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The genus *Mallomonas* (Mallomonadales, Synurophyceae) in several Southeast Asian urban water bodies – the biogeographic implications

by

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Abstract: We report the occurrence of 10 *Mallomonas* taxa from several urban water bodies in four Southeast Asian cities in Malaysia, Singapore and Indonesia. Apart from some cosmopolitan or pantropic species, the two presumed Asian synurophyte endemics (*Mallomonas grata* and *Mallomonas ocellata*) were found. We discuss the patterns of their geographic distribution that could contravene Finlay's neutral model of ubiquitous dispersal of microbial eukaryotes for these two species.

Introduction

The members of the class Synurophyceae, whose cells are covered with species-specific inorganic silica scales, are widely considered model organisms for studies of microalgal distribution and biogeography (Siver 1991, Kristiansen 2000, 2001, 2002, Kristiansen & Lind 2005). In this study, we concentrate on the synurophycean flagellates of the genus *Mallomonas*. Up to present, about 175 of species and infraspecific taxa have been described within this genus (Kristiansen 2002). There are now about 200 floristic and ecological studies reporting *Mallomonas* species composition in localities from all over the world, from all kinds of freshwater habitats (Siver 1991, Kristiansen 2002, Němcová et al. 2003). For numerous species, some ecological preferences were detected and *Mallomonas* species are now widely used for biomonitoring purposes (Smol et al. 1984, Hartmann & Steinberg 1989; Siver et

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al. 1996, Nováková et al. 2004). Mass occurrences of *Mallomonas* species in freshwater phytoplankton have mostly been reported from temperate and subarctic ecosystems (Eloranta 1995, Nicholls 1995). Even in tropical and subtropical ecosystems, however, there are now numerous studies documenting the occurrence of *Mallomonas* in these types of biotopes (e.g. Cronberg 1989, Vyverman & Cronberg 1993, Kristiansen & Menezes 1998, Wei & Yuan 2001, Wujek & Bicudo 2004, Menezes et al. 2005, Vigna et al. 2005).

Biogeography of microalgae has recently become a frequently discussed topic with the formulation of the neutral model of ubiquitous microorganismal dispersal (Finlay 2002, Fenchel & Finlay 2004; Finlay & Fenchel 2004; Finlay et al. 2004). The core of the neutral model hypothesis can be summarized as follows:

- The metapopulations of free-living microorganisms are sufficiently abundant to have a world-wide distribution and these extreme population numbers of individual species lead to their equable dispersion over the planet in a short evolutionary time.

- There are no historically determined biogeographic areas in microorganisms and the only geographic pattern that can be detected results from ecological requirements of individual species (e.g. temperature requirements).

Therefore, the relative frequency of the occurrence of an individual microbial species within a particular climatic zone on different continents or hemispheres should be similar according to the neutral model. Ubiquitous distributional patterns were demonstrated in different algal and protozoan groups (e.g. by Finlay & Clarke 1999, Finlay et al. 1999, Esteban et al. 2001, Wilkinson 2001, Fenchel & Finlay 2004), but the generalization of the neutral model to all eukaryotic microorganisms still remains a controversial issue (e.g. Foissner 1999; Lachance 2004). In the genus *Mallomonas*, the patterns of distribution were demonstrated for many species (Kristiansen 2000, 2001, 2002, Kristiansen & Lind 2005). The presumed distributional patterns suggested for individual taxa include those with cosmopolitan distribution, those with distributions restricted to particular climatic zones, and those which are endemic to individual continents or regions. However, according to the neutral dispersal model, the global distributions of species should follow presumably the latitudinal (based on general temperature gradient) or cosmopolitan patterns. Given the microbial nature of *Mallomonas*, none of the floristic studies that are based on EM investigations of scales from plankton or sediment samples, can claim to represent a comprehensive account of all species present at investigated localities. Rather, only the locally abundant species occurring in detectable numbers can be found using the floristic approach. Nevertheless, given the state of knowledge of the world distribution of *Mallomonas*, we can ask for the approximate probability of their ubiquitous distribution - either world-wide or within particular climatic zones.

