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Review of the European species of the genus *Sphaerium* (Mollusca, Bivalvia, Pisidioidea)

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The group of fingernail clams, treated in Russian literature as genus *Sphaerium* while as subgenus *Sphaerium* s.str. in western countries, is revised. Qualitative characters of shell and soft body were investigated, and their diagnostic value evaluated. As a result, 6 species are distinguished in the European fauna, and the group is divided into 3 genera, regarded earlier as subgenera *Sphaerium* s.str. (3 species), *Nucleocyclas* (2 species) and *Parasphaerium* (1 species). The quantitative morphometric analysis reveals some new differences between species, but their diagnostic value is restricted because of great individual and inter-populational variability. Diagnoses for all European genera and species and the key for their identification are given. Phylogenetic relationships within fingernail clams are analyzed in the light of the new data.

Обзор европейских видов рода *Sphaerium* (Mollusca, Bivalvia, Pisidioidea)

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Проведена ревизия группы, обозначаемой в отечественной литературе как род *Sphaerium*, а в зарубежной — как подрод *Sphaerium* s.str. Изучены качественные признаки раковины и мягкого тела и оценена их пригодность для диагностики. Установлено, что в европейской фауне представлено 6 видов изучаемой группы. Последняя разделена на 3 самостоятельных рода, соответствующих установленным ранее подродам *Sphaerium* s.str. (3 вида), *Nucleocyclas* (2 вида) и *Parasphaerium* (1 вид). Количественный анализ морфометрических признаков выявил новые различия между видами, однако их диагностическое значение ограничено вследствие значительной индивидуальной изменчивости. Приведены родовые и видовые диагнозы, а также определительная таблица. В свете новых данных проанализированы филогенетические отношения родов сферид.

INTRODUCTION

Being widely distributed and abundant in many freshwater communities, fingernail clams (genus *Sphaerium* Scopoli, 1777 sensu lato) are well known not only to professional malacologists. Nevertheless, this group of molluscs is still one of the most complicated for identification, as different taxonomic schools have developed incompatible approaches to its systematics.

The group traditionally designated as the subgenus *Sphaerium* s.str. is especially intricate. In the classic Westerlund's review [Westerlund, 1890], it included as many as 16 species. Odhner [1921-1929] reduced the number of valid names. Since that time specialists of the West European countries distinguished only two species: *Sphaerium corneum* (L.,1758) and *S. nitidum* (Clessin in Westerlund, 1877). But in the USSR the group was revised once again in the late 1960s [Starobogatov, Streletskaja, 1967; Alimov, Starobogatov, 1968]. As a result, some old species names were reviwed, a new species from Siberia was described, the whole group became a genus and was divided into 3 subgenera: *Sphaerium* s.str., *Nucleocyclas* Alimov et Starobogatov, 1968 (type species *Sphaerium nucleus* (Studer,1820)) and *Parasphaerium* Alimov et Starobogatov, 1968 (type species *S. rectidens* Starobogatov et Streletskaja, 1967).

Later on, some anatomical data, mainly on the breeding organs, were involved in the taxonomic discussion [Starobogatov, Korniushin, 1986]. However, they were not complete

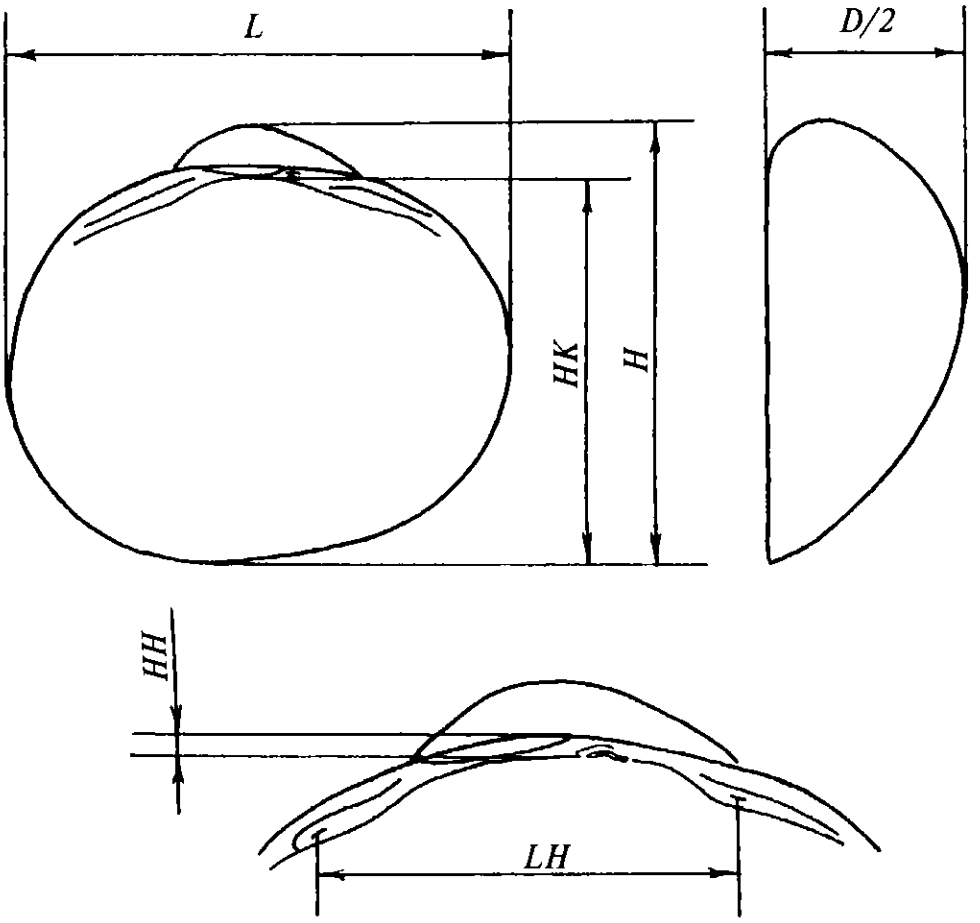

FIG. 1. Shell measurements used in morphometric investigation: L — shell length, H — shell height, D — shell thickness, HK — comissural height, HH — height of a hinge plate, LH — hinge length (distance between the cusps of lateral teeth).

РИС. 1. Промеры раковины, используемые в морфометрическом исследовании: L — длина раковины, H — высота раковины, D — выпуклость, HK — комиссуральная высота, HH — высота замочной площадки, LH — длина замка (расстояние между вершинами латеральных зубов).

and the new data on *Sphaerium* anatomy obtained recently made us to continue the revision of the group.

MATERIAL AND METHODS

This investigation is based on numerous samples collected by the author in Ukraine, Belarus, Russia and Estonia, as well as on rich collection of Zoological Institute in St.-Petersburg (ZIN), including some samples from the Westerlund's collection, and on materials presented by the colleagues. Type specimens of *Sphaerium nitidum* Clessin in Westerlund, 1877 were loaned to Dr. Y.a.I.Starobogatov by the Naturhistoriska Rijksmuseet, Stockholm (NRM).

For the species identification, so called "comparatorial" method [Shikov, Zatrawkin, 1991] was applied. Outlines of examined valves (cross sections) were compared to those of the type specimens (when available), or the specimens chosen as standard.

Further ivestigation dealt with various conchological and anatomical characters: surface sculpture, shell pores, muscle scars, hinge teeth, brood sacs and nephridia. As many as 34 samples, each including at least 5 specimens, were chosen for a detailed statistic analysis. Shell measurements were made with ocular micrometer. Altogether, 246 valves were measured, 6 parameters being registered (Fig. 1). Then, values of 5 indexes were calculated for each shell: I1 — relative height (H/L), I2 — relative thickness (D/H), I3 — relative comissural height (HK/L), I4 — relative height of the hinge plate (HH/H), I5 — relative hinge length (LH/L). All the data were subjected to the usual statistic procedure. The linear and the multiplicative models, developed earlier [Alimov, 1967], were applied to investigation of the dependence between three principal measurements (length, height and thickness). Besides that, the factor analysis was carried out, involving 11 metric parameters and indexes mentioned above. All calculations were made with the help of the CSS computer program.

Quantitative anatomical characters were studied in 266 specimens. Registration was made of number of the brood sacs and that of the embryos per sac which characterize fecundity.

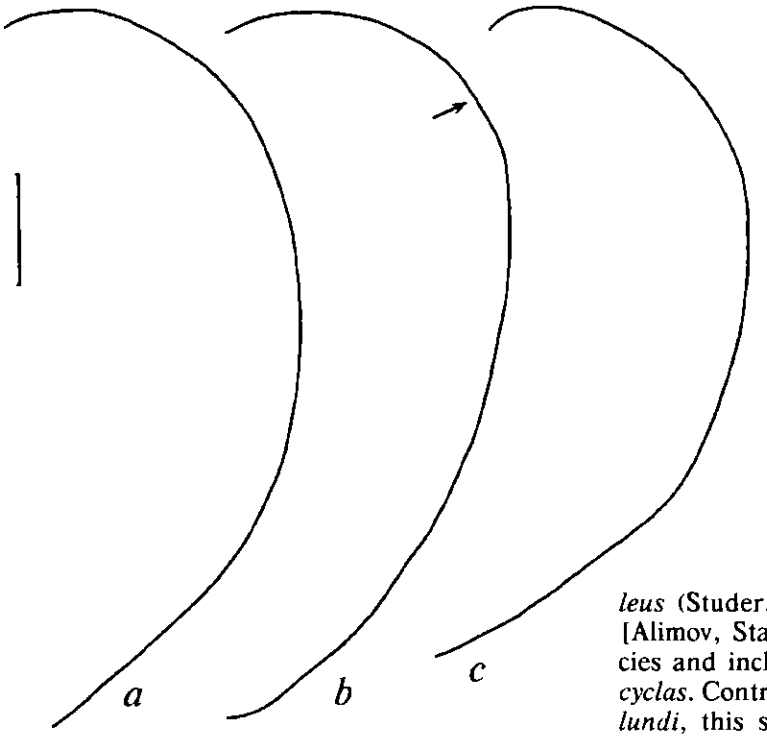

FIG. 2. Standard outlines of the cross section (frontal view) of a valve in *Sphaerium corneum* (a), *S. mamillanum* (b) and *S. westerlundi* (c). An arrow indicates the break at the margin of embryonic shell. Here and in all figures the scale bar is 1 mm

РИС. 2. Стандартные контуры фронтального сечения створки *Sphaerium corneum*, *S. mamillanum* и *S. westerlundi*. Стрелкой указан излом контура у внешнего края эмбриональной раковины. Здесь и далее масштабная линейка 1 мм.

