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Distribution of the Genus *Mallomonas* (Synurophyceae) – Ubiquitous Dispersal in Microorganisms Evaluated

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The neutral dispersal model in protists was suggested as a general principle resulting in either cosmopolitan or ecologically restricted distribution of individual species. The high local diversity results in “flat” species–area curves of individual protist groups. We investigated the local and regional diversity of the genus *Mallomonas* in the alluvial plain of upper Lužnice in the Czech Republic. About 86.5% of species previously reported from all types of freshwater biotopes within the country were found in our investigated localities. However, there was a considerable increase of species numbers in relation to the total area of available habitats on the continent and global scales. In three species found in our localities, the floristic data indicate a possible geographically restricted distributional pattern. Here, we discuss possible reasons for this phenomenon.

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Introduction

The neutral model of ubiquitous dispersal of microorganisms (Fenchel and Finlay 2004; Finlay 2002; Finlay and Clarke 1999a; Finlay et al. 2002) has contributed much to our understanding of microbial diversity and distribution. Ubiquitous distributional patterns were demonstrated in different groups of protists (Fenchel and Finlay 2004; Finlay and Esteban 2001; Finlay and Fenchel 2004; Finlay et al. 2004; Wilkinson 2001). However, the generalization of the neutral model to all microorganisms still remains a controversial issue (see e.g. Coleman 2002; Foissner 1999; Lachance 2004).

The core of the neutral model hypothesis can be summarized as: (1) metapopulations of free-living microorganisms are sufficiently abundant to have a world-wide distribution; (2) the extreme population numbers of individual species lead to their equable dispersion over the planet in a negligible time from an evolutionary point of view; (3) consequently, microbial species richness of individual localities is large and represents a significant proportion of global diversity; (4) consequently, the individual species occur in detectable numbers wherever suitable environmental conditions are available; (5) there are no historically determined biogeographic areas of microorganisms; and (6) the only geographic pattern that can be detected results from individual ecological requirements of species.

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Individual species are therefore cosmopolitan and they occur in detectable numbers in their favored environment (e.g. peat bog pools or eutrophic freshwater). The only biogeographic pattern that can be discerned over large areas, continents, or climatic zones is connected with temperature and, consequently, with latitude. We found species that cannot tolerate freezing and therefore occur in a pantropic pattern, or species preferring colder environments whose distribution has a bipolar pattern. Therefore, Finlay et al. (2004) attempted to disprove the presumed occurrence of some species in one hemisphere only.

A major obstacle for the neutral dispersal model is the existence of many endemic microbial species that have been reported rarely and often only from a single locality. However, the authors of the neutral model demonstrated that numerous slowly growing protist species are so rare in nature that the probability of their discovery is negligible. In these species, their findings depend on the sampling effort and undersampling is the crucial problem for evaluation of distributional patterns (Finlay and Clarke 1999b; Finlay et al. 2004). The “single-report” occurrence explains nothing about their global distribution.

In many protist groups, existing ambiguous species concepts, possibly incorporating numerous biological species within a single traditionally delimited morphospecies, have argued against the neutral dispersal model (Lachance 2004). Therefore, distributional studies focused on those microorganisms with more consistent species concepts are desirable to evaluate the neutral model hypothesis.

In this study, we concentrate on the synurophycean autotrophic flagellates of the genus *Mallomonas*, whose cells are covered with species-specific inorganic silica scales (Lavau et al. 1997; Siver 1991; Wee 1997). This makes *Mallomonas* a very good model group for evaluating the neutral dispersal model. The silica scales enable ultrastructural identification of individual species from plankton and also from the sediments of freshwater habitats. Since the 1950s, the taxonomy of the genus has been based on their ultrastructural morphology (Asmund and Kristiansen 1986; Fott 1955; Harris and Bradley 1960). To date, 176 species and infraspecific taxa have been described within the genus and almost 200 floristic and ecological studies reporting *Mallomonas* species include all kinds of freshwater habitats from around the world (Kristiansen and Lind 2005). In many species, the ecological preferences were determined and *Mallomonas* species are widely

used for biomonitoring purposes (Hartmann and Steinberg 1989; Lott and Siver 2005; Siver and Marsicano 1996).

