0	4.73	0.67	7.2	55.0	78.0	50
3	27.8	27.0	1.72	0.24	6.2	25.0	32.0	50
1:2	0.7	0.7	0.04	0.01	5.7	0.6	0.8	50
Hyalosphenia papilio Population 5								
1	118.3	121.0	9.65	0.96	8.2	95.0	137.0	100
2	71.4	72.5	5.98	0.60	8.4	60.0	85.0	100
3	33.0	35.0	5.16	0.52	15.7	24.0	43.0	100
1:2	0.6	0.6	0.03	0.00	4.8	0.52	0.69	100
Schoenbornia humicola Population 1								
1	57.2	56.0	3.73	0.53	6.5	45.0	65.0	50
2	34.7	35.0	2.73	0.39	7.9	28.0	40.0	50
3	18.6	18.0	2.10	0.30	11.3	13.0	23.0	50
1:2	0.6	0.6	0.04	0.01	6.7	0.5	0.7	50
Schoenbornia humicola Population 2								
1	35.0	35.0	3.99	0.56	11.4	26.0	45.0	50
2	21.2	22.0	2.52	0.36	11.9	15.0	25.0	50
3	9.9	10.0	1.34	0.19	13.5	8.0	13.0	50
1:2	0.6	0.6	0.05	0.01	7.7	0.5	0.7	50

Table 1 (contd.)

Schoenbornia humicola Population 3								
1	38.1	38.0	1.74	0.25	4.6	33.0	42.0	50
2	24.6	25.0	1.05	0.15	4.3	22.0	27.0	50
3	10.5	10.0	1.31	0.19	12.5	7.0	14.0	50
1:2	0.7	0.7	0.03	0.01	4.3	0.6	0.7	50
Schoenbornia humicola Population 4								
1	37.9	37.0	1.79	0.25	4.7	35.0	45.0	50
2	22.7	23.0	1.24	0.18	5.5	20.0	27.0	50
3	9.3	9.0	1.20	0.59	12.9	7.0	38.0	50
1:2	0.6	0.6	0.03	0.01	5.0	0.5	0.7	50
Difflugiella oviformis								
1	21.4	22.0	2.12	0.30	9.9	16.0	27.0	50
2	17.8	17.0	1.87	0.26	10.5	15.0	21.0	50
3	11.2	11.0	1.56	0.22	13.9	8.0	13.0	50
1:2	0.8	0.8	0.07	0.01	8.1	0.7	0.9	50
Phryganella acropodia								
1	39.5	40.0	1.80	0.25	4.6	34.0	44.0	50
2	19.8	20.0	1.12	0.16	5.7	17.0	23.0	50
3	19.6	19.0	1.67	0.24	8.5	17.0	22.0	50
1:2	0.5	0.5	0.01	0.00	3.0	0.4	0.5	50
Wailesella eboracensis Population 1								
1	26.4	26.0	1.60	0.23	12.6	23.0	29.0	50
2	14.5	14.0	0.97	0.14	12.1	12.0	17.0	50
3	5.5	5.5	0.58	0.08	23.2	5.0	7.0	50
4	5.5	5.0	0.58	0.08	24.0	5.0	7.0	50
5	9.7	10.0	0.56	0.08	9.3	8.0	11.0	50
6	11.2	11.0	0.93	0.13	8.4	9.0	15.0	50
Wailesella eboracensis Population 2								
1	27.2	27.0	3.43	0.49	12.6	23.0	48.0	50
2	15.0	15.0	1.80	0.25	12.0	13.0	26.0	50
3	5.6	5.0	1.31	0.18	23.2	5.0	14.0	50
4	5.5	5.0	0.50	0.07	9.2	5.0	6.0	50
5	9.8	10.0	0.91	0.13	9.3	5.0	11.0	50
6	11.6	12.0	0.99	0.14	8.5	9.0	14.0	50
Assulina muscorum								
1	45.1	45.0	3.53	0.35	7.8	32.0	50.0	100
2	34.0	35.0	3.47	0.35	10.2	18.0	42.0	100
3	12.9	13.0	2.10	0.21	16.3	5.0	16.0	100
1:2	0.8	0.8	0.07	0.01	9.0	0.5	1.0	100
Tracheleuglypha acolla								
1	41.8	42.0	2.37	0.34	5.7	38.0	46.0	50
2	26.6	27.0	3.44	0.49	12.9	21.0	34.0	50
3	8.8	9.0	1.41	0.20	16.1	6.0	11.0	50
Trinema lineare								
1	28.6	30.0	5.04	0.80	17.6	21.0	40.0	40
2	11.8	11.0	2.76	0.44	23.5	8.0	18.0	40
3	6.8	7.0	1.68	0.26	24.8	4.0	11.0	40
1:2	0.4	0.4	0.05	0.01	13.0	0.3	0.6	40

