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Protostelids of the "Stolby" State Reserve (Siberia, Eastern Sayan)

Alena P. Kosheleva[1], Martin Schnittler[2] and Yuri K. Novozhilov[1]

[1] *V.L. Komarov Botanical Institute of the Russian Academy of Sciences, St.Petersburg, Russia*

[2] *Institute of Botany and Landscape Ecology, Ernst-Moritz-Arndt University, Greifswald, Germany*

Summary

This study presents the first survey of protostelids in the Russian Federation and the second one in boreal forests. Altogether, 158 cultures of protostelids were prepared, with samples taken from the bark surface of living trees, rotten bark of logs and decaying plant litter in 2005 and 2006. Samples were processed in 2008 and 2007, respectively. Storing the air-dried substrate samples for three years instead of one did not result in a loss of species, but extended development time of the fructifications for about 2 days. In total, 184 records representing 15 protostelid species from nine genera were made. As for most other surveys of protostelids, *Protostelium mycophaga* and *Schizoplasmodiopsis pseudoendospora* were found to be very abundant. However, bark of living trees, a substrate not studied in most other surveys of protostelids, yielded *Protosporangium articulatum* as the second most common species, occurring almost exclusively on this substrate type. In taiga communities, bark of coniferous trees was found to be the most productive substrate, whereas in steppe communities ground litter was more productive than bark. A comparison of 11 different regions where protostelid biota has been studied showed a high similarity of the regional species assemblages (average Cs=0.86) except for differences caused by the selection of different substrata.

Key words: ecology, distribution, epiphytic species, Eumycetozoa, forests, taiga, microhabitat, slime molds, spore longevity .

Introduction

Protostelids are a small group (37 described species) of simple slime molds with amoeboid trophic cells and simple fruiting bodies in their life cycle (Olive and Stoianovitch, 1960). Together with the two other groups of slime molds, the myxomycetes and the dictyostelids, they make up the taxonomic group *Eumycetozoa* (Adl et al., 2005). Protostelids are eukaryotic, phagotrophic bacteriovores. They have minute fructifications, consisting of one or several spores 5-40 μm in diameter on a delicate

acellular stalk 5 to 150 μm in length, except for the genus *Ceratiomyxa*, which forms a large compound fructification. Although some species seem to display a preference for certain substrata, protostelids are mostly opportunists, able to develop on a broad spectrum of substrata: dead aerial parts of plants, litter, bark of living trees, bark and wood of dead trees and logs, soil and herbivore dung (Olive, 1975; Best and Spiegel, 1984; Moore and Spiegel, 1995, 2000a, b). In addition, some species were reported from aquatic habitats (Lindley et al., 2007; Tesmer and Schnittler, 2008).

So far, most surveys on protostelid diversity were carried out in different types of ecosystems of North and Central America, e.g. in tropical forests of Puerto Rico (Moore and Spiegel, 2000b; Stephenson et al., 1999) and Costa Rica (Moore and Stephenson, 2003), in boreal forests and tundra of Alaska (Moore et al., 2000), in beech and pine forests of Ohio (Best and Spiegel, 1984), and in the temperate habitats of Arkansas (Moore and Spiegel, 2000a). In comparison to the New World, the protostelid assemblages of Europe are almost unstudied. One investigation was made in old-growth beech forests in northeastern Germany (Tesmer et al., 2005), one in temperate broadleaf forests of northwestern Spain (Aguilar et al., 2007), and one in oak forests of the Ukraine (Glustchenko et al., 2002). Tropical regions of the Old World are also poorly studied, the few examples being one survey from Australia (Powers and Stephenson, 2006) and one from temperate montane forests of northern India (Shadwick and Stephenson, 2004).

This study presents the first survey of protostelids from the Russian Federation andthe second one, after Moore et al. (2000), from boreal forests. Therefore, the primary objective of this study was to document the assemblage of protostelids for the study region. As a second goal, we wanted to determine substrate preferences of protostelid species by comparison of series of cultures made with typical substrata, such as litter, and those made with the bark of living trees, a microhabitat neglected in almost all former surveys of protostelids. Due to limitations in laboratory space, air-dried substratum samples were stored for different periods of time; a circumstance used to derive some data about the longevity of protostelid spores.