RESULTS

Investigation of the qualitative characters and the problem of species diagnostics

Some forms traditionally synonymized with *Sphaerium corneum* (L., 1758) were recognized as valid species in the latest classification [Starobogatov, Korniushin, 1986]. Application of "comparatorial" method to the Westerlund's materials stored in ZIN visualized the differences between them and the typical *Sphaerium corneum* (Fig. 2).

The species designated in the cited paper as *Sphaerium suecicum* Westerlund, 1871 is represented by two samples with *Sphaerium mamillanum* Westerlund, 1871 and *S. mamillanum* var. *suecicum* Clessin in Westerlund, 1871 identified by C.Westerlund and labelled: "Suecia, Dalsland, Osterby". Both series share a peculiar shell character: the outer edge of embryonic portion is marked by the break in growth, clearly visible on the cross section of a valve. Outlines of all the specimens fairly fit each other. Therefore the two forms are conspecific and the older name "*mamillanum*" should be accepted as a valid one. Specimens with the same characteristic contour of the cross section were found in many samples from various localities. Westerlund's specimens of *Sphaerium westerlundi* Clessin in Westerlund, 1873 (originated from "Suecia, Ronneby") are distinguished by considerable convexity of the cross section.

No diagnostic features except the differences in the shell outlines were found for both above mentioned species. Thus, the problem of their status cannot be finally settled.

Another form of *Sphaerium*, namely *S. nucleus* (Studer, 1820), was also recognized earlier [Alimov, Starobogatov, 1968] as a "good" species and included in the new subgenus *Nucleocyclas*. Contrary to *S. mamillanum* and *S. westerlundi*, this species is distinct in many aspects. Two diagnostic features (sharply bent cardinal teeth and the high number of youngs in each sac) have been mentioned already by N.Odhner [1929]. Our data fairly confirm his observations.

Besides that, the valves of *S. nucleus* have a peculiar "silky" glitter and lack coloured concentric bands. Differences in the patterns of porosity between this species and *S. corneum* are also conspicuous. In *S. nucleus*, the density of pores is much higher and their distribution over the shell surface is more even. It was shown earlier that the pores may fulfil some respiratory function [Alekseev, 1988], and their arrangement depends on ecological factors [Adler, Fiechtner, 1992]. Really, the species with high density of pores inhabit swampy waters with low oxygen content. However, we observed the differences in patterns of porosity in the species occuring in the same water body. It means, that this character is not determined directly by local conditions and therefore has a diagnostic value.

Taxonomic significance of the muscle scar arrangement was discovered by Starobogatov and Streletskaja [1967]. The strongest pair of siphonal retractors is attached to each valve near the upper-anterior angle of the posterior adductor. Position of the scar of this retractor depends on its length [Starobogatov, Korniushin, 1986]. According to our recent observations, in *S. nucleus* the scars are clearly distinct, while in *Sphaerium corneum*, as well as in *S. mamillanum* and *S. westerlundi*, the scar of the siphonal retractor is merged with that of the adductor.

At last, the most conspicuous distinction of *Sphaerium nucleus* was revealed by the investigation of excretory organs [Korniushin, 1992]. Contrary to *Sphaerium corneum*, the dorsal lobe of nephridium is broad, and its branches tightly

adjoin each other, completely covering the coils of the pericardial duct (closed type of nephridium). This difference is no less than the difference between *S. corneum* and the small northern form identified by N.Odhner [1921] as *S. nitidum* Clessin in Westerlund, 1877 and recognized unanimously as a "good" species. Thus, *Sphaerium nucleus* (Studer, 1820) should have an equal status.

Another form of *Sphaerium*, similar to *S. nucleus*, occurs in the investigated area. It has the same silky glitter of a shell, dense pores, sharply bent inner cardinal tooth of the left valve and distinct scars of siphonal retractors. However, its shell is much larger, less convex and more elongated. The shape of nephridium is peculiar: the organ is of the open type (the coils of the pericardial duct are visible from the dorsal surface), as in the majority of fingernail clams, but the dorsal lobe is broadened as in *S. nucleus*. Identification of this form is rather complicated. Ya.I.Starobogatov [Starobogatov, Korniushin, 1986] considers it conspecific to *S. nitidum* Clessin in Westerlund, 1877. Really, cross section of its valves coincides with that of the Clessin's specimens from Dudino (Dudinka) loaned by NRM. Earlier, N.Odhner identified the same specimens as the small northern form characterized by regular ribbing in the umbonal part and extremely elongated closed nephridia [Odhner, 1921]. Thus, two different opinions concerning *S. nitidum* should be discussed.

Unfortunately, the type specimens are dry, and their anatomy cannot be studied. Some important conchological characters (pores, muscle scars, etc.), which can distinguish the above described form from other species of *Sphaerium*, were neglected earlier. But in the original description reproduced in the Westerlund's monograph [Westerlund, 1890], the bent cardinal teeth and the shell glitter were mentioned. These characters speak in favour of Starobogatov's point of view, which we accept here. However, a re-investigation of the type specimens is necessary.

The form which we call here "*Sphaerium nitidum*" is surely conspecific with *S. levinodis* var. *radiatum* Westerlund, 1897. The type specimens of the latter, kept in ZIN collection, have all characteristic conchological features mentioned above.

Some specimens of the species discussed here are transitional in conchological aspect between *S. nucleus* and *S. nitidum*. But the differences in the shape of nephridium are always clear and are recommended as the most reliable diagnostic feature.

The northern form, studied by N.Odhner, was subsequently synonymized with *Sphaerium suecicum* Clessin in Westerlund, 1871 [Alimov, Starobogatov, 1968]. This identification is surely erroneous, because Westerlund's specimens of *S. suecicum* (dried shells) mentioned above lack umbonal ribbing, which is one of the two diagnostic features mentioned by Odhner [1921]. On the other hand, the type series of *S. rectidens* Starobogatov et Streletskaja, 1967 posseses both the ribbing and the elongated nephridia. We confirmed the identity of the available European specimens with the holotype from Siberia by the comparison of contours of their valves.

Thus, fingernail clams are represented in Europe by 6 species. Among them, *Sphaerium corneum*, *S. mamillanum* and *S. westerlundi* are almost identical in all aspects except the contour of the cross section of valve and should be included in the subgenus *Sphaerium* s.str. *S. (Parasphaerium) rectidens* differs first of all in umbonal sculpture and configuration of nephridium. No other *Sphaerium* species share these peculiarities, that is why the subgenus *Parasphaerium* Alimov et Starobogatov, 1968 should be regarded now as a monotypic taxon. The third group corresponds to the subgenus *Nucleocyclas* Alimov et Starobogatov, 1968 and includes *S. nucleus* and the form designated here as *S. nitidum*. In some aspects (hinge teeth configuration and muscle scars arrangement) it is more related to the subgenus *Cyrenastrum* of the genus *Amesoda* (*Sphaerium solidum* group) than to the *Sphaerium corneum* group. *Parasphaerium* also stands nearer to *Cyrenastrum* than to *Sphaerium* in respect to surface sculpture. Taking into account also differences in nephridium configuration between *Sphaerium* s.str., *Parasphaerium* and *Nucleocyclas*, which are of generic level, we come to the conclusion, that the subgeneric groups of *Sphaerium* should be regarded as distinct genera.

The principal diagnostic characters for the three groups discussed here are shown in Fig. 3.

Analysis of the quantitative characters

Shell measurements and indexes are traditionally included into descriptions and identification keys. They are also used as an argument in the taxonomic discussion. In order to obtain reliable mean values of these parameters, we have studied individual variability of each species.

Despite the great variability of metric parameters and indexes within each population, there are some interspecific differences (Table 1 — see p. 48). Thus, *S. westerlundi* can be distinguished from *S. corneum* by higher relative thickness of the shell (mean value of I2 exceeds 0.8). The difference between *Nucleocyclas nucleus* and *N. nitidum* in this parameter is not so prominent, but as a rule it is noticeable in sympatric populations of the two species. Both *Nucleocyclas* species differ from *S. corneum* in the height of the hinge plate. The hinges of *N. nitidum* and especially of *Parasphaerium rectidens* are relatively shorter (on the average) as compared to those of *S.corneum*. However, all the differences mentioned are not statistically significant.