Bivariant frequency distribution diagrams (Fig. 6) allow us to estimate not only the degree of polymorphism in testate amoebae populations, but also the discreteness of total variability. In this way it is possible to distinguish monomorphic populations (for example, *Cyclopyxis eurystoma* v. *parvula*), polymorphic populations with correlated characters (*Difflugia urceolata, D.corona, Assulina muscorum*) and populations with a high phenotypic plasticity, non-correlated characters and the elements of discreteness (*Difflugiella oviformis, Wailesella eboracensis*).

Populations of the same species in different biotopes may differ from each other not only as to size (Table 4) but also as to the degree of correlation between characters (Tables 5, 6). This phenomenon may be considered as an adaptation mechanism in testate amoebae.

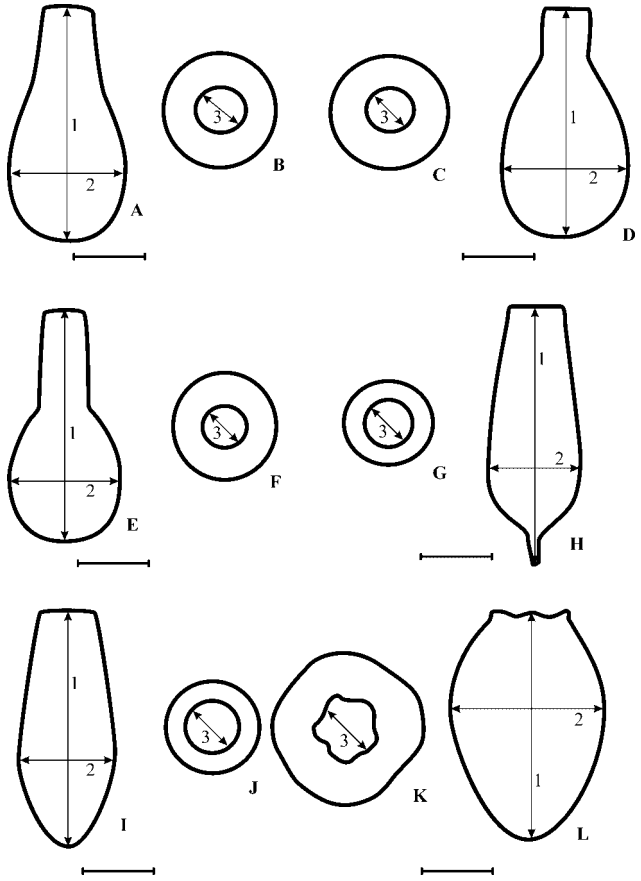

Fig. 1. Outline of shells and position of measured axis. **A, B** - *Difflugia oblonga*; **C, D** - *D. pyriformis*; **E, F** - *D. parva*; **G, H** - *D. acuminata*; **I, J** - *D. lanceolata*; **K, L** - *D. labiosa*. 1 -shell length, 2 - shell breadth, 3 - aperture diameter. Scale bars 50 µm.