Based on floristic reports, the biogeography of the genus *Mallomonas* was established. Presumed distributional patterns of individual taxa range from cosmopolitan, over distributions restricted to particular continents or climatic zones, to endemic (Kristiansen 2001a, b; Kristiansen and Lind 2005). More than 40 species have been considered as endemics of individual continents (including the “single-report” species). Interestingly, old freshwater lakes such as Lake Biwa in Japan or Lake Baikal in Russia, known by the high endemism of their fauna and macrophytic flora, do not contain any endemic *Mallomonas* species (Kristiansen and Lind 2005).

According to the neutral dispersal model, global distributions of microorganisms follow latitudinal or cosmopolitan patterns. Of course, given the microbial nature of *Mallomonas*, none of the floristic studies that are based on EM investigations of scales from plankton or sediment samples could claim to be a comprehensive account of all species present at the investigated localities. Rather, locally abundant species occurring in detectable numbers can be found using a floristic approach. Nevertheless, given the present findings of individual species, we can ask for the probability of their ubiquitous distribution — either worldwide or in particular climatic zones.

Let us imagine a simple example. In total, we have 10 independent floristic accounts. Seven of them are situated in a region *N* (e.g. temperate northern hemisphere), and the three remaining are in a region *S* (e.g. temperate southern hemisphere). The species *x* was reported three times — and actually, it was from the region *N* only. Now, the probability *p* that the distribution of the species *x* in temperate zones of the planet follows the neutral dispersal model is:

$$p = [Z/A] \times [(Z-1)/(A-1)] \\ \times \dots \times [(Z-(x-1))/(A-(x-1))],$$

where *Z* is a number of independent reports (floristic studies) from a particular region (e.g. continent, hemisphere, or climatic zones), *A* is a number of all independent reports (floristic studies) worldwide, and *x* is a number of independent reports of a particular investigated species.

In our example, $p = [7/10] \times [(7-1)/(10-1)] \times [(7-2)/(10-2)] = 0.291$. Therefore, we can see that in our example the probability that the presumed pattern of the occurrence restricted to

the region *N*, based on three reports out of 10 independent studies could have emerged by chance is fairly high 29.1%. In this fashion, we can investigate probabilities of non-random distribution of those *Mallomonas* taxa, with the presumed distribution pattern, which seemingly contradicts the neutral model (Kristiansen 2002).

Here, we present our floristic data of *Mallomonas* distribution and species richness in alluvial pools of upper Lužnice in the Czech Republic, a result of a 4 year systematic study aimed at the enumeration of *Mallomonas* species. We present the species-area curve for the genus *Mallomonas* based on these results.

Results and Discussion

For systematic monitoring, we chose the T2 pool, an alluvial pool with an area of 330 m² and

maximum depth of 2 m (Pithart 1997). We took about 25 whole water and sediment samples that were analyzed for the presence of *Mallomonas* scales. The total TEM investigation time was about 100 h. Simultaneously, we investigated the *Mallomonas* species richness in the alluvial ecosystem as a whole, where the total average area of freshwater pools is about 40 ha. Six *Mallomonas* species from the area are new to the Czech Republic (*M. corymbosa*, *M. cyathellata*, *M. eoa*, *M. mangofera* f. *mangofera*, *M. lelymene*, *M. torquata*) (Fig. 1). In the T2 pool — a single small mesotrophic locality — 38 *Mallomonas* species were found (Table 1). The list of species from the T2 pool represents 84.5% of the total species number from the whole investigated alluvial complex. The whole alluvial complex (including the T2 pool) contained 86.5% of the total species number found in the Czech Republic in about