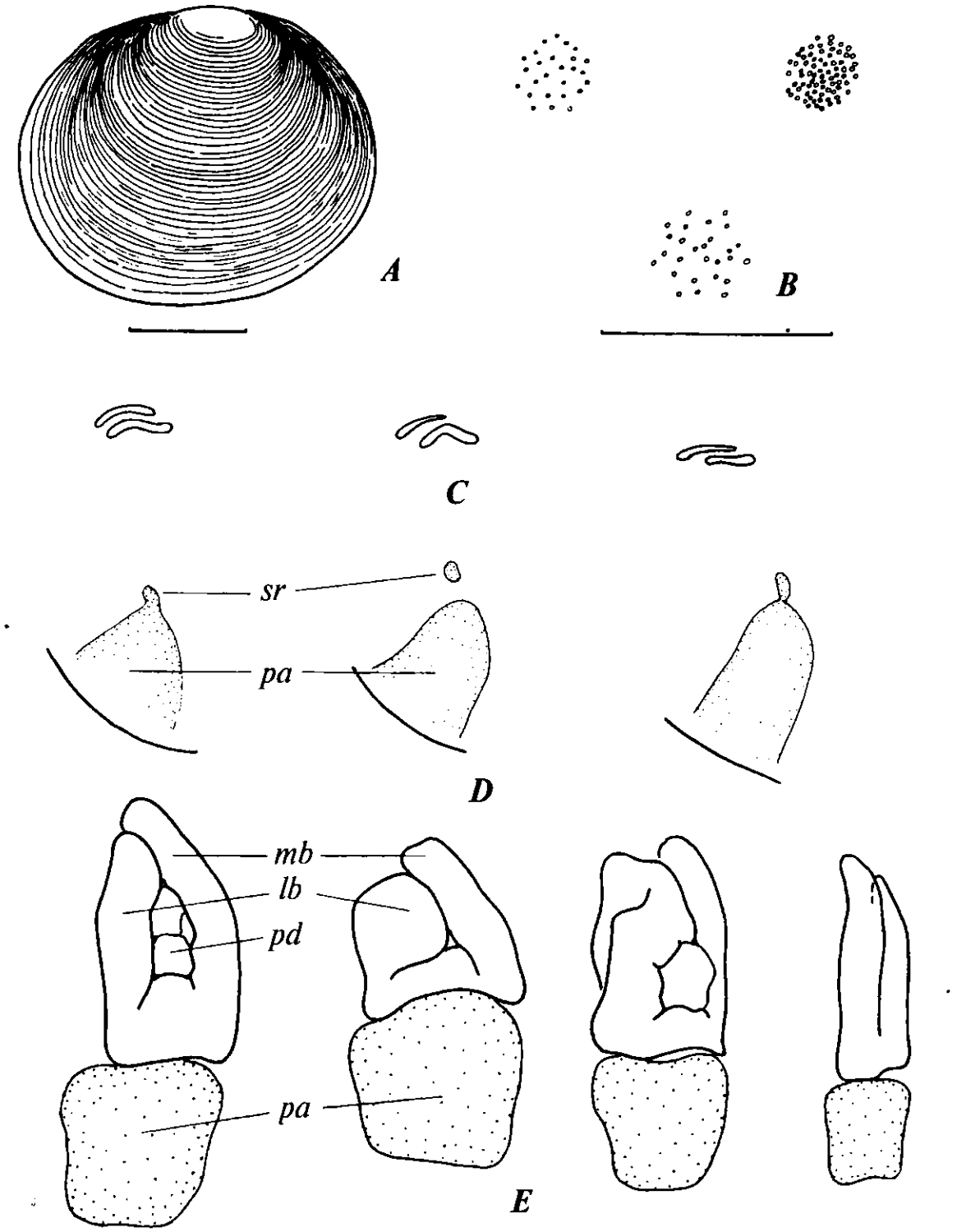

FIG. 3. Diagnostic characters of the groups distinguished within *Sphaerium* s. lato: A. Umbonal sculpture of *Parasphaerium*; B. Shell pores in *Sphaerium* s.str. (on the left), *Nucleocyclas* (on the right) and *Parasphaerium* (below); C. Cardinal teeth in the left valve of *Sphaerium* s.str. (on the left), *Nucleocyclas* (in the centre) and *Parasphaerium* (on the right); D. Arrangement of the posterior adductor (pa) and siphonal retractor (sr) scars on the inner valve surface, in the same order; E. Dorsal view of nephridium (from left to right): *Sphaerium* spp., *Nucleocyclas nucleus*, *N. nitidum* and *Parasphaerium rectidens*, mb — medial branch of the dorsal lobe, lb — lateral branch, pd — pericardial duct.

РИС. 3. Диагностические признаки таксонов, выделяемых в пределах *Sphaerium* s. lato: А. Макушечная скульптура *Parasphaerium*; В. Поры раковины *Sphaerium* s.str. (слева), *Nucleocyclas* (справа) и *Parasphaerium* (внизу); 5. Кардинальные зубы левой створки *Sphaerium* s.str. (слева), *Nucleocyclas* (в центре) и *Parasphaerium* (справа); 6. Расположение отпечатков аддуктора (pa) и сифонального ретрактора (sr) на внутренней поверхности створки (в том же порядке); 7. Вид нефридия с дорсальной стороны (слева направо): *Sphaerium* spp., *Nucleocyclas nucleus*, *N. nitidum* и *Parasphaerium rectidens*, mb — медиальная ветвь дорсальной лопасти, lb — латеральная ветвь, pd — перикардиальный проток.

Table 1. Mean values and variation limits (in brackets) of shell indexes in the investigated species.

Таблица 1. Средние значения и пределы изменчивости (в скобках) индексов у исследованых видов.

Species	n	Indexes				
		H/L	D/H	HK/L	HH/H	HL/L
Sphaerium corneum	87	0.83±0.020 (0.77-0.87)	0.76±0.070 (0.57-0.90)	0.77±0.020 (0.68-0.82)	0.032±0.006 (0.019-0.047)	0.57±0.030 (0.49-0.63)
S. mamillanum	34	0.84±0.020 (0.79-0.88)	0.80±0.050 (0.71-0.89)	0.78±0.020 (0.71-0.82)	0.032±0.008 (0.014-0.061)	0.58±0.020 (0.45-0.63)
S. westerlundi	19	0.83±0.019 (0.80-0.87)	0.84±0.065 (0.65-0.92)	0.77±0.018 (0.74-0.82)	0.032±0.005 (0.020-0.041)	0.56±0.024 (0.49-0.60)
Nucleocyclas nitidum	50	0.83±0.030 (0.72-0.87)	0.73±0.110 (0.56-0.94)	0.78±0.020 (0.73-0.81)	0.042±0.007 (0.026-0.055)	0.54±0.020 (0.49-0.58)
N.nucleus	47	0.84±0.020 (0.78-0.88)	0.76±0.110 (0.53-0.97)	0.78±0.020 (0.73-0.92)	0.043±0.007 (0.033-0.059)	0.58±0.030 (0.48-0.63)
Parasphaerium rectidens	19	0.84±0.010 (0.81-0.87)	0.75±0.090 (0.59-0.89)	0.79±0.020 (0.76-0.83)	0.029±0.005 (0.018-0.038)	0.52±0.032 (0.44-0.57)

Table 2. Parameters of relationship between shell thickness (D) and shell height (H): D=a×Hb, calculated for local samples (1, min-max) and for pooled data (2)

Таблица 2. Параметры зависимости между выпуклостью и высотой раковины: D=a×Hb, вычисленные для отдельных проб (1, min-max) и всей видовой выборки (2)

Species	Log.corr. (r)	Parameter a		Parameter b	
		1	2	1	2
Sphaerium corneum	0.972	0.29-0.47	0.42	1.25-1.50	1.30
S. mamillanum	0.982	0.63-0.79	0.64	1.03-1.12	1.12
S. westerlundi	0.935	—	0.69	—	1.12
Nucleocyclas nucleus	0.957	0.18-0.26	0.30	1.57-1.79	1.53
N. nitidum	0.982	0.21-0.34	0.28	1.37-1.65	1.50
Parasphaerium rectidens	0.978	—	0.45	—	1.37

The great variability of the shell indexes can be partly explained by nonlinearity of the dependence between the metric parameters. All the shell ratios depend to a certain extent upon the age of specimens. The most strict correlation was found between the relative shell breadth (I2) and the height of a shell (H): *r* value exceeds 0.7 in all species. In some samples, low (0.4-0.6) but significant values of the correlation coefficient were obtained for other indexes. Generally, in the course of growth the shells become more elongated and convex, and the relative height and length of the hinge decrease. A.F.Alimov [1967] proposed an allometric (multiplicative) function as an adequate description of the shell growth. According to our data, each species can be characterized by peculiar values of parameters (the slope and the intercept) of logD-logH regression (Table 2). However, the differences between populations of one and the same species are also great.

Application of the factor analysis allows to describe the morphometric variation by 5 factors (Table 3). The first factor has the largest loadings on the shell measurements and on the index of convexity (I2). The factor value steadily increases in the course of ontogenesis and can be regarded as a generalized measure of the shell growth. The second factor has the largest loadings on the indexes of the shell elongation (I1 and I3). The third one is associated with the absolute and relative height of the hinge plate (HH and I4 respectively). The fourth factor is also a hinge characteristic, having the most conspicuous loading on the index of hinge length. At last, the fifth one appears to be the factor of convexity, it is closely associated with relative shell thickness (I2) and determines the component of its variation, indifferent to the absolute shell dimensions.

The last two factors ensure the best species discrimination, if the mean values for each sample are plotted (Fig. 4). But if the individual variation of the factor values is taken into account, then the areas, covered on the diagram by each species, overlap. Thus, the factor analysis fails to reveal interspecific gaps in the metric characters of the shell. This means that no such a character nor a combination of characters can be used as a good diagnostic feature for the species identification.

We have studied 2 characteristics of fecundity proposed earlier [Starobogatov, Korniushin, 1986] for diagnostics of species and subgenera: the number of ovisacs in each demibranch and the number of youngs per ovisac. The first one has no taxonomic value within the investigated group, since in all the species an equal number of sacs

Table 3. Normalized factor loadings (normalized varimax rotation) for 5 principal factors computed from R matrix of metric shell characters.

Таблица 3. Нормализованные факторные нагрузки 5 главных факторов, вычисленные по корреляционной матрице для метрических признаков раковины.

Character	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4	FACTOR 5
L	.980626	-.120530	.012475	-.005914	.134021
H	.986823	-.020133	.021139	.002077	.141633
D	.902432	-.007352	-.019282	-.013407	.415441
HK	.990646	-.036351	.016144	.008293	.126278
HH	.625510	.034512	.763188	.000686	.046431
LH	.962724	-.095747	.006950	.200343	.131718
I1	-.025860	.995506	.030681	.060032	.061249
I2	.389141	.032791	-.086244	.020434	.915500
I3	-.227199	.719278	-.016686	.071198	-.098663
I4	-.180188	.009520	.976487	.016749	-.100005
I5	.072430	.080466	.014992	.993646	.014522

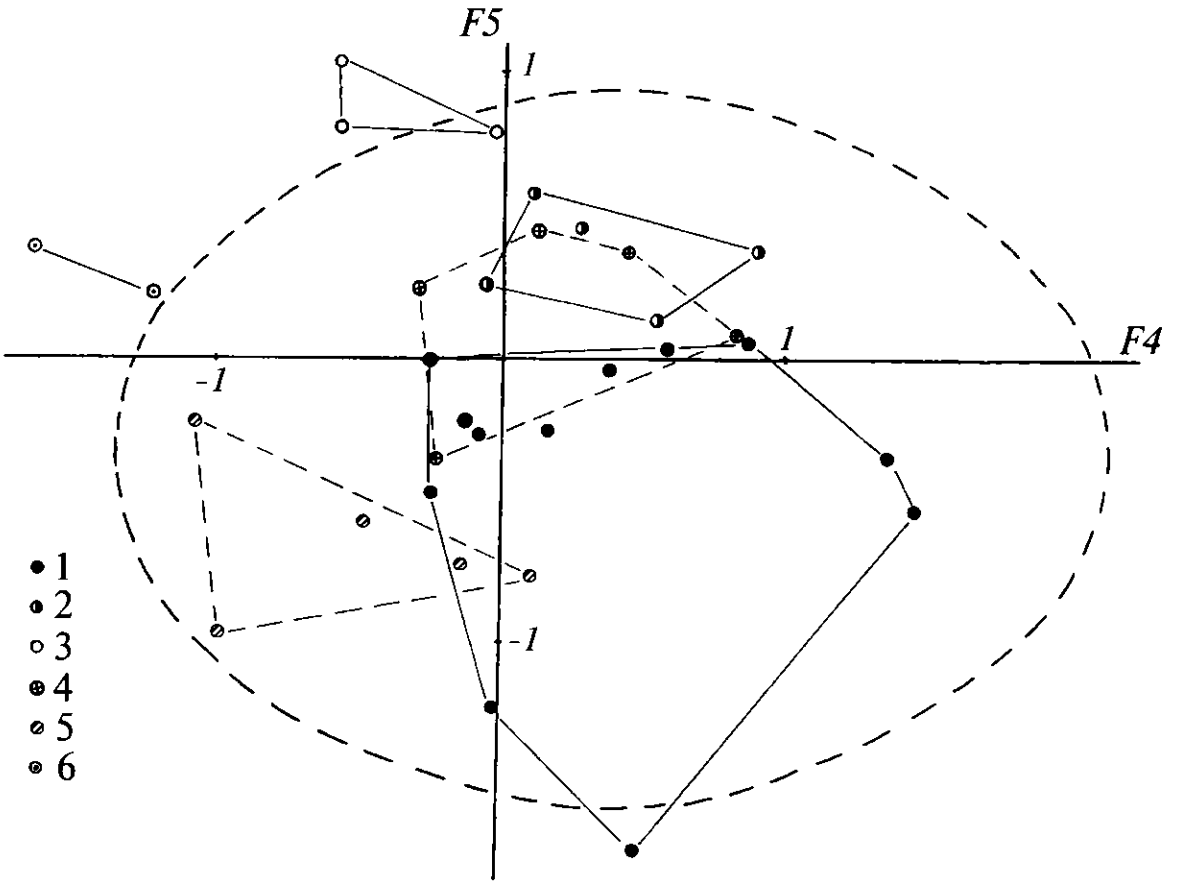

FIG. 4. Individual and inter-populational variation of factors 4 (horizontal axis) and 5 (vertical axis) in the investigated species. Mean values for samples: 1 — *Sphaerium corneum*, 2 — *S. mamillanum*, 3 — *S. westerlundi*, 4 — *Nucleocyclas nucleus*, 5 — *N. nitidum*, 6 — *Parasphaerium rectidens*. An ellipse shows the range of individual variation in *S. corneum* — it includes all values whose deviation from the average does not exceed doubled standard deviation.