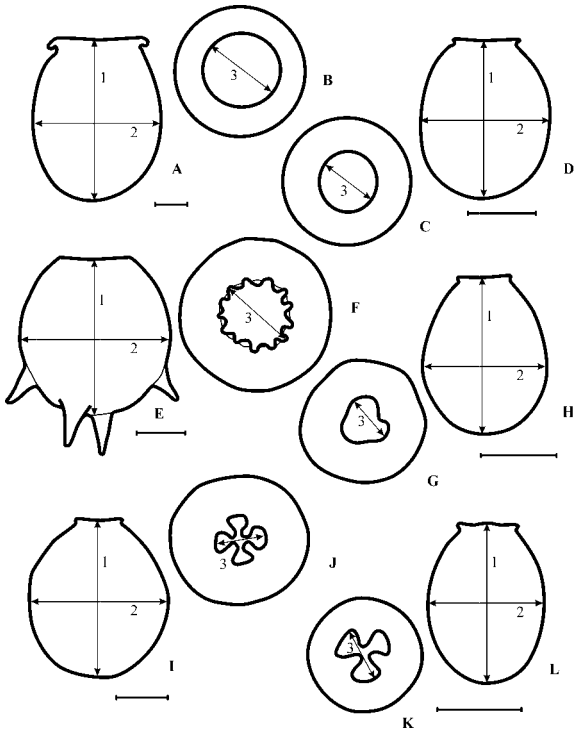

Fig. 2. Outline of shells and position of measured axis. **A, B** - *Difflugia urceolata*; **C, D** - *D. lithophila*; **E, F** - *D. corona*; **G, H** - *D. limnetica*; **I, J** - *D. lobostoma*; **K, L** - *D. gramen*. 1 - shell length, 2 - shell breadth, 3 - aperture diameter. Scale bars 50 µm.

These variants of variability occur in species with all types of shell (organic, with xenosomes or idiosomes), species representing various life forms, inhabiting freshwater bodies, sphagnum bogs, soils, species from different phyletic branches (Filosea, Lobosea).

DISCUSSION

The analysis of the variability of testate amoebae in natural populations reveals several general patterns: (a) the variability in natural populations of testate amoebae is expressed either in the changes of the shell size (correlated) or in the changes of the size of separate characters (non correlated). Frequently one character can be decreased in size, and another - to be enlarged. This results in a significant broadening of phenotypic spectrum in populations; (b) the size of the pseudostome is the most variable character. Moreover, this character, as a rule, changes independently from the others. Taking into account that the aperture of the shell is the main way of the organism's interaction with the environment, variations of its size are likely to be adaptive; (c) the pattern of variability (degree and correlativity) differs not only in different species but in different populations of the same species. It might be supposed that the variability of populations is due to the environmental conditions of the habitat where the population is formed.

A pronounced polymorphism of testate amoebae has been recorded by many researches. For example, Schönborn (1992) has shown the phenospectra of *Trinema complanatum* in litter and humus soil horizons of a spruce forest to include 6 morphological variations in each horizon. Only a part of morphological variants were common for both horizons.

The results of the analysis of variability in natural populations of testate amoebae are supplemented by the