Material and Methods

Study sites

The state reserve "Stolby" is located ca. 3 km SW of Krasnoyarsk city between 92°40' to 92°55' E and 55°30' to 55°38' N at the Krasnoyarskiy or Kuysumskiy mountain ridge of northwestern foothills of the Eastern Sayan, adjacent to the right bank of the Yenisei River. The area of the reserve is 47,200 ha (Shcherbakov and Kirillov, 1962; Kozlov, 1958). The continental climate is characterized by winter temperatures as low as –45°C, while average January and July temperatures are –16.2°C and +16.8°C, respectively. The mean annual precipitation in this region is 679 mm, with approximately one-third falling as rain in July and August (Andreeva, 2005). The study of Kosheleva et al. (2008) supplies detailed data about the study region.

Sampling, culture and identification of species

In August of 2005 and 2006 the first author collected several series of samples from various substrates in four study sites located in two vegetation belts (light and dark coniferous forest) and in one study site located in the extrazonal steppe:

Moist fir taiga (*Abies sibirica* Ledeb.) with rich green moss and sedge cover, plot 52 of the forest reserve "Stolbinskoe" near the station "Kaltat" (dark coniferous forest belt, 92°50'34" N 55°26'09" E), samples (bark of living trees, bark of decaying logs and sedge-dominated ground litter) collected in 2005;

Aspen forest (*Populus tremula* L.) with rich grass cover, plot 52 of the forest reserve "Stolbinskoe" near the station "Kaltat" (dark coniferous forest belt, 92°51'23" N 55°26'15" E), samples (bark of decaying logs and grass-dominated ground litter) collected in 2005;

Pine taiga (*Pinus sylvestris* L.) with rich grass and sedge cover, ca. 600 m N of "Vtoroy Stolb" ("Second Column") rock (light coniferous forest belt, 55°26'49" N 92°43'34" E), samples (bark of living trees, needle ground litter) collected in 2006;

Alder forest (*Alnus glutinosa* (L.) Gaertn.) with rich fern and grass cover on plot 18 of the forest reserve "Stolbinskoe" near the Laletina stream (light coniferous forest belt, 92°44'48" N 55°26'54" E), samples (leafy ground litter) collected in 2005;

Shrub steppe at the southwestern slope of the "Chertov paletc" ("Devil's Finger") rock (most common vegetation are the shrubs *Cotoneaster lucidus* Schlecht. and *Caragana arborescens* Lam. and grasses), ca. 300 m N of the Laletina control post (extrazonal steppe , 92°45'16" N 55°27'07" E), samples (bark of living shrubs, mixed ground litter) collected in 2006.

All surveyed plant communities were represented by two classes of substrata, bark of living trees and ground litter, except for the alder forest (only ground

litter was sampled). In addition, rotten bark from fallen logs was sampled in the fir taiga (Table 1).

Primary isolation plates were prepared for pine taiga and steppe in March 2007 (after one-year storage), and for fir taiga, alder and aspen forest in Ma 2008 (after three-year storage), using a modification of the technique described by Olive (1975). Using sterile tweezers, four rows (called hereafter streaks), each consisting of 3-6 substrata pieces of 1-3 mm size, were placed on weak malt yeast agar (0.002 g malt extract, 0.002 g yeast extract, 0.75 g potassium hydrogen phosphate, and 15 g agar/L distilled water) poured 3-5 mm deep in Petri dishes of 9 cm diameter. All the cultures were maintained at room temperature (21-23°C) and checked on days 3, 5, 7, 9 and 11 after plating them out, using the 10x and 20x objectives of a compound microscope. The entire margin of a substrate piece and the surrounding agar surface was systematically scanned for the presence of protostelid fructifications. Species were keyed out according to Spiegel et al. (2005). Since all taxa mentioned in this study have already been described, permanent cultures were not established.

The pH values were determined using an Orion 610 pH meter with a touch-down probe in separate cultures prepared with substrata samples on pre-wetted filter paper adjusted with deionized water and KOH to pH 7.0 (Kosheleva et al., 2008).