РИС. 4. Индивидуальная и популяционная изменчивость факторов 4 и 5 у исследованных видов. Средние значения для выборок: 1 — *Sphaerium corneum*, 2 — *S. mamillanum*, 3 — *S. westerlundi*, 4 — *Nucleocyclas nucleus*, 5 — *N. nitidum*, 6 — *Parasphaerium rectidens*. Эллипс показывает размах индивидуальной изменчивости у *S. corneum*, он включает все значения, отклоняющиеся от среднего не более чем на две величины стандартного отклонения.

(usually 3 to 5, sometimes up to 7) can be observed in each demibranch. This character depends on the dimensions of the mother, the stage of the life cycle and the season [Beriozkina, 1991]. The influence of local conditions is less significant.

The number of embryos per ovisac is a highly variable character (Table 4, see Fig. 5 for loca-

lization of samples). The differences between conspecific populations, inhabiting different habitats or geographical regions, appears to be more significant than it was supposed earlier [Starobogatov, Korniushin, 1986]. All species, except *Sphaerium westerlundi* and *Parasphaerium rectidens*, demonstrate common trends of variation. Northwards, the mean number of youngs decreases while their relative dimensions increase. This rule can be explained by climatic factors. The minimum fecundity is registered in some lakes: Onega (Fig. 5, *5*) in Russia, Chudskoye (Fig. 5, *7*) in Russia and Estonia, Naroch (Fig. 5, *10*) in Belarus. For the last two lakes, the constancy of fecundity characteristics is confirmed by the comparison of samples taken with an interval of more than 20 years (Table 4). For *Sphaerium mamillanum*, we demonstrate the decrease of fecundity in the lake Naroch with respect to the overgrown channels and ditches situated nearby (Table 4). However, in the Shatsk lake district (Ukraine) (Fig. 5, *14*) such a phenomenon does not take place.

Limits of variation for *Sphaerium corneum* and *S. mamillanum*, as well as for *Nucleocyclas nitidum* and *N. nucleus* almost coincide. On the contrary, intergeneric differences are evident, despite the geographic variation described. In *Nucleocyclas*, the mean number of youngs exceeds 2.5 in almost all sampled populations, while in *Sphaerium* such values are registered only in the most southern samples. When species of the two genera inhabit the same locality, the differences in fecundity are, as a rule, statistically significant (Table 4).

The quantitative analysis presented here demonstrates some differences between the taxa studied. It is necessary to mention, however, that these differences can be revealed only in the comparison of large samples, and a particular specimen cannot be reliably identified by its shell parameters or number of youngs in brood sacs. Thus, the diagnostic value of the quantitative characters is restricted.

Table 4. Number of embryos (per sac) in different populations of investigated species.

Таблица 4. Число эмбрионов (в пересчете на 1 сумку) в различных популяциях исследованных видов.

Locality	Habitat	Number of specimens	Number of examined sacs	Number of embryos: range of variation	mean value	standard deviation
Sphaerium corneum						
4	lake	6	16	1-5	2.4	0.43
6	ditch	9	44	1-4	2.0	0.12
9	lake	8	24	1-4	1.6	0.18
11	river	9	17	1-6	2.1	0.17
14	lake	9	30	1-5	2.3	0.17
14	ditch	7	27	1-5	2.2	0.19
15	pond	6	14	1-5	3.3	0.35
18	pond	8	20	1-6	2.8	0.28
20	pond	3	9	1-5	2.6	0.50
22	river	7	23	2-5	2.8	0.17
Sphaerium mamillanum						
5	lake	7	24	1-2	1.0	0.04
7 (1910)	lake	5	10	1-3	1.6	0.16
7 (1983)	lake	4	10	1-2	1.3	0.15
8	river	5	25	1-3	1.4	0.12
10 (1968)	lake	5	10	1-2	1.1	0.10
10 (1991)	lake	5	18	1-3	1.3	0.14
10 (1991)	channel	7	17	1-4	1.9	0.25
12	lake	5	15	1-4	1.7	0.25
17	pond	13	36	1-6	2.5	0.21
20	pond	5	14	2-4	2.6	0.19
Sphaerium westerlundi						
4	lake	5	7	2-3	2.4	0.20
Nucleocyclas nucleus						
5	lake	7	14	1-4	2.6	0.23
10	stream	3	7	2-8	4.5	0.72
11	bog	10	17	1-5	2.8	0.35
16	river	6	8	2-5	2.9	0.35
19	wet meadow	4	9	1-7	3.2	0.55
Nucleocyclas nitidum						
10	lake	7	16	1-4	2.8	0.21
10	stream	6	13	1-4	2.9	0.29
13	pond	10	13	1-4	2.3	0.41
16	river	10	22	1-5	3.1	0.30
21	river	12	24	2-7	4.7	0.29
Parasphaerium rectidens						
1	lake	3	9	1-4	2.3	0.33
2	lake	7	17	1-3	2.0	0.19
3 (1969)	lake	9	17	1-2	1.2	0.11
3 (1990)	lake	4	8	1-3	1.5	0.33

Diagnoses of the taxa

Genus *Sphaerium* Scopoli, 1777

Shell broad-oval, in some species almost spherical, with rounded outline, tumid, thin-walled, smooth or irregularly striated, usually with clear lines of growth breaks. Embryonic shell smooth. The maximum convexity is in the upper portion of a valve (cross section heart-shaped). Umbones broad, prominent. Shell colour extremely variable: usually several concentric bands or zones of contrast colours (yellowish to dark grey or brown) are present. Shell pores concentrated in the umbonal part, where their density is relatively high; near the external margin the pores are scarce. The scar of the upper siphonal retractor merged with posterior adductor scar.

Hinge plate narrow, especially in its mid-portion (under the umbones). In the left valve, the cardinal teeth are of almost equal length, situated parallel to each other, slightly bent, inner tooth often double bent (S-shaped). In the right valve,

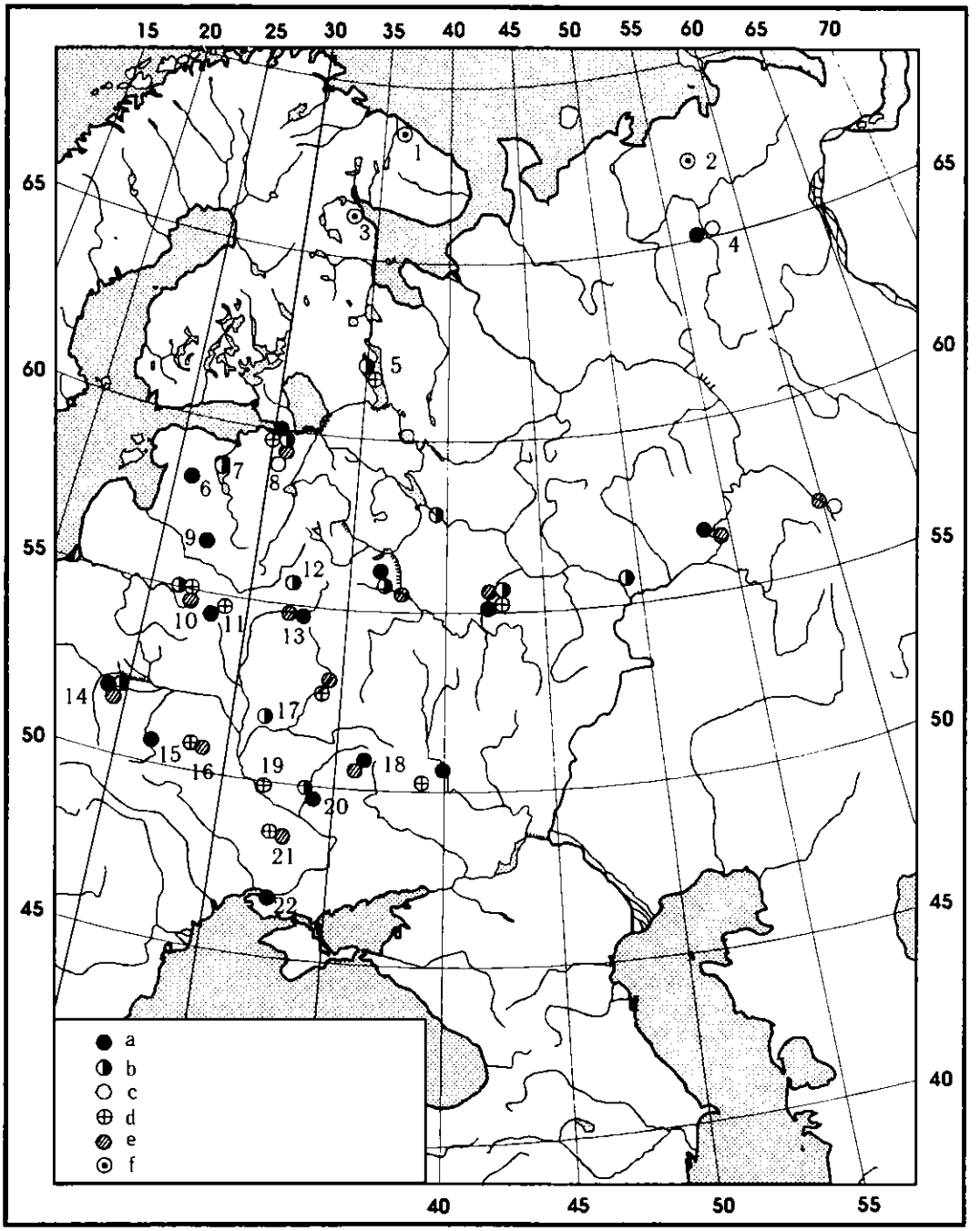

FIG. 5. Records of *Sphaerium corneum* (a), *S. mamillanum* (b), *S. westerlundi* (c), *Nucleocyclas nucleus* (d), *N. nitidum* (e) and *Parasphaerium rectidens* (f). Numbered are the large samples studied anatomically and represented in Table 4.