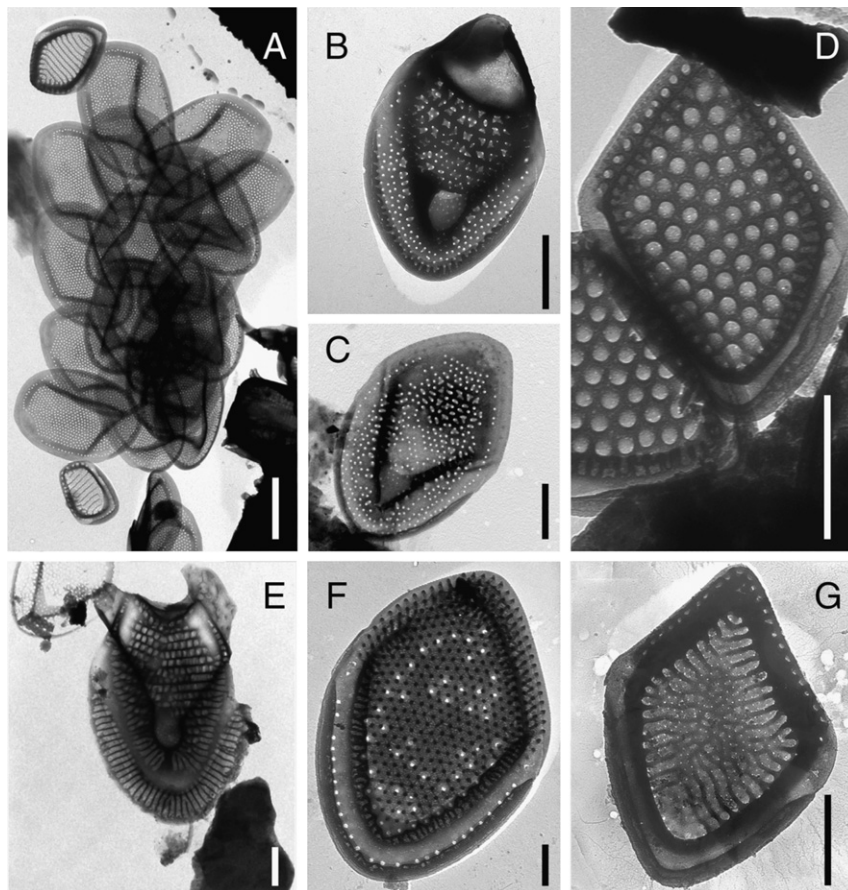


Figure 1. (A) *Mallomonas corymbosa*. Body scales. Bar: 2 μ m. (B, C) *Mallomonas cyathellata*. Body scales. Bars: 1 μ m. (D) *Mallomonas eoa*. Body scale. Bar: 1 μ m. (E) *Mallomonas lelymene*. Body scale. Bar: 1 μ m. (F) *Mallomonas mangofera* var. *mangofera* f. *mangofera*. Body scale. Bar: 0.5 μ m. (G) *Mallomonas torquata* f. *torquata*. Body scale. Bar: 0.5 μ m.

Table 1. *Mallomonas* species found in alluvial pools of upper Lužnice, the Czech Republic. The parameters Z, A, and x of the formula following the neutral dispersal model are given for species with northern temperate distribution. Low probabilities of bipolar distribution were found for three species (marked by an asterisk).