Data analysis

A species accumulation curve was constructed for (i) all records per sample (culture) and (ii) all records per streak using the program EstimateS (Colwell, 2006) based on the rarefaction formula. Following Raaijmakers (1987), a hyperbolic regresion according to the formula $y = ax/(b+x)$, resulting in a curve shape coming very close to a broken-stick model (Magurran, 2004), was used to fit both sets of data. In this model, the parameter a estimates the maximum number of species to be expected for a particular kind of substrate.

Species diversity (alpha-diversity) was calculated using Shannon's diversity index $H' = -\sum P_i \ln P_i$, where P_i is the relative abundance (the proportion of the total number of individuals or records represented by species) of a particular species (Shannon and Weaver, 1963; Magurran, 2004).

Results

Of the 158 samples cultured in total, 84 (53.2 %) cultures were positive for protostelids (Table 1). The 53 samples cultured after one year of storage yielded 96 records of ten species, the remaining 105 samples cultivated after three years of storage yielded 88 records from eleven species. There was an obvious difference in development times between the two cohorts (Fig. 1). Protostelids from samples stored for one year developed mostly after 3-5 days (mean 4.1 days), while those from three-year old samples usually developed after 5-7 days (mean 6.7 days), this difference being statistically significant (Mann-Whitney rank sum test, $P<0.001$).

Species accumulation curves were constructed on the basis of records per culture as well as records per streak (technically, the four streaks per culture

Table 1. Culture statistics for samples cultivated for protostelid diversity from five different plant communities of the "Stolby" nature reserve.

Plant community	Substrate type[a]	Samples	Stored (yrs)[b]	pH mean ± SEM	positive cultures
Pine taiga	b	13	1	4.97 ± 0.14	12 (92.3%)
	l	14	1	5.46 ± 0.13	4 (28.6%)
Fir taiga	b	15	3	3.85 ± 0.37	6 (40.0%)
	rb	15	3	5.18 ± 0.50	12 (80.0%)
	l	15	3	6.97 ± 0.66	1 (6.7%)
Aspen forest	rb	15	3	6.98 ± 0.64	9 (60.0%)
	l	15	3	6.80 ± 0.65	4 (26.7%)
Alder forest	l	30	3	n.d.	16 (53.3%)
Steppe	b	12	1	7.34 ± 0.12	7 (58.3%)
	l	14	1	7.45 ± 0.08	11 (78.6%)
Total		**158**			**84 (53.2%)**

[a] Substratum types are b – bark of living trees, l - ground litter, and rb – rotten bark of fallen logs.

[b] tored as air-dried samples for one or three years.

can be considered as pseudoreplicates). If the Chao2 estimator was used, species richness estimates for both data sets were nearly identical (15.5 species, Fig. 2). Estimates of the hyperbolic model differed slightly more (15.7 species for the analysis based on streaks, 16.1 for the culture-based analysis). Comparing these figures with the real number of species retrieved (14), the survey can be said to be complete to 87 per cent.

A total of 14 species of protostelids was detected in agar cultures. During a survey of myxomycetes (Kosheleva et al., 2008), one other species (*Ceratiomyxa fruticulosa* (O.F. Müll.) T. Macbr.) has been found in the field, but these records are not considered in this paper. Data on the occurrence of protostelids in the five communities and substrate types are given in Table 2. The most common species on all types of substrates, except for the needle litter

Table 2. Occurrence of 15 protostelid species within substrata and communities of the "Stolby" nature reserve. Record data are given for cultures (first value) and streaks (pseudoreplicates, second value).