РИС. 5. Местонахождения *Sphaerium corneum* (a), *S. mamillanum* (b), *S. westerlundi* (c), *Nucleocyclas nucleus* (d), *N. nitidum* (e) и *Parasphaerium rectidens* (f). Пронумерованы выборки, изученные анатомически и представленные в табл. 4.

the cardinal tooth in fine, bent, its posterior arm being slightly cleft. Ligament relatively long.

Nephridia of the open type (pericardial duct visible on the dorsal surface), dorsal lobe elongated (length twice as much as breadth), its medial branch being longer than lateral one.

TYPE SPECIES — *Telina cornea* L., 1758 (by monotypy).

Sphaerium corneum (L., 1758)

Fig.6.

Linné, 1758, p.678 (*Tellina*); Westerlund, 1890, p.8; Shadin, 1952, p.321 (part), Stadnichenko, 1984, p.194 (part.)

—*mamillanum var.tomentosum* Westerlund,1871,p.154, 1890, p.13;

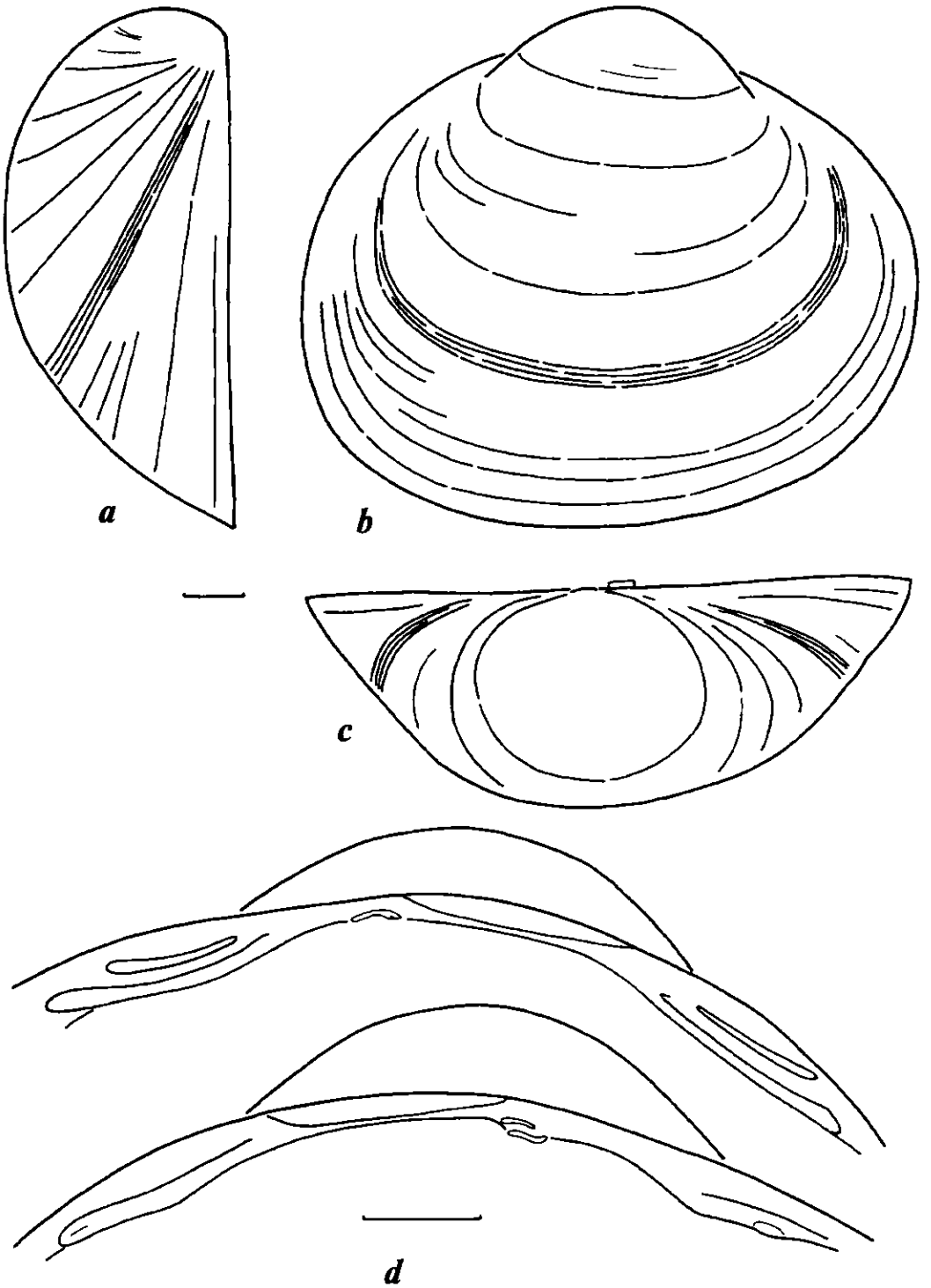

FIG. 6. *Sphaerium corneum* (L.), river Vorskla in Belgorod Region, Russia: frontal (a), lateral (b) and dorsal (c) view of a valve, and hinge (d). Collection of the author.

РИС. 6. *S. corneum* (L.), р. Ворскла в Белгородской обл. (Россия): створка спереди (a), сбоку (b) и сверху (c), замок (d). Коллекция автора.

TYPE LOCALITY: Sweden?

Shell large, broad-oval: length up to 12.4 mm, height up to 9.5 mm, thickness (of two valves) up to 8.4 mm. Average relative shell height (H/L) varies in different populations from 0.80 to 0.85. The largest specimens may be more elongated (H/L=0.77-0.80). Shell moderately convex: average relative thickness (D/H) 0.67 to 0.80. The contour of the cross section smooth, without marks of break in growth.

Mean number of embryos per ovisac, evaluated for different populations, varies from 2.0 to 3.3.

The species is distributed throughout Europe (Fig. 5). Its occurence in other regions is doubtful (in the latest Russian publications the Asian forms of *Sphaerium* are regarded as distinct species).

Most frequent and abundant in small lakes and ponds. Occurs also in large lakes and rivers with quiet flow. Prefers habitats with dense vegetation.

Sphaerium mamillanum Westerlund, 1871

Fig. 7

Westerlund, 1871, p.154, 1890, p.13;
— *mamillanum var.suecicum* Clessin in Westerlund, 1871, p. 154, 1890,p.13
— *corneum f.westerlundi* Shadin, 1952, p. 321 (part.)
— *suecicum* Starobogatov et Korniushin, 1986, p. 36(part.).

TYPE LOCALITY: Sweden, Osterby.

Shell large, rounded: length up to 11.0, height up to 9.4, thickness up to 8.0 mm. Average relative height 0.83 to 0.85. Contour of the cross section with distinctly marked embryonic portion. Average relative thickness 0.76 to 0.83.

Offspring usually scarce, in samples from large lakes it numbers 1.0 to 1.7 per sac (on the average). In specimens from small ponds offspring is more numerous: 2.5 embryos per sac, on the average.

Distributed throughout Europe. According to Westerlund [1890], occurs in Russia, Scandinavian countries and Germany. Our records are shown in Fig. 5.

It is ecologically similar to *S. corneum* but, more frequent in large lakes. Occurs also in ponds, small rivers and running-water ditches. Also associated with vegetation.

Sphaerium westerlundi Clessin in Westerlund, 1873

Fig. 8

Westerlund, 1873, p. 508, 1890, p. 13.
— *corneum* f. *westerlundi* Shadin, 1952, p. 321 (part.)

TYPE LOCALITY: Sweden, Ronneby.

Shell of medium size, spherical: length up to 9.6, height up to 7.7, thickess up to 6.6 mm. Dimensions of Westerlund's specimens in ZIN collection: 8.6×7.3×3.3; 8.0×6.8×3.1 mm. Average relative height 0.83. Average relative thickness 0.82 to 0.84 (in Westerlund's specimens relative thickness up to 0.91). Contour of the cross section with several marks caused by breaks in growth.

Mean number of embryos per sac 2.4 (only one population sampled).

Distributed in the northern Palearctic [Starobogatov, Korniushin, 1986]. In Europe known from Sweden [Westerlund, 1890; materials of ZIN collection] and northern Russia (Fig. 5). Records from the more southern territories (central Russia, etc.), published earlier, should be referred to other *Sphaerium* species, mainly to *S. mamillanum*.

Ecological preference is the same as in *S. mamillanum*.

Genus *Parasphaerium* Alimov et Starobogatov 1968

Shell spherical or broad-oval, moderately convex, smooth, or with lines of periodic growth breaks, thin-walled. Outline with clear angles at the anterior and posterior ends of the dorsal margin. Embryonic shell with regular thin ribs. The maximal convexity of a shell is in its middle portion. Umbones comparatively narrow, prominent. There are concentric bands of contrast colours. The scar of upper siphonal retractor is connected with the posterior adductor scar. Porosity as in the nominotypical subgenus.

Hinge plate very narrow. Hinge short. Cardinal teeth reduced, almost straight in the left valve and slightly bent in the right one. The right cardinal not cleft. Ligament short.

Nephridium of the closed type, its dorsal lobe being extremely elongated (the length more than 3 times as much as the breadth). Lateral portion of the dorsal lobe longer than medial one.

TYPE SPECIES: *Sphaerium rectidens* Starobogatov et Streletskaja, 1967 (original designation).

Parasphaerium rectidens Starobogatov et Streletskaja, 1967

Fig. 9

Starobogatov, Streletskaja, 1967, p. fig. (*Sphaerium*)
—*nitidum* Odhner, 1921, p. 124 (*Sphaerium*); Shadin, 1952, p. 322 (*Sphaerium*) (part.)
—*suecicum* Starobogatov, Korniushin, 1986, p.36 (*Sphaerium*) (part.).

TYPE LOCALITY: Lower Kolyma basin, Sakha (Yakutia) Republic, Russia.

Shell small, almost spherical: length up to 7.3, height up to 6.3, thickness up to 5.6 mm. Average relative height 0.84 to 0.85, relative thickness 0.75 to 0.76. Breaks in growth usually marked, but the embryonic shell not distinct.

The mean number of youngs is 1.5 to 2.3 per sac.