Taxon	T2 pool	Other alluvial pools	Distribution types	Z	A	x	Probability of bipolar distribution
<i>Mallomonas acaroides</i>	1		Widely distributed				
<i>M. actinoloma</i> var. <i>maramuresensis</i>	1		Northern temperate (arct., temp.)	119	125	14	0.483
<i>M. akrokornos</i>	1	1	Cosmopolitan				
<i>M. alata</i>	1	1	Widely distributed				
<i>M. alpina</i>	1		Cosmopolitan				
<i>M. alveolata</i>	1		Scattered				
<i>M. annulata</i>	1	1	Widely distributed				
<i>M. areolata</i>	1	1	Widely distributed				
<i>M. calceolus</i>	1	1	Widely distributed				
<i>M. caudata</i>	1	1	Widely distributed				
<i>M. corcontica</i>	1		Northern temperate (arct., temp., subtr.)	151	173	12	0.184
<i>M. corymbosa</i>	1	1	Bipolar				
<i>M. costata</i>	1		Widely distributed				
<i>M. crassisquama</i>	1	1	Widely distributed				
<i>M. cratis</i>	1		Widely distributed				
<i>M. cyathellata</i>	1	1	Widely distributed				
<i>M. doignonii</i>	1	1	Northern temperate (arct., temp., subtr.)	151	173	14	0.137
<i>M. elongata</i>	1	1	Widely distributed				
<i>M. eoa</i>	1	1	Widely distributed				
<i>M. flora</i>	1		Widely distributed				
<i>M. heterospina</i>	1	1	Widely distributed				
<i>M. intermedia</i>	1	1	Endemic to Europe				
<i>M. lelymene</i>	1	1	Scattered, but widely distributed				

<i>M. mangofera</i> f. <i>mangofera</i>	1	1	Cosmopolitan				
<i>M. matvienkoeae</i>	1	1	Cosmopolitan	151	173	36	0.004*
<i>M. multiunca</i>	1	1	Northern temperate (arct., temp., subtr.)	151	173	28	0.015*
<i>M. oviformis</i>	1	1	Northern temperate (arct., temp., subtr.)	151	173		
<i>M. papillosa</i>	1	1	Cosmopolitan				
<i>M. parvula</i>	1	1	Widely distributed				
<i>M. paxillata</i>	1	1	Widely distributed				
<i>M. pillula</i> f. <i>valdiviana</i>	1	1	Bipolar				
<i>M. portae-ferreae</i>	1	1	Cosmopolitan				
<i>M. prora</i>	1	1	Bipolar				
<i>M. pumilio</i> var. <i>pumilio</i>	1	1	Bipolar				
<i>M. pumilio</i> var. <i>silvicola</i>	1	1	Endemic to Europe				
<i>M. punctifera</i> var. <i>punctifera</i>	1	1	Northern temperate (arct., temp., subtr.)	151	173	56	0.000*
<i>M. retifera</i>	1	1	Scattered				
<i>M. schwemmleri</i>	1	1	Northern temperate (arct., temp., subtr.)	151	173	19	0.065
<i>M. striata</i>	1	1	Widely distributed				
<i>M. teilingii</i>	1	1	Northern temperate (arct., temp.)	119	125	27	0.224
<i>M. tonsurata</i>	1	1	Cosmopolitan				
<i>M. torquata</i> f. <i>simplex</i>	1	1	Northern temperate (arct., temp.)	119	125	21	0.323
<i>M. torquata</i> f. <i>torquata</i>	1	1	Bipolar				
<i>M. transsylvanica</i>	1	1	Northern temperate (arct., temp.)	119	125	15	0.457
<i>M. trummensis</i>	1	1					

135 localities ranging from mountainous peat bogs to alkaline eutrophic fish ponds (Němcová et al. 2002, 2003; Řezáčová et al. 2004). The corresponding species—area curve is supplemented with the data for total species number as reported from Europe and worldwide to date (Franceschini and Kristiansen 2004; Forsström et al. 2005; Kristiansen 2002; Lott and Siver 2005; Řezáčová and Škaloud 2005; Siver et al. 2005; Vigna and Siver 2003; Carty and Wujek 2003; Wujek and Ogundipe 2003; Wujek et al. 2004) (Fig. 3). The species—area curve was compiled in the same way as the species—area data as presented in Fenchel and Finlay (2004). We took the log data of the area of freshwater habitats across different scales: the T2 pool, the alluvial ecosystem of upper Lužnice (Pithart 1997), the Czech Republic (Viček 1984), Europe and the world (CIA 2006; Revenga et al. 2000), and the *Mallomonas* species number reported from floristic studies.