Species	All records	Pine taiga		Fir taiga			Aspen forest		Alder forest	Steppe	
		b [a]	l	b	rb	l	rb	l	l	b	l
Cavostelium apophysatum Olive	1/1										1/1
Ceratiomyxa fruticulosa (O.F. Műll) T. Macbr.[b]	2	1					1				
Echinosteliopsis oligospora Reinhardt & Olive	1/1								1/1		
Nematostelium gracile (Olive & Stoian.) Olive & Stoian.	7/7		1/1		1/1			1/1	3/3		1/1
Nematostelium ovatum (Olive & Stoian.) Olive & Stoian.	3/3	1/1									2/2
Protosporangium articulatum Olive & Stoian.	26/38	9/21	2/2	10/10	2/2					2/2	1/1
Protostelium arachisporum Olive	3/3		1/1					1/1	1/1		
Protostelium mycophaga Olive & Stoian.	59/68	10/12			12/12	1/1	15/15	5/5	4/4	5/7	7/13
Protostelium pyriformis Olive & Stoian.	3/3	3/3									
Schizoplasmodiopsis amoeboidea Olive & K.D. Whitney	13/13	1/1			2/2		2/2	1/1	5/5		2/2
Schizoplasmodiopsis micropunctata Olive & Stoian.	1/1								1/1		
Schizoplasmodiopsis pseudoendospora Olive, G.W. Martin, & Stoian.	23/29	6/10	1/2		4/4			1/1	3/3	2/3	6/6
Schizoplasmodiopsis vulgaris Olive & Stoian.	8/8				8/8						
Soliformovum irregularis (Olive & Stoian.) Spiegel	6/6								2/2		4/4
Tychosporium acutostipes Spiegel, D.L. Moore & J. Feldman	2/2								2/2		
Total: records	**158/180**	**30/48**	**5/6**	**10/10**	**29/29**	**1/1**	**17/17**	**9/9**	**22/22**	**9/12**	**24/30**
Total: species for substrate classes		**7**	**4**	**1**	**6**	**1**	**2**	**5**	**9**	**3**	**8**
Total: species for plant communities	**15**	**9**			**6**		**6**		**9**	**8**	
Shannon H'	**1.47**	**1.39**	**1.33**	**0.00**	**1.48**	**0.00**	**0.36**	**1.30**	**1.21**	**1.00**	**1.61**

[a] Substratum classes are b – bark of living trees, l - ground litter, and rb – rotten bark of fallen logs.

[b] Observed only in the field.

of pine and bark of fir, is *Protostelium mycophaga* (68 records from 59 cultures). Except for fir bark, this species seems to prefer bark of living and dead trees (67% of all records), but avoids litter, especially that of coniferous trees. *Protosporangium articulatum* is common as well (38 records from 26 cultures), but exhibits a strong preference for bark of coniferous living trees (92% of all records), especially pine bark (21 records) and fir bark (10 records). Beside this obviously corticolous species, only two protostelid species among the seven most common ones (>5 records) exhibited clear substrate preferences: *Schizoplasmodiopsis vulgaris* was recovered exclusively (8 records) from samples of rotten bark, whereas *Nematostelium gracile* and *Soliformovum irregulare* were both more common on litter (6 of 7 and 6 of 6 records, respectively). Another seven species were recorded less than five times.

Among the substrate types, bark was the most productive one (70 records from 40 samples); to a lesser extent this holds true for bark of decaying logs (46 records from 30 samples). However, only six species were found on bark of living trees, and another two on dead bark. Among these, only *Protosporangium articulatum* was highly specific to this substratum (33 records from living bark, two from dead bark, three from ground litter). Ground litter was clearly less productive (68 records from 88 samples), but more diverse (12 species, with *Cavostelium apophysatum, Echinosteliopsis oligospora, Protostelium arachisporum, Schizoplasmodiopsis micropunctata, Soliformovum irregularis* and *Tychosporium acutostipes* observed only on litter. However, of the six species found on living bark, there are three common ones (exceeding 10 records); ground litter has 12 species but only two of them are common. For this reason, the Shannon diversities of the two substratum types are comparable (bark of living trees 1.04, ground litter 0.97).

Looking at the percentage of positive cultures, bark was generally more productive than litter. However, productivity depended strongly on the tree species: pine was most productive (92.3% positive cultures), followed by bark of steppe shrubs (*Cotoneaster lucidus* and *Caragana arborescens*, 58%), whereas bark of living fir yielded only 40% of positive cultures. Among litter, leafy litter performed better (79%) than needle litter of pine (29%), and litter of sedges was very unproductive (7% positive cultures).

Discussion

Although this study is the first published survey of protostelids from Russia, the species assemblage observed is sufficiently similar to those recorded in other parts of the world to suggest that most of the species known from temperate zones can be found in Russia as well.