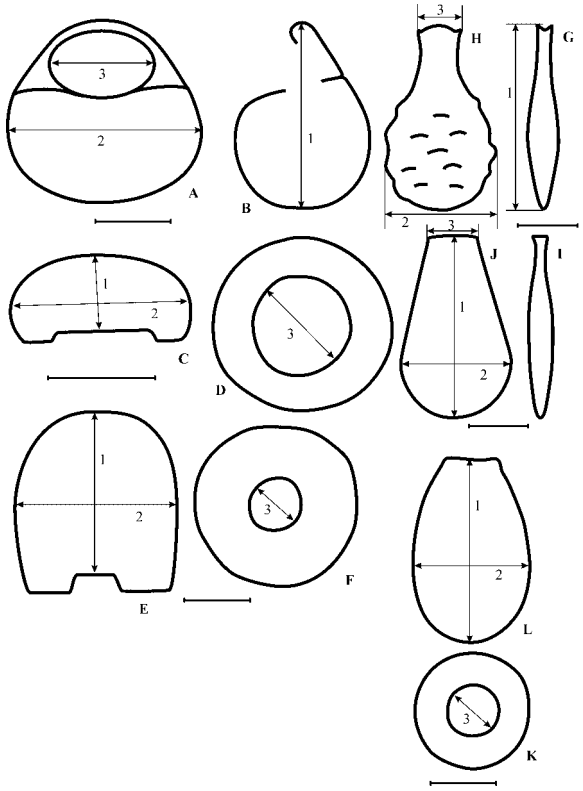

Fig. 3. Outline of shells and position of measured axis. **A, B** - *Centropyxis sylvatica* ; **C, D** - *Cyclopyxis eurystoma* v. *parvula*; **E, F** - *Cyclopyxis puteus*; **G, H** - *Hyalosphenia elegans*; **I, J** - *Hyalosphenia papilio*; **K, L** - *Schoenbornia humicola*. 1 - shell length, 2 - shell breadth, 3 - aperture diameter. Scale bars 50 µm (A, B, E-J); 20 µm (C, D, K, L).

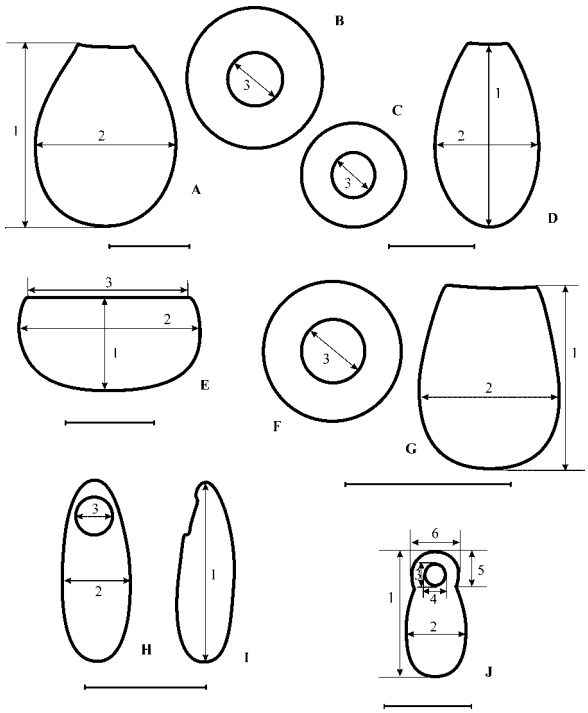

Fig. 4. Outline of shells and position of measured axis. **A, B** - *Assulina muscorum*; **C, D** - *Tracheleuglypha acolla*; **E** - *Phryganella acropodia*; **F, G** - *Difflugiella oviformis*; **H, I** - *Trinema lineare*; **J** - *Wailesella eboracensis*. **A-I** - 1 - shell length, 2 - shell breadth, 3 - aperture diameter. **J** - 1 - shell length, 2 - shell breadth, 3 - aperture length, 4 - aperture breadth, 5 - length of "head region", 6 - breadth of "head" region. Scale bars 20 µm.

investigations of clonal cultures. The question to be solved is whether individual variability in testacean populations is due to genotypic features or to environmental impact (trophic interactions, abiotic factors, etc.).

In laboratory experiments on *Trinema lineare* and *Euglypha laevis* clones Schönborn (1992) has shown that in stable controlled conditions the variation coefficients of morphometrical parameters considerably grows with the time of conducting the clonal culture. Consequently, individual variability is likely to be genetically conditioned, and it is not always directly adaptive. In other words, in a genotype spontaneous size fluctuations within certain intervals are incorporated. In concrete biotopes the selection is for a total phenotypic spectrum, i.e., from all possible morphological and morphometrical variations of a species those individuals are represented in the population that possess the advantages of a better adaptation to concrete conditions. Localities being heterogeneous, in a population there may be several phenotypes, adapted to different microlocalities. However, there will not always be a uniform sample of phenotypes in a homogeneous locality, either. In the experiments of Schönborn (1992), individual variability was recorded even in stable conditions of clonal cultures. Thus, species in natural populations possess an extremely complex phenotypic spectrum. It is expressed differently in different species. If we take this into account, it becomes even more surprising that individual variability in the majority of species is rather low and the species is stable.