Comparing these data with the results of Finlay (2002) and Fenchel and Finlay (2004), we can see a similar “flat” species—area pattern in our data when followed up to the area of the Czech Republic. This pattern agrees well with the “high local diversity — low global diversity” paradigm assumed by the neutral dispersal model (Finlay 2002). The extremely low slope of the species—area curve of microorganisms in contrast to larger organisms, e.g. insects (Finlay 2002), indicates their easy and frequent dispersal leading to their ubiquitous distribution in a given area. There is a certain increase of the slope in continent-wide and global parts of the curve when compared with the corresponding curves of Fenchel and Finlay (2004). We propose two possible explanations of this phenomenon: (1) higher ecological diversification of worldwide freshwater habitats when compared to marine ecosystems; and (2) inadequate sampling at smaller scales of our curve.

Firstly, we presume that the increase of species number at continent-wide and global levels (boosting the slope of our species—area curve) is connected with the increase of available habitats — probably mainly in the subtropical and tropical localities without an annual freezing period. In our opinion, these results indicate generally higher numbers of microbial species whose distribution is restricted to a particular climatic zone in freshwater ecosystems in comparison to marine ecosystems.

Secondly, we cannot exclude that there is also an inadequate sampling of *Mallomonas* in the Czech Republic. Although this country has been

one of the centers of *Mallomonas* floristic research (Fott 1955; Němcová et al. 2003), species new to the Czech Republic are still being found during detailed EM investigations of many samples (e.g. Němcová et al. 2003; Neustupa et al. 2001; Nováková et al. 2004; Řezáčová et al. 2004).

Looking at the distributional patterns of *Mallomonas* taxa found in the investigated pools (Table 1), we see that 25 of them can be considered cosmopolitan or widely distributed according to Kristiansen (2002), which means that they were found in different continents and in different climatic zones. In addition, there are five taxa known as bipolar in their distribution — thus occurring in colder regions of the planet. The distributional patterns of these species conform to the neutral dispersal model. However, there are 10 taxa that were reported as northern temperate by Kristiansen (2002), which means that they were found in arctic/temperate to subtropical localities in the Northern Hemisphere only. Looking at the probabilities that these patterns could have emerged by chance on the basis of available floristic data (Table 1), we can see that in most of these taxa, probabilities of bipolar temperature-dependent distribution are very high (for convenience, we take the 5% probability as the highest possible level that should attract our attention to distribution of a particular taxon). Three species — *M. multiunca*, *M. oviformis*, and *M. punctifera* var. *punctifera* (Fig. 2) seemingly do not conform to the neutral dispersal model due to their highly non-random distribution in subtropic to subarctic zones of the Northern Hemisphere (Fig. 3).

Nevertheless, their reported absence from the Southern Hemisphere may be due to inadequate sampling and scarcity of studies from these regions investigating appropriate habitats conforming to ecological preferences of these species. *Mallomonas multiunca* was found in 36 independent studies ranging from subtropical to subarctic Europe, North and Central America, and Asia. It occurs at a pH range from 4.0 to over 9.0 and tolerates a wide spectrum of lake types, including oligotrophic, dystrophic, and eutrophic localities (Siver 1991; Takahashi 1978). *Mallomonas oviformis* has been reported in 28 studies from subtropical to subarctic Europe, North America, and Asia (Kristiansen 2002). Siver (1989) and Němcová et al. (2003) found *M. oviformis* mainly in alkaline and relatively eutrophic conditions at conductivities above $80 \mu\text{S cm}^{-1}$. *Mallomonas punctifera* var. *punctifera* belongs to one of the most frequently reported taxa within the genus. There are 56 reports of this species from subtropic