Since the survey was carried out with series of samples from selected substrate types, the statistics of the species accumulation curves indicates the survey to be nearly complete for this selection. The analysis of streaks (functioning as pseudoreplicates) is well comparable with the analysis of cultures; the same holds true for a comparison of the non-parametric Chao2 estimator with a hyperbolic regression. The latter was often found to underestimate the number of species to be expected (Unterseher et al., 2008). However, it has to be mentioned that all these analyses are valid only for the substrate types investigated and can not serve as estimates of protostelid species numbers for the whole region. Nevertheless, our results show that for a given type of substratum it is sufficient to culture 15 samples with four streaks as pseudoreplicates (equalling 180-360 substratum pieces of 1-3 mm size).

In contrast to myxomycetes, whose spores were found to germinate after decades of herbarium storage (Erbisch, 1964), there are currently no data about spore longevity of protostelids. In this study we used air-dried substrate samples which were stored dry for one year (53 samples) and for three years (105 samples). Comparing the two cohorts of samples, we did not find any significant loss in frequency (64%

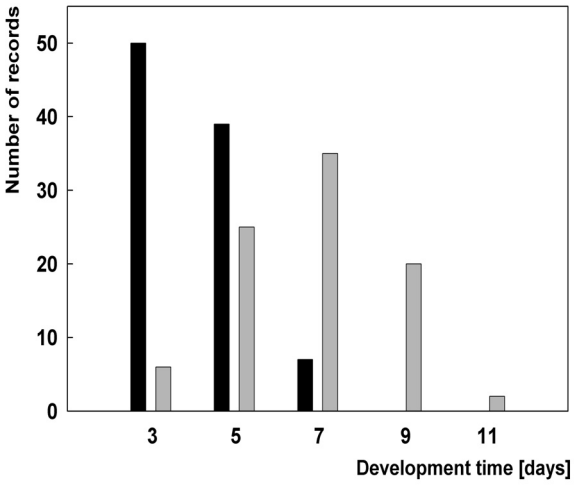

Fig. 1. Development time of protostelids (number of observations on the respective days) in 53 cultures prepared from substrate samples stored for one year (black bars) and in 105 cultures prepared from substrate samples stored for three years (grey bars).

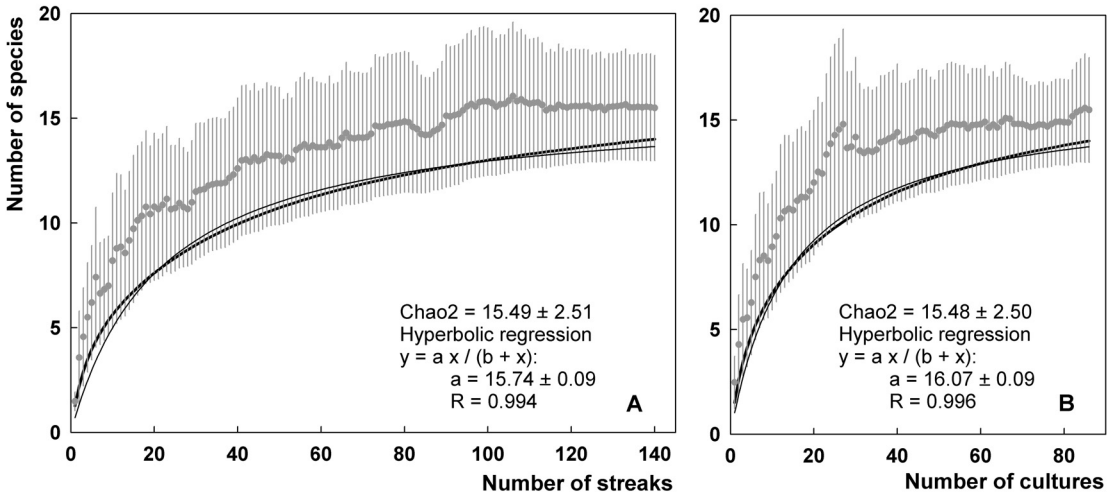

Fig. 2. Species accumulation curves (solid lines) for protostelids calculated for 140 positive streaks (A) and from 86 positive cultures (B, thick lines). Curves were fitted according to a hyperbolic model y = *a*x/(*b*+x), with *a* as the maximum number of species to be expected (thin lines). In addition, the mean Chao2 estimator (grey dots) ± SD (grey bars) is shown and its final values are given.