The results of the experiments of Schönborn (1992) could be also explained in another way. Deterioration of conditions in the culture in the course of experiments (changes of a trophic regime, accumulation of metabolites in the growing culture, an increasing population density) could results in the expansion of the morphological spectrum of the population. This hypothesis could be supported by an increase in the number of organisms of

Table 2. Variation coeffcients in different testate amoebae groups. n - number of characters investigated, $\bar{x}$ - arithmetic mean, Min - minimum, Max - maximum, SD - standard deviation.

Life - forms	n	$\bar{x}$	Min	Max	SD
Simple acrostomia	75	12.2	3.2	29.8	5.77
Compressed acrostomia	152	11.4	2.3	35.2	6.40
Centrostomia	38	13.4	2.4	35.3	9.18
Plagiostomia	91	13.5	2.5	35.3	6.96
Biotope inhabited	**n**	**$\bar{x}$**	**Min**	**Max**	**SD**
Freshwater	66	12.0	3.1	26.2	5.78
Sphagnum	62	10.5	2.3	32.1	7.04
Soil	256	12.6	2.4	35.3	6.78
Class	**n**	**$\bar{x}$**	**Min**	**Max**	**SD**
Lobosea	266	11.3	2.3	35.3	6.18
Filosea	114	14.0	2.5	35.3	7.45

Table 4. Statistical significance (Student's t-test) of shell measurements between populations of *Schoenbornia humicola* and populations of *Hyalosphenia papilio*. P1-P4 - populations (see Materials and Methods).

	Schoenbornia humicola				*Hyalosphenia papilio*		
	P1	P2	P3		P1	P2	P3
P2	***			P2	NS		
	***				***		
P3	***	***		P3	***	***	
	***	***			***	***	
P4	***	***	NS	P4	***	***	***
	***	***	***		***	***	***

1st line - shell length; 2nd line - shell width. *** $P < 0.001$; NS - not significant.

Table 3. Pearson correlation coefficients between shell measurements of the investigated testate amoebae species. L - length of the shell, B - breadth of the shell, Dp - aperture diameter; *** $P < 0.001$; ** $0.01 > P > 0.001$; * $0.05 > P > 0.01$; $^{+}$ $0.1 > P > 0.05$; ^{NS} - not significant.

Species	L-B	L-Dp	B-Dp
Centropyxis sylvatica	0.71***	0.46**	0.51***
Cyclopyxis eurystoma v. *parvula*	0.89***	0.74***	0.68***
Cyclopyxis puteus	0.31^{+}	0.42**	0.31+
Difflugia acuminata	0.47**	0.51**	0.83***
Difflugia corona	0.46**	-0.05^{NS}	-0.06^{NS}
Difflugia labiosa	0.69***	0.60***	0.70***
Difflugia lanceolata	0.46***	0.32**	0.78***
Difflugia limnetica	0.48**	0.29^{+}	0.70***
Difflugia lobostoma	0.76***	0.01^{NS}	-0.10^{NS}
Difflugia gramen	0.83***	0.51**	0.73***
Difflugia lithophila	0.17^{NS}	0.32^{NS}	-0.03^{NS}
Difflugia oblonga	0.40**	0.35**	0.13^{NS}
Difflugia pyriformis	0.72***	0.62**	0.48*
Difflugia parva	0.27^{NS}	0.40*	-0.06^{NS}
Difflugia urceolata	0.78***	0.79***	0.87***
Hyalosphenia elegans	0.41**	0.04^{NS}	0.43***
Hyalosphenia papilio Population 5	0.84***	0.84***	0.85***
Schoenbornia humicola Population 2	0.80***	0.48***	0.55***
Difflugiella oviformis	0.67***	0.64***	0.57***
Phryganella acropodia	0.89***	0.84***	0.85***
Wailesella eboracensis Population 1	0.45**	0.26^{NS}	0.27^{NS}
Assulina muscorum	0.60***	0.49***	0.78***
Tracheleuglypha acolla	0.82***	0.64***	0.66***
Trinema lineare	0.82***	0.84***	0.83***

Table 5. Correlation coefficients between shell measurements of 2 populations *Wailesella eboracensis* from *Sphagnum* in Malozemel shrubbery tundra. 1st line - Population 1, 2nd line - Population 2. Statistical significance (Student's t-test) between 2 populations $P < 0.05$.