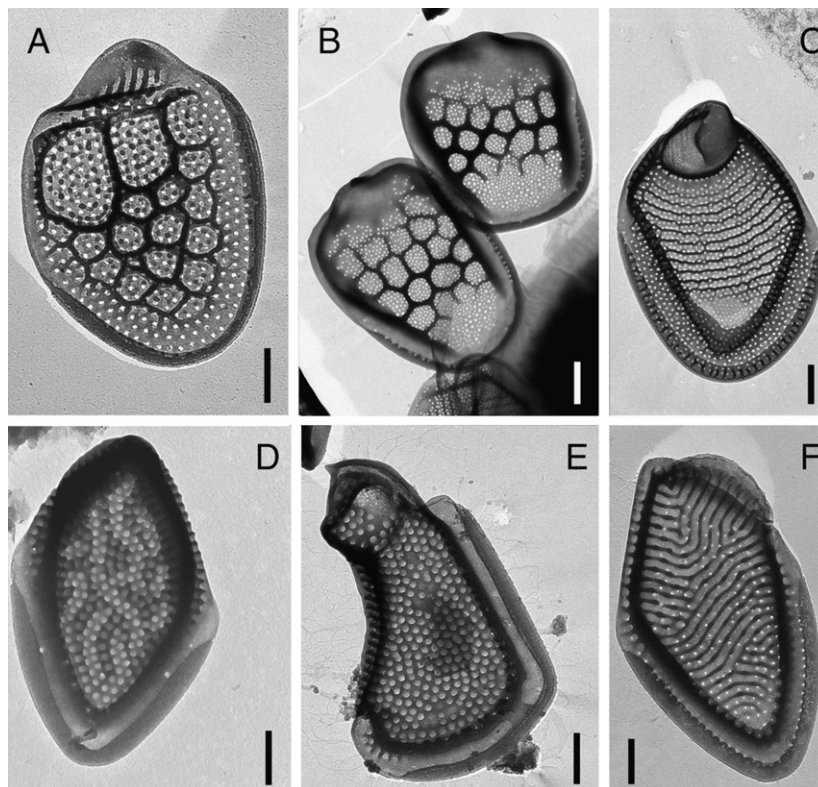


Figure 2. (A) *Mallomonas multiunca*. Body scale. Bar: 0.5 μm. (B) *Mallomonas punctifera* var. *punctifera*. Body scales. Bar: 1 μm. (C) *Mallomonas portae-ferreae*. Body scale. Bar: 1 μm. (D, E) *Mallomonas prora*. (D) Body scale. (E) Apical scale. Bars: 0.5 μm. (F) *Mallomonas schwemmlei*. Body scale. Bar: 0.5 μm.

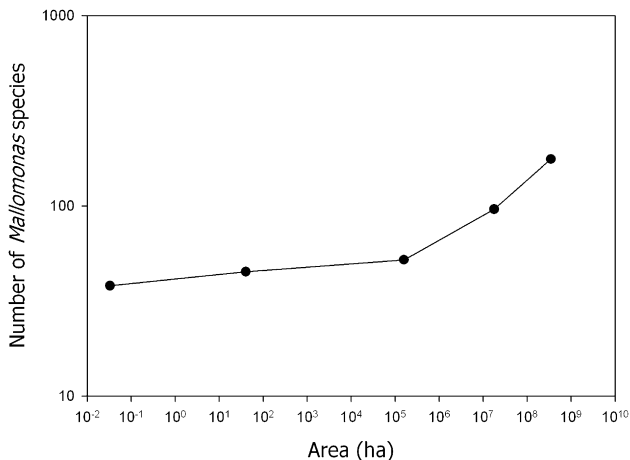


Figure 3. Species—area curve based on *Mallomonas* species from alluvial pool T2 from the whole alluvial complex of upper Lužnice, the Czech Republic, Europe, and the whole world.