versus 49% positive cultures, respectively) or species richness (10 versus 11 species recorded). Except for *Schizoplasmodiopsis vulgare*, all of the more common protostelid species (represented by more than three records) were found in both cohorts. However, the average developmental time increased from 4.1 to 6.7 days (Fig. 1), and the average productivity of cultures decreased from 1.81 to 0.84 records per culture. It has to be noted, however, that the first cohort of substrata included samples from drier vegetation types (extrazonal steppe and pine forest), which, as it was observed in similar surveys, tend to be more productive. Thus, our results do not allow one to derive quantitative data on spore survival, though we can conclude that most species of protostelids can survive prolonged periods of drought. Indirect confirmation comes from the frequent occurrence of protostelids in deserts, as observed in Kazakhstan (Novozhilov, pers. comm.) and Oman (Schnittler, unpubl. data).

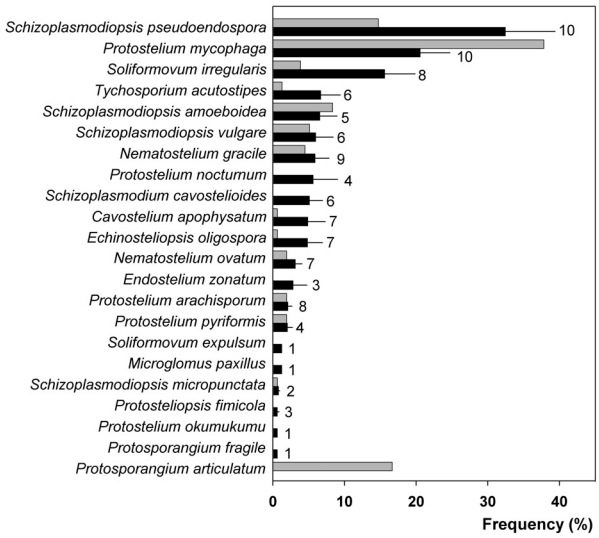

Fig. 3. Mean frequency of 22 protostelid species found in this survey (grey bars, 158 records) and their mean frequency in ten surveys from various regions of the world (black bars, altogether 4891 records, see Table 3 for citations), including the standard error of means. Numbers near black bars indicate the number of surveys in which the species was recorded.

In contrast to almost all other studies of protostelid diversity, we cultured bark of living trees and found this substrate to be often more productive than ground litter. Similarly to myxomycetes, protostelids seem to include corticolous species, as indicated by the high specificity of *Protosporangium articulatum* to bark. This was confirmed by a large study in the country of Oman, where this species and the related *P. conicum* were found to grow mostly corticolously (Schnittler, unpubl. data). The whole genus *Protosporangium* seems to be corticolous; to note, there are several entirely corticolous genera of myxomycetes (Ku, 1969; Pendergrass, 1976; Stephenson, 1989). Similarly to corticolous myxomycetes, corticolous protostelids tolerate low substrate pH but to a certain degree. Pine bark with 92% positive cultures had the mean pH of 4.97, while fir bark with a mean pH of 3.85 was already less productive (40% positive cultures).

Except for the corticolous *Protosporangium articulatum*, frequencies of protostelid species found by us are mostly comparable with the average frequency figures (Fig. 3) derived from ten surveys in the world (Aguilar et al., 2007; Best and Spiegel, 1984; Powers and Stephenson, 2006; Moore and Spiegel, 2000a, b; Moore and Stephenson, 2003; Moore et al., 2000; Shadwick and Stephenson, 2004; Spiegel and Stephenson, 2000; Tesmer et al., 2005). All these studies except Aguilar et al. (2007) did not include bark of living trees, and so only occurrences on litter substrates are comparable. As in this study, *Protostelium mycophaga* and *Schizoplasmodiopsis pseudoendospora* were found to be among the two most abundant species in, respectively, 8 and 7 of the ten surveys evaluated; these two species were also the only ones found in every survey. A comparison of protostelid assemblages from 11 different regions confirms this pattern (Table 3). The adjusted incidence-based Sørensen similarity index Cs (Chao et al., 2005) calculated for all pair wise combinations of the regions shows a mean value of 0.86 (range 0.36 to 1.00), indicating a high level of similarity between protostelid assemblages of all the regions studied. The mean similarity index for the "Stolby" reserve with other regions is 0.88. Due to the often small number of cultures used in many surveys, substratum preferences and occurrences of rare species are hardly comparable.