2	3	4	5	6	Character
0.45	0.26	0.26	0.14	0.13	1
0.86	0.89	0.09	0.51	0.00	
	0.27	0.33	0.29	0.29	2
	0.86	0.00	0.57	-0.04	
		0.97	0.33	0.04	3
		0.00	0.57	-0.09	
			0.37	0.09	4
			0.45	0.36	
				0.26	5
				0.59	

Table 6. Correlation coefficients between shell measurements of 4 populations *Hyalosphenia papilio* and 4 populations *Schoenbornia humicola* from different biotopes. L - length of the shell, B - breadth of the shell, Dp - aperture diameter.

Population	L:B	L:Dp
H. papilio Population 1	0.21	0.23
H. papilio Population 2	0.21	0.33
H. papilio Population 3	0.70	0.65
H. papilio Population 4	0.52	0.55
Sch. humicola Population 1	0.61	0.45
Sch. humicola Population 2	0.80	0.48
Sch. humicola Population 3	0.50	0.38
Sch. humicola Population 4	0.41	0.05

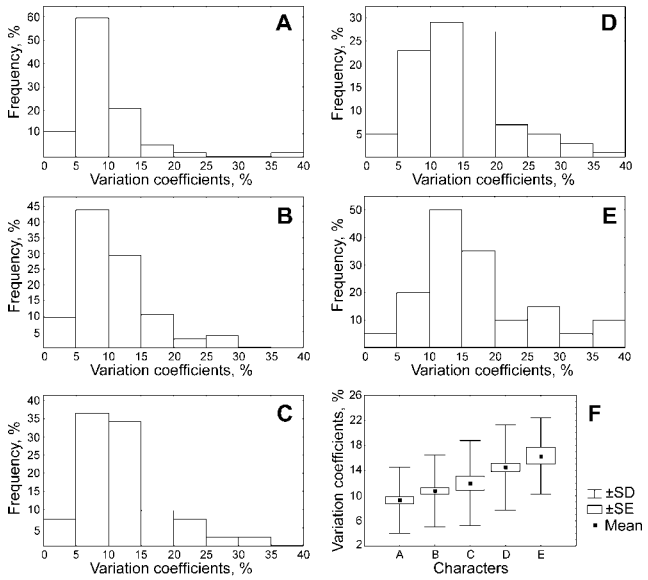

Fig. 5. Frequency distribution of variation coefficients in shell length (**A**), shell breadth (**B**), shell depth (**C**), aperture length (**D**) and aperture breadth (**E**). Mean variation coefficients of different characters (**F**). SD - standard deviation, SE - standard error of mean. The differences between variation coefficients are significant (Mann-Whitney U test: $p < 0.05$) for all character combinations (exception B *vs.* C).

smaller size closer to the end of the experiment. In the same investigation (Schönborn 1992), the experiments with clonal strains of large and small individuals were carried out. Our calculations on the basis of Schönborn's (1992) data have shown that in clonal strains of large individuals the average values of shell size remain the same in the course of the experiment, and only occasionally are a little reduced. As for the minimum values, they are reduced by 14.4-25.9 %, whereas the maximal ones, by 0-17.6 %. In other words, in populations, which have initially consisted of large individuals, the number of smaller organism increases. In clonal strains of small testaceans the average size was increasing with time in the majority of experiments. The increase of the average size took place first of all is due to the growth of the number of large amoebae (in one of the clones the shell dimensions increased more than by 50 %), and not due to the elimination of small testate amoebae.

Thus, individual variability in experimental conditions depends on the duration of the experiment and thus on varying conditions of the medium, and also on the phenotype of the mother cell chosen for the clonal culture.