Distributed in the northern Palearctic. In Europe recorded in Scandinavian countries (as *Sphaerium nitidum*) [Odhner, 1921; Kuiper et al., 1989], Kola peninsula and Komi Republic (Fig. 5).

Inhabits small lakes.

Genus *Nucleocyclas* Alimov et Starobogatov, 1968

Shell spherical or broad-oval, sometimes elongated, comparatively thick-walled, smooth, with a peculiar silky glitter. Outline without angles.

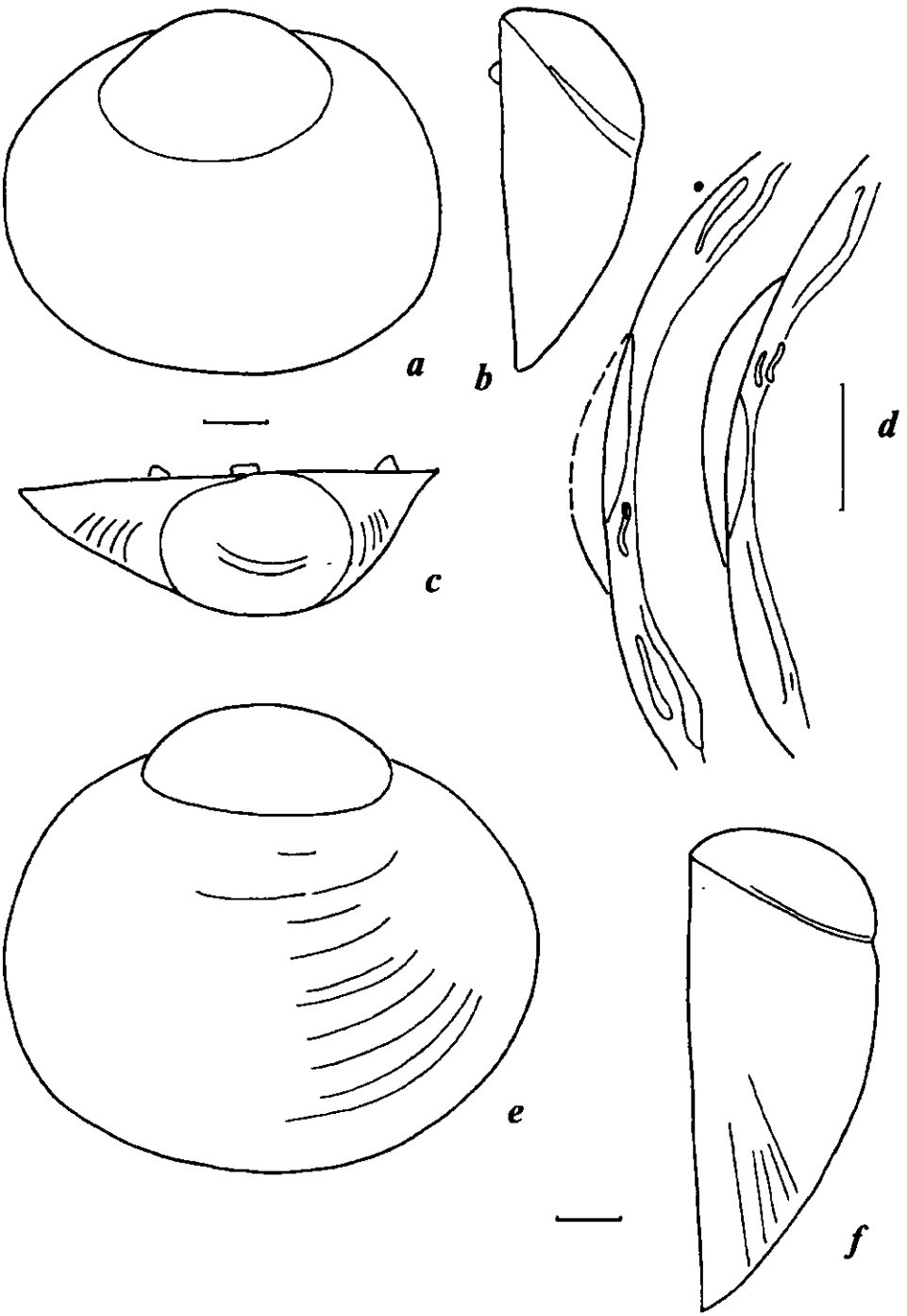

FIG. 7. *Sphaerium mamillanum* Westerlund, 1871: a-d — specimen of the original Westerlund's series from Osterby, Sweden labelled as *S. mamillanum* (ZIN); e-f — specimen from the same locality labelled as *S. mamillanum* var. *suecicum*.

РИС. 7. *Sphaerium mamillanum* Westerlund,1871: a-d — экз. Вестерлунда из Швеции, обозначенный как типичная форма *S. mamillanum* (ЗИН); e-f — экз. из той же местности, обозначенный как *S. mamillanum* var. *suecicum*.

The maximal convexity of a shell is in its mid-portion. Umbones more or less broad, not prominent. The shell is yellow, grey or brown, usually without contrast bands. The whole shell surface densely covered with pores. The scar of the upper siphonal retractor is separated from that of the posterior adductor.

Hinge plate comparatively broad. Inner cardinal tooth of the left valve sharply bent (hook-like), outer one situated obliquely above and behind it, stretching only to its mid-point. Cardinal tooth of the right valve also bent, its posterior arm bifurcated. Ligament comparatively long. Nephridia of the closed or open type. Dorsal lobe always broad (the length is equal to the breadth), especially its lateral branch.

TYPE SPECIES: *Cyclas nucleus* Studer, 1820 (original designation).

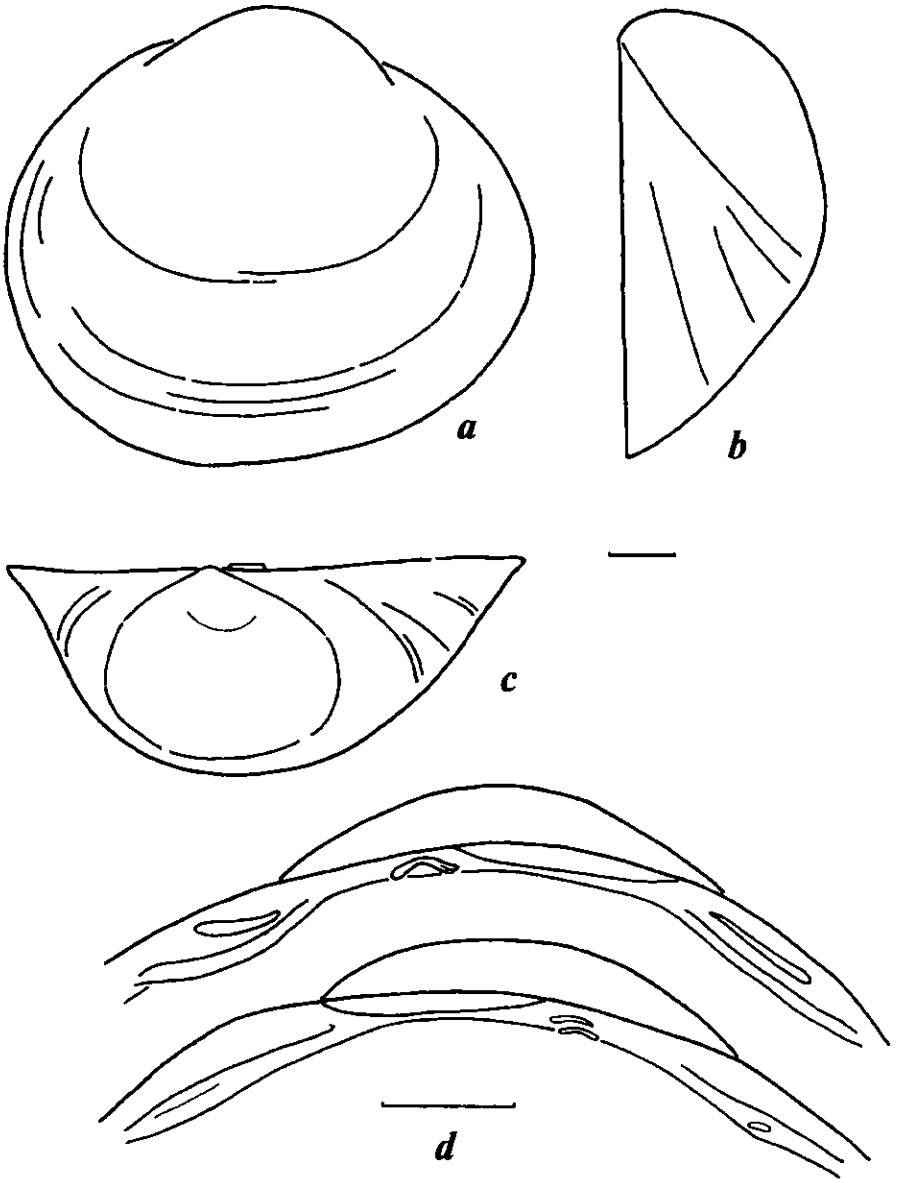

FIG. 8. *Sphaerium westerlundi* Clessin in Westerlund, 1873, specimen of the original Westerlund's series, Ronneby, Sweden (ZIN). Lettering the same as in the Fig. 6.

РИС. 8. *Sphaerium westerlundi* Clessin in Westerlund, 1873, экз. Вестерлунда из Швеции (ЗИН). Обозначения те же, что на рис. 6.

Nucleocyclas nucleus (Studer, 1820)

Fig. 10

Studer, 1820, p. 93 *(Cyclas)*
— *corneum var.nucleus* Westerlund, 1890, p.9 (*Sphaerium*)
— *nucleus* Stadnichenko, 1984, p.200 (*Sphaerium*)

TYPE LOCALITY: Germany?

Shell comparatively small, from broad-oval to spherical: length up to 9.1, height up to 7.6, thickness up to 7.0 mm. Average relative hight 0.82 to 0.86, relative thickness 0.72 to 0.88. Umbones relatively narrow.

Nephridium of the closed type.

Mean number of youngs 2.6 to 4.6 per sac.

Distributed throughout Europe. In addition to the localities shown in Fig.5, a sample from Germany (Bavaria, Dinkelscherben) identified by S.Clessin should be mentioned (ZIN collection).

Most frequent in swamps, where inhabits bogs, small streams and ditches. Also occurs in wet meadows.

Remark. Discrimination between this species and *Sphaerium corneum* based on the shell convexity (as practicized earlier) is not reliable. Investigation of pores, muscle scars and nephridia is recommended for better identification.