Although still very fragmentary, the pattern of protostelid occurrences within different regions in the world delineated here seems to be in accord with the ubiquist model of Finlay (2002, 2004). An exception may be the genus *Ceratiomyxa* with macroscopic fructifications, where two species are confined to the tropics (Stephenson et al., 2008; Rojas et al., 2008). In the related group of myxomycetes, which have larger and more complex fructifications, a high proportion of species has a more narrow distribution (Stephenson et al., 2008), lending evidence in support of the moderate endemicity model postulated by Foissner (2006, 2008) for most groups of protists. Further studies on protostelid and myxomycete diversity may elucidate if there is indeed an relationship between the distribution range, on the one hand, and size of fructifications and the related biological parameters, e.g. developmental time, on the other hand.

Table 3. Pair wise comparison of protostelid biotas recorded for eleven different regions of the world. Total numbers of all records from cultures were used for the calculation of the adjusted incidence-based Chao-Søerensen similarity index. Both the similarity index (upper right) and number of species shared (lower left) are given.

	St	Au	I	Sp	G	PR	Co	AR	OH	M	AL
St	-	0.81	0.86	0.97	0.93	0.80	0.85	0.88	0.95	0.79	0.79
Au	9	-	0.72	0.80	0.91	0.98	0.94	0.93	0.96	0.84	0.73
I	9	6	-	0.88	1.00	0.89	0.85	1.00	0.93	0.70	0.70
Sp	13	9	11	-	1.00	0.76	0.70	0.96	0.90	0.90	0.65
G	11	8	9	13	-	0.92	0.88	0.99	0.96	0.92	0.82
PR	8	7	8	9	8	-	0.98	0.98	0.99	0.76	0.83
Co	8	6	7	8	7	7	-	0.87	0.82	0.36	0.86
AR	11	8	11	14	13	9	8	-	0.99	0.93	0.76
OH	9	7	7	10	9	8	6	9	-	0.74	0.74
M	5	4	4	6	6	3	2	6	3	-	0.58
AL	6	4	5	6	6	4	5	6	4	3	-

Notes: Study regions are abbreviated as St = "Stolby" reserve, Krasnoyarsk region, Russia (14 species recorded / 158 samples cultured); Au = Australia, the tropical forests, woodlands and deserts (12 / 1039; Powers and Stephenson 2006); I = India, northern forests (12 / 30; Shadwick and Stephenson ,2004); Sp = northeastern Spain, deciduous forests of Somiedo Biosphere Reserve (21 / 160; Aguilar et al., 2007); GE = northeastern Germany, old-grown beech forests (14 / 128; Tesmer et al., 2005); PR = Puerto Rico, Caribbean National forest (10 / 97; Moore and Spiegel, 2000); Co = Costa Rica, tropical wet forests of La Selva Biological Station (9 / 145; Moore and Stephenson, 2003); AR = Arkansas, USA, forests and grasslands (15 / 3132; Moore and Spiegel, 2000); OH = Ohio, USA, deciduous forest of Hueston woods state park (16 / 105; Best and Spiegel, 1984); M = Macquarie Island, tundra, Tasmania, Australia, Antarctic (6 / 54; Spiegel and Stephenson, 2000); AL = Alaska, boreal forests and tundra (6 / 370; Moore et al., 2000).

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Address for correspondence: Yuri K. Novozhilov, Komarov Botanical Institute of the Russian Academy of Sciences, 197376, St.Petersburg, Russia, e-mail: yurinovozhilov@gmail.com