Later Wanner (Wanner 1994a, b; Wanner and Meisterfeld 1994; Wanner *et al.* 1994) in a series of laboratory experiments with clones and natural populations of *Cyclopyxis kahli, C. eurystoma* v. *parvula, Euglypha strigosa, E. rotunda, Trinema lineare, T. enchelys* has shown the influence of light intensity, temperature, fertilising and pesticides, and the nature of food upon morphometrical characteristics of testate amoebae. The analysis of the Wanner's data (Wanner 1994a) has shown that the variability of different morphological parameters in clonal cultures varied, preserving its values practically irrespective of experimental conditions. For example, at *Cyclopyxis kahli* the varia-

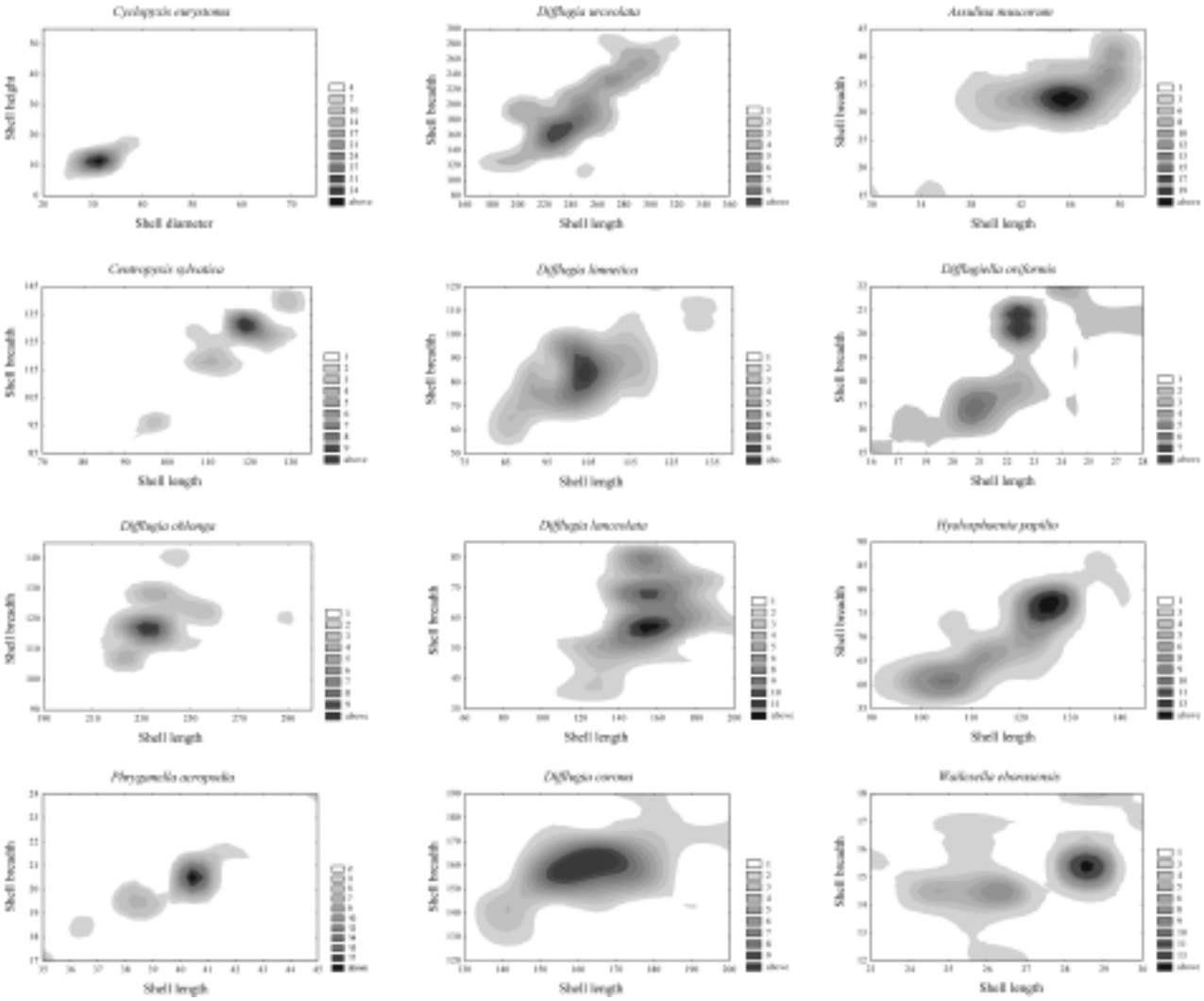

Fig. 6. Bivariant frequency distribution of characters in different testate amoebae species.

tion coefficient of the pseudostome diameter in almost all variants of experiments was almost three times higher than the coefficient of variation of the shell diameter. The degree of variability of various morphological characters is most likely to be determined by the species genotype. So the species realize its adaptive strategy by means of the most variable characters and due to variability of these ones the species can be polymorphic or polytypic.