Nucleocyclas nitidum (Clessin in Wersterlund, 1877)

Fig. 11

Westerlund 1877, p. 66, 1890, p. 13 (*Sphaerium*); Shadin, 1952, p. 322 (part.) (*Sphaerium*); Stadnichenko, 1984, p. 204 (*Sphaerium*)
— *radiatum* Starobogatov, Streletskaja, 1967, p. 243 (*Sphaerium*)

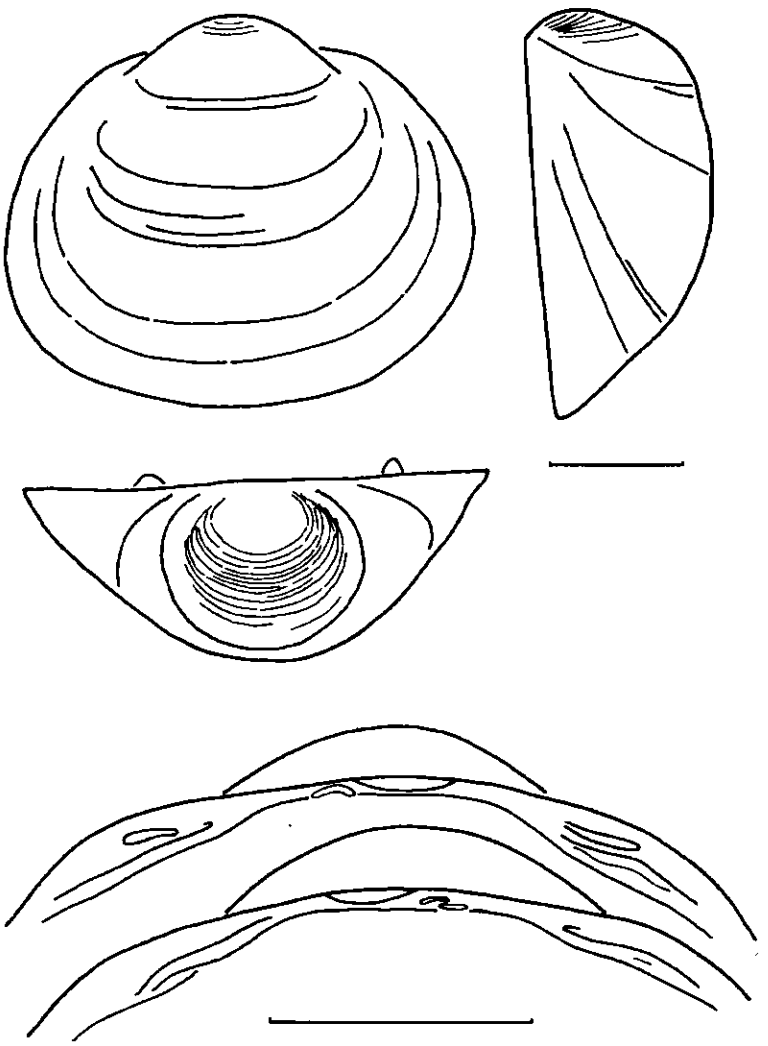

FIG. 9. *Parasphaerium rectidens* (Starobogatov et Streletskaja, 1967), northern Karelia, collected by A.F.Alimov (ZIN).

РИС. 9. *Parasphaerium rectidens* (Starobogatov et Streletskaja, 1967), северная Карелия, сбор А.Ф.Алимова (ЗИН).

TYPE LOCALITY: Dudino (Dudinka), Yenisey River, Russia.

Shell large, oval: length up to 14.3, height up to 11.7, thickness up to 11 mm. Average relative height (in different populations) 0.81 to 0.85. Large specimens often elongated (relative height 0.72), young shells rounded (relative height up to 0.87). Cross section convex, but with flat umbonal portion. Average relative thickness 0.68 to 0.82.

Offspring numerous, on the average 2.3 to 4.7 youngs per sac.

Distributed, presumably, all over the Palearctic region. Originally described from Siberia, Yenisey river. Localities of samples, identified or checked up in the course of the present investigation, are shown in Fig 5. Samples from Pontarlier (France) and Przemysl (Poland, identified by C.Wesrterlund as *Sphaerium ulicnyi*) should be added to them. Data of Western authors [Odhner, 1921; Kuiper et al., 1989] concerning *Sphaerium nitidum* refer to *Parasphaerium rectidens*.

Intermediate in ecology between *Sphaerium* species and *Nucleocyclas nucleus*. Inhabits lakes of different types, including swampy, as well as rivers with quiet flow. Rare, but in some localities is abundant.

REMARKS. *Nucleocyclas nitidum* can be distinguished from *N. nucleus* by the larger shell size and relatively short hinge (low values of HL/L index). Young specimens are less convex than in *N. nucleus*. However, identification on the purely conchlogical basis is not reliable, and only investigation of nephridia makes it possible to discriminate between the two species of *Nucleocyclas*.

DISCUSSION

Considerations on the phylogeny of fingernail clams

Concluding our investigation on *Sphaerium* species, we present a short review of phylogenetic

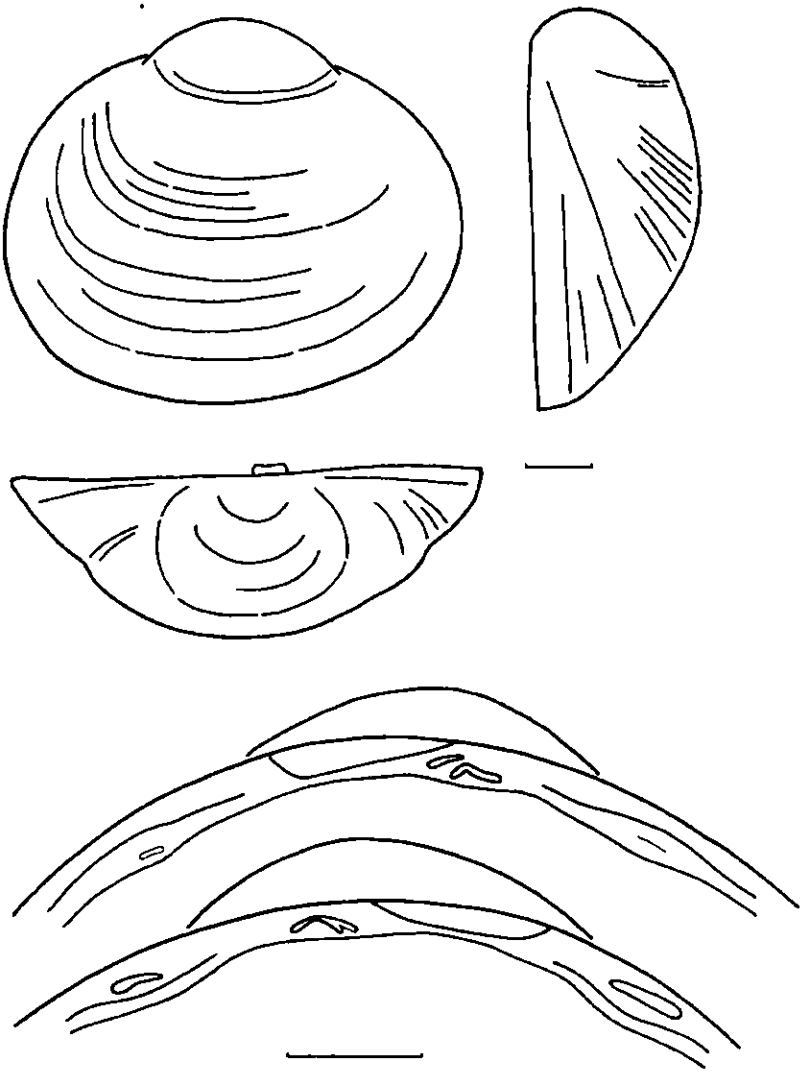

FIG. 10. *Nucleocyclas nucleus* (Studer, 1820), Dinkelscherben, Bavaria, collected and identified by S.Clessin (ZIN).

РИС. 10. *Nucleocyclas nucleus* (Studer, 1820), Бавария, сбор и определение С.Клессина (ЗИН).

relationships in the whole group of fingernail clams. The principal problem lies in distinguishing apomorphic and plesiomorphic conditions of characters. It is difficult to give now a final decision for all characters studied, but some suppositions can be put forward.

Freshwater fingernail clams evidently originated from a certain marine or brackish-water group, presumably of the suborder Astartoidei [Starobogatov, 1992]. Therefore, the shell of most primitive sphaeriids should be similar to the shell of marine bivalves. In all probability, it was comparatively large, thick-walled, with ribbed surface, strong and sharply bent cardinal teeth and an extraverted ligament. Among Recent fingernail clams, the genus *Rivicoliana* Servain, 1888 (*Sphaerium rivicola* group) best of all corresponds to this description, with only exeption of the lack of ribs. *Cyrenastrum* (*Sphaerium solidum* group) also has many plesiomorphic shell characters including the ribbing, but the ligament is of more advanced (enclosed) type. The ribbing of the umbonal, embryonic part of shell peculiar for *Parasphaerium rectidens* is presumably a rudiment of strong sculpture of an *Amesoda*-like ancestor [Odhner, 1926] and thus is a plesiomorphic character.

Shells of *Sphaerium* s.str. and *Musculium* demonstrate signs of profound specialization: diminution of calcification and reduction of surface sculpture and hinge teeth. It is necessary to mention that at least in one species with *Musculium*-like shell, namely in *Sphaerinova transversa* (Say, 1829), the ligament is extraverted. This means that the group including *Sphaerinova* and *Musculium* is rather ancient and the reduction of its shell and hinge is independent from the reduction taking place in *Sphaerium*.