to subarctic ecosystems of Europe, North America, and Asia. It is characterized as an alkaliphilic to pH-neutral species (Němcová et al. 2003;

Roijackers and Kessels 1986). A second variety of the species, *M. punctifera* var. *brasiliensis*, was found 14 times in North and South America, including the tropical equatorial localities (Kristiansen and Menezes 1998). From a taxonomic point of view, both varieties are well delimited and easily discernible (Kristiansen 2002; Kristiansen and Menezes 1998). All three taxa form relatively large and easily discernible scales.

Other *Mallomonas* species with many independent floristic reports but geographically restricted distribution were detected in subtropical/tropical ecosystems (e.g. *M. ocellata* and *M. ceylanica* in South and East Asia, *M. plumosa* in South-East Asia and Australia) and in temperate ecosystems (*M. hamata* in the Northern Hemisphere, *M. clavus* in Europe, and *M. duerrschmidtiae* in arctic North America) (Kristiansen 2002; Kristiansen and Lind 2005). While it seems that, given the present amount of floristic data, the neutral model can successfully be applied to the distribution of most *Mallomonas* species (at least those found in our study), the non-neutral geographic patterns of these several species should be investigated for

possible underlying explanatory mechanisms. There could be three possible theoretical explanations of seemingly non-neutral, geographically restricted distribution in freshwater microbial organisms such as *Mallomonas*: (1) a species could be very young from an evolutionary point of view and, so far, it was not able to colonize the available habitats worldwide; (2) distributional abilities of the species could be distinctly lower than in other taxa of the genus. In *Mallomonas*, this could involve the lower survival rate of cysts and palmelloid stages that are probably the most easily dispersible stages of the life cycle (Kristiansen 2001b; Wee et al. 2005). In addition, the rate of dispersal depends on the absolute abundance of individual species so that locally rare species should disperse more slowly; and (3) there could be presently unknown environmental factors, e.g. obligatory biotic interactions with biogeographically restricted larger organisms, that “hold” a species in a restricted area and whose absence from the rest of the world results in failure of dispersal attempts.

None of these three possible explanations has ever been tested in chrysophytes or synurophytes. Nevertheless, the first two hypothetical mechanisms in fact represent the historically determined distribution. They could be addressed in specifically designed experimental studies investigating either the evolutionary age or cyst formation and their survival characteristics in individual *Mallomonas* species. If there would be any significant differences between cosmopolitan or bipolar species and species with seemingly non-neutral distribution that have many times been found within some restricted region or hemisphere, then these taxa could be considered to contradict the neutral dispersal model.

Although, we do not consider the existence of an unknown ecological factor restricting the occurrence of a species in a single continent or hemisphere as a likely phenomenon, it always remains a possibility. However, unless there is any single proved example of such a mechanism in free-living protists, such as *Mallomonas*, this explanation remains entirely speculative.

Methods

All investigated localities are alluvial pools in the floodplains of the upper Lužnice, the Czech Republic. For systematic monitoring, we chose the T2 pool, an alluvial pool with an area of 330 m² and a depth of about 2 m (Pithart 1997). The range

of pH values in the T2 pool was 6.0–7.5 and conductivity was between 150 and 240 μS cm⁻¹. In 2002 and 2003, we took 1.5 l whole water samples for investigation of synurophyte species composition monthly. In 2005, we investigated the samples of the upper 1 cm of benthic sediment for the presence of *Mallomonas* scales. In 2003, we investigated the alluvial ecosystem as a whole, with a total area of freshwater pools of about 40 ha (Pithart 1997). For this investigation, we chose 12 pools lying in an 8 km long strip along the river. The pH values were 6.0–7.3 and conductivity values were 140–280 μS cm⁻¹. All samples were prepared for examination by TEM (for methods see Řezáčová et al. 2004).

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