Summing up, all available data indicate to a rather high variability of testate amoebae. The existing morphological types are grouped around a limited number of adaptive peaks, formed under the influence of ecological factors. However, these peaks are often weakly expressed, their discreteness is frequently insignificant, there being a lot of transitional forms. Thus the space of morphometrical characters as a whole is characterized by both continuality and discreteness. In different cases (different biotopes or different complexes of closely related species) it is possible to distinguish discrete units with a varying accuracy. Nevertheless, the systematicists have traditionally tried to designate the extreme forms as taxonomical units (subspecies or forms) irrespective of whether there are clear boundaries between them. The imprecision of differential diagnoses stems from the features of the object classified (asexual protists with

continuous variability). All this entails great difficulties in the diagnostics of testacean species and in the applicability of the "species" concept for them.

Recently the "morphospecies" concept (Finlay *et al.* 1996, Finlay 1998) has been suggested with reference to protists. The morphological criterion is put forward as a predominant one. On the one hand, this makes possible to avoid numerous difficulties associated with the separation of genetically isolated systems of organisms, not differing morphologically (syngenes), and, on the other hand, this is a rather convenient approach for the ecologists, as morphology to a great extent reflects the characteristics of the ecological niche occupied by an organism. However, the problems in connection with asexual protists are arisen. The notion of "species aggregates" has been offered (Finlay 1998) for clusters of species, which are morphologically indiscernible or form a continuum of morphologically overlapping forms. However, such an approach is likely to result in the loss of some ecological information reflected in the total morphological variability of the object or the number of transitional forms (distinguished as subspecies or forms). A high level of morphological variability within the population can indicate the heterogeneity of the biotope, where several morphs, including transitional ones, can exist simultaneously. A narrow phenospectrum, on the contrary, is more likely to arise in a homogeneous microbiotope or under severe abiotic conditions.

On the other hand, the account of all morphological diversity, not divided into discrete units, introduces significant difficulties into systematics and unambiguous species diagnosis. The problem is also complicated by the incompleteness of the descriptions of many taxa.

Earlier it was proposed to define the species of testate amoebae as wide phenetic clusters in which specimens are linked to each other through intergradation (Medioli and Scott 1983). However, there arises a question of what value of phenotypic variability can be accepted as infraspecific. In the work of Medioli and Scott (1983) an extreme degree of "lumping" can be seen. They have divided all diversity within Arcellinida into 14 species.

Detailed study of different species complexes presented recently by Foissner and Korganova (1995, 2000) is an excellent way of clarifying the problems outlined.

We propose the following scheme of the close related species analysis: (a) Revealing morphological variability of populations from various localities, and also variability within groups of closely related species; (b) A detailed biometric analysis of variability within the complex of close species studied and the evaluation of the possibility to distinguish more or less discrete units; in case of impossibility of unambiguous differentiation of taxa in the species complex demonstrating a high degree of polymorphism, the description of extreme variants and the indication of continuity of changes; (c) Redescription or establishing the synonymy of poorly described species; (d) Taking in account the environmental constraints determining morphological variability.

As a result of such research we will obtain a clearer understanding of the characteristics of phenotypic space of testate amoebae natural populations at a morphological level. From the systematic point of view it would help to outline the borders between species of testate amoebae more clearly. The adaptive strategy of testate amoebae is diverse. Its mechanisms are different at different species, and the knowledge of its variants realised would help to build the hierarchy of morphological characters as to their significance in different taxa.

A research like this could increase our knowledge of the causes and factors producing changes in shell morphology in ecological and paleoecological investigations. It would considerably expand the interpretation possibilities of rhizopode analysis, as it has already been shown for the rhizopode population of oligotrophic moors (Bobrov *et al.* 1999).

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