Primitive shell characters are associated with strong siphonal musculature, especially upper retractors of the branchial siphon. If the latters are long enough, their scars are clearly separated

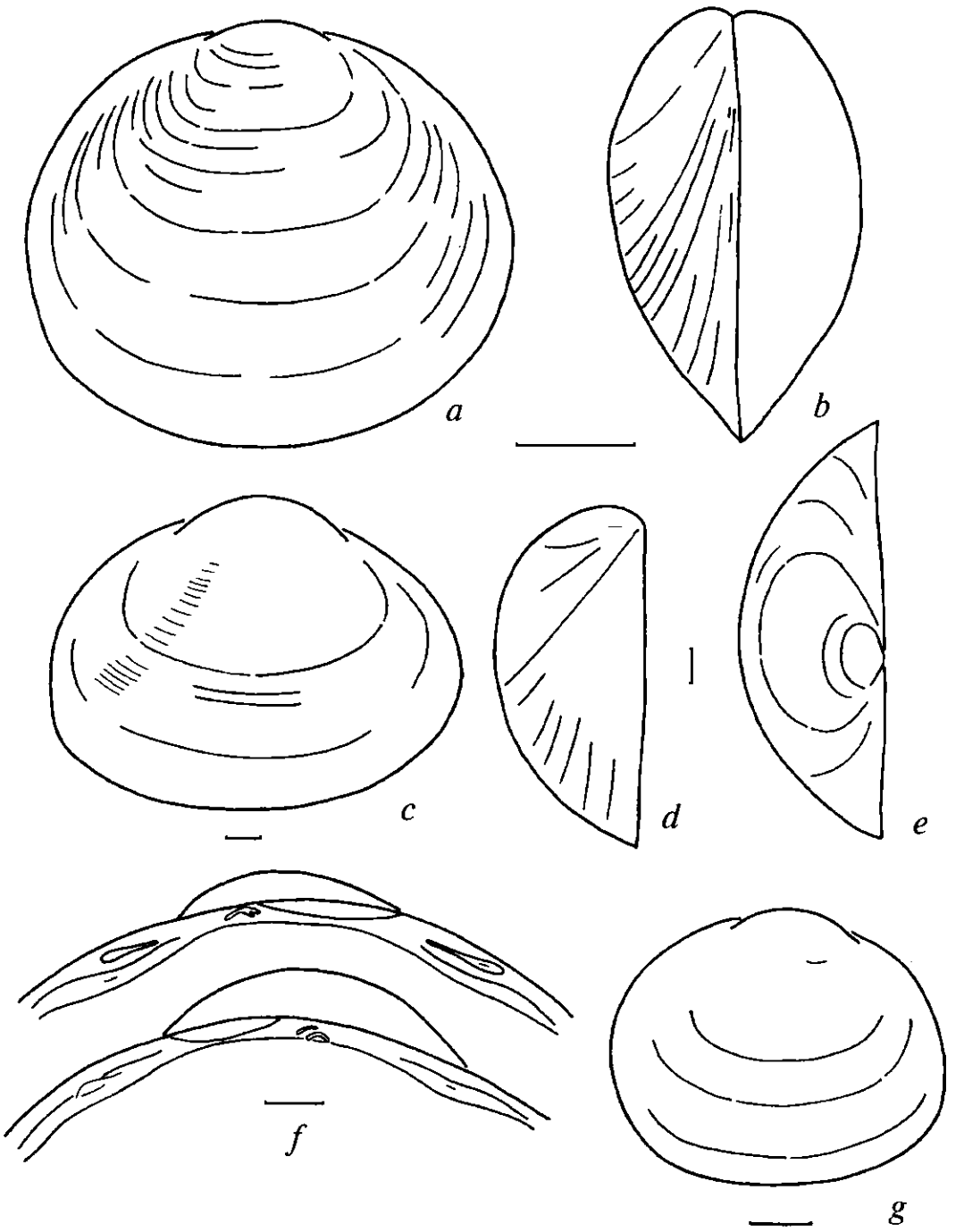

FIG. 11. *Nucleocyclas nitidum* (Clessin in Wersterlund, 1877) a-b — one of the syntypes from Dudino (Dudinka), Russia (NRM), figured by Ya.I.Starobogatov; c-f — large specimen from the Dnieper river near Smolensk, personal collection of the author; g — young specimen from the same locality.

РИС. 11. *Nucleocyclas nitidum* (Clessin in Wersterlund, 1877) a-b — один из синтипов из Дудино (Дудинка) (NRM), рис. Я.И.Старобогатова; c-f — крупный экз. из Смоленска, р. Днепр, коллекция автора, g — молодая особь из того же сбора.

from the scars of posterior adductors. Such condition we observe in *Rivicoliana, Amesoda, Nucleocyclas* and *Sphaerinova* and consider plesiomorphic. Apomorphic condition (muscle scars merged) is peculiar of *Sphaerium* s.str., *Parasphaerium* and *Musculium*. The first two genera are surely related, but in *Musculium* we presumably deal with a parallelism.

As we have supposed earlier [Korniushin, 1992], simultaneous development of several brood sacs in a single gill is an evolutionary novation. Developing this point of view, we come to the conclusion, that the genus *Rivicoliana*, characterized by the largest number of sacs (up to 9), is the most advanced group of the fingernail clams in respect to the breeding organs.

Characters of the excretory organs are also rather informative. An extended excretory sac,

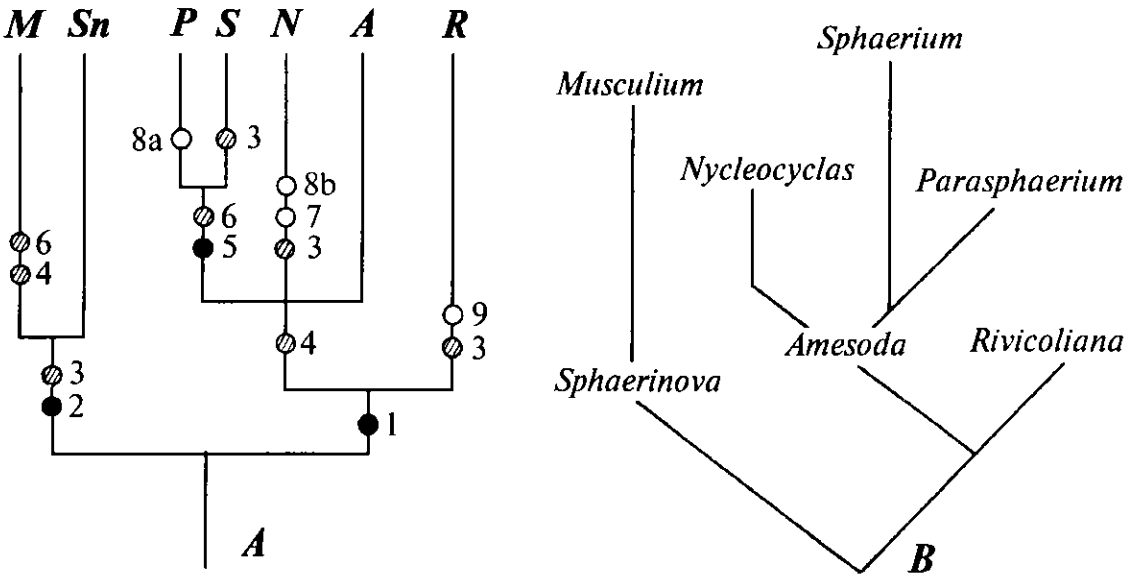

FIG. 12. Phylogenetic relationships in fingernail clams.
A. Distribution of apomorphies: black circles — synapomorphies, open circles — autapomorphies, hatched circles — parallelisms (reductions); 1 — extended excretory sac, 2 — "musculiid" shape of shell (narrow umbones and hinge plate, reduced teeth, etc), 3 — total reduction of the surface sculpture, 4 — enclosed ligament, 5 — parallel cardinal teeth, 6 — merged siphonal retractor and adductor scars, 7 — increased porosity, 8a — broadened and 8b — extremely elongated nephridia, 9 — numerous brood sacs; *M — Musculium, Sn — Sphaerinova, P — Parasphaerium, S — Sphaerium, N — Nucleocyclas, A — Amesoda, R — Rivicoliana.*
B. Probable evolutionary interrelations of genera.

РИС. 12. Филогенетические отношения шаровок.
А. Распределение апоморфий: черные кружки — синапоморфии, белые — аутапоморфии, заштрихованные — параллелизмы (редукции); 1 — увеличенный выделительный мешок, 2 — "мускулиидная" форма раковины (узкие макушки и замочная площадка, редуцированные зубы и т.д.) , 3 — полная редукция скульптуры, 4 — закрытый лигамент, 5 — параллельное расположение кардинальных зубов, 6 — слитые отпечатки заднего аддуктора и сифонального ретрактора, 7 — многочисленные поры, 8а — расширенные и 8b — удлиненные нефридии, 9 — увеличение числа выводковых сумок. *M — Musculium, Sn — Sphaerinova, P — Parasphaerium, S — Sphaerium, N — Nucleocyclas, A — Amesoda, R — Rivicoliana.*
В. Вероятные эволюционные отношения родов.

observed in all fingernail clams except *Musculium* [Dreher-Mansur, Meier-Brook, 1992; our data], is presumably a synapomorphy. Unfortunately, we know nothing about nephridia of *Sphaerinova*, which has two plesiomorphic characters (extraverted ligament and separated muscle scars) and is probably an ancestor of *Musculium*.

Analyzing the shape of the dorsal lobe, we suppose that the moderately elongated configuration observed in such conchologically different groups as *Sphaerium*, *Amesoda* and *Rivicoliana*, is plesiomorphic in respect to the shortened dorsal lobe of *Nucleocyclas* and extremely elongated one of *Parasphaerium*.

The pattern of phylogenetic relationships within Sphaeriidae, concluded from the considerations presented above, is shown in Fig. 12.

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ПРИЛОЖЕНИЕ

Таблица для определения европейских видов группы *Sphaerium* s.lato

1. Раковина небольшая. Эмбриональные части створок несут четко выраженную концентрическую скульптуру. Кардинальные зубы почти прямые. Нефридии сильно вытянуты в длину, закрытые, латеральная ветвь дорсальной лопасти длиннее медиальной *Parasphaerium rectidens*

— Раковина средних размеров или крупная. Эмбриональные части створок гладкие или неравномерно исчерчены. Кардинальные зубы изогнуты. Нефридии открытые либо закрытые, но в последнем случае дорсальная лопасть всегда короткая и широкая. Латеральная ветвь дорсальной лопасти короче медиальной 2

2. Периостракум имеет характерный шелковистый блеск. Раковина пронизана многочисленными равномерно расположенными порами. Отпечаток верхнего ретрактора бранхиального сифона отделен от отпечатка заднего аддуктора. Внутренний кардинальный зуб левой створки изогнут, внешний расположен косо позади него, не заходя за точку перегиба. Нефридии открытые или закрытые. Дорсальная лопасть нефридия короткая и широкая (род *Nucleocyclas*) 3

— Шелковистого блеска нет. Поры сравнительно редки и сконцентрированы в макушечной части створки. Отпечатки сифонального ретрактора и аддуктора слиты. Кардинальные зубы левой створки слегка изогнуты, наружный зуб почти такой же длины, как и внутренний, располагается параллельно последнему и краю замочной площадки. Нефридии открытые, дорсальная лопасть удлинена (род *Sphaerium*) 4

3. Раковина средних размеров (длина не более 9 мм), шаровидная. Молодые раковины выпуклые.
Нефридии закрытые *Nucleocyclas nucleus*
— Раковина крупная (длина до 14 мм), овальная. Молодые раковины округлые, но уплощенные. Нефридии открытые *N.nitidum*

4. Контур фронтального сечения створки с отчетливо обособленной эмбриональной частью *Sphaerium mamillanum*

— контур плавный, эмбриональная часть не обособлена 5

5. Раковина сильно выпуклая, индекс выпуклости превышает 0.82 *Sphaerium westerlundi*

— Раковина умеренно выпуклая, индекс выпуклости, как правило, не более 0.80 *S.corneum*