The tropical and subtropical *Mallomonas* flora has now been reported in more than 70 floristic and ecological studies and 30 taxa are hitherto known only from tropical or subtropical climatic zones (Kristiansen 2002, Wujek et al. 2004, Vigna et al. 2005, Wujek & Dziedzic 2005). In this paper we concentrate on several urban water bodies in the equatorial region of Southeast Asia that were sampled in the years 2003-2005 in the course of field studies concerned primarily with terrestrial algae (Neustupa 2005). We have carefully investigated the whole water samples aiming at the enumeration of *Mallomonas* species occurring in phytoplankton of the localities and at the evaluation of their distributional patterns.

Material and methods

The 1000 ml whole water samples were taken at individual localities. The samples were immediately fixed with standard Lugol's solution. Water temperature and pH were measured in the field using a Hannah field pH-meter. The samples were rinsed in distilled water in a centrifuge, dried on to Formvar coated copper grids and shadowcast with chromium (Řezáčová et al. 2004). The grids were examined with Philips T 300 and JEOL 1011 transmission electron microscopes.

The samples were taken at the following localities:

1) a pool in Bogor Botanical Garden, West Java, Indonesia, altitude 200 meters a.s.l., area ca 100 m^2, pH 7.8, temperature 29°C, coll. 8.2. 2003.

2) a pool in Woodlands city area, Singapore, altitude 15 meters a.s.l., area ca 400 m^2, pH 7.2, temperature 25°C, coll. 4.2. 2003.

3) an artificial lake in Singapore Botanical Garden, altitude 45 meters a.s.l., area ca 1 ha, pH 6.8, temperature 31°C, coll. 31.1. 2005.

4) a pool in Chinese Bonsai Garden, Singapore, altitude 30 meters a.s.l., area ca 100 m^2, pH 8.3, temperature 30°C, coll. 31.1. 2005.

5) an artificial lake in Tasik Perdana city park, Kuala Lumpur, Malaysia, altitude 120 meters a.s.l., area ca 2.5 ha, pH 8.0, temperature 28°C, coll. 1.2. 2003.

6) an artificial lake in Seremban city park, Negeri Sembilan province, Malaysia, altitude 150 meters a.s.l., area ca 2 ha, pH 7.1, temperature 26°C, coll. 29.1. 2005.

Results

In total, 10 *Mallomonas* species were found in the investigated samples (Table 1).

Mallomonas cyathellata Wujek & Asmund Figs 1, 2

The scales with characteristic irregularly shaped pits on the secondary shield were observed. The observed struts on proximal border resemble *M. cyathellata* var. *chilensis* Dürrschmidt, but the rear scales with hare's ear-like protuberances were not observed, so that we report the occurrence of this alga on the species level only. This species was repeatedly reported from tropical to temperate localities world-wide (Kristiansen 2002), with a higher incidence in warm waters.

Mallomonas grata Takahashi in Asmund & Takahashi Figs 3, 4

We observed the body and collar scales with several more or less clearly demarcated subcircular depressions on the shield well corresponding with scales from the original description of this species (Takahashi 1963). So far, this species was reported in 10 floristic studies from Asia (Japan, China and India) (Kristiansen 2002). The recent

Table 1. List of species found at the investigated localities (for the description of localities - see section Material and methods). The numbers given in columns indicate the total number of scales observed.

	1	2	3	4	5	6
Mallomonas cyathellata Wujek & Asmund					4	
Mallomonas grata Takahashi in Asmund & Takahashi		5			1	
Mallomonas mangofera Harris & Bradley var. *mangofera* f. *reticulata* Cronberg					1	
Mallomonas mangofera Harris & Bradley var. *sulcata* Dürrschmidt				2		
Mallomonas matvienkoae (Matvienko) Asmund & Kristiansen var. *matvienkoae* f. *matvienkoae*				8	10	
Mallomonas matvienkoae (Matvienko) Asmund & Kristiansen var. *grandis* Dürrschmidt & Cronberg			6			1
Mallomonas multisetigera Dürrschmidt			11			
Mallomonas ocellata Dürrschmidt & Croome				2		
Mallomonas rasilis Dürrschmidt		6				
Mallomonas tonsurata Teiling em. Krieger var. *tonsurata*	12	7		3		2

floristic account of this species from Belize (Carty & Wujek 2003) we consider as dubious as the presented scales do not correspond to *M. grata*.

Mallomonas mangofera Harris & Bradley var. **mangofera** f. *reticulata* Cronberg Fig. 5

The identification of this taxon was based on the presence of characteristic raised ridges connecting the papillae on the shield (Kristiansen 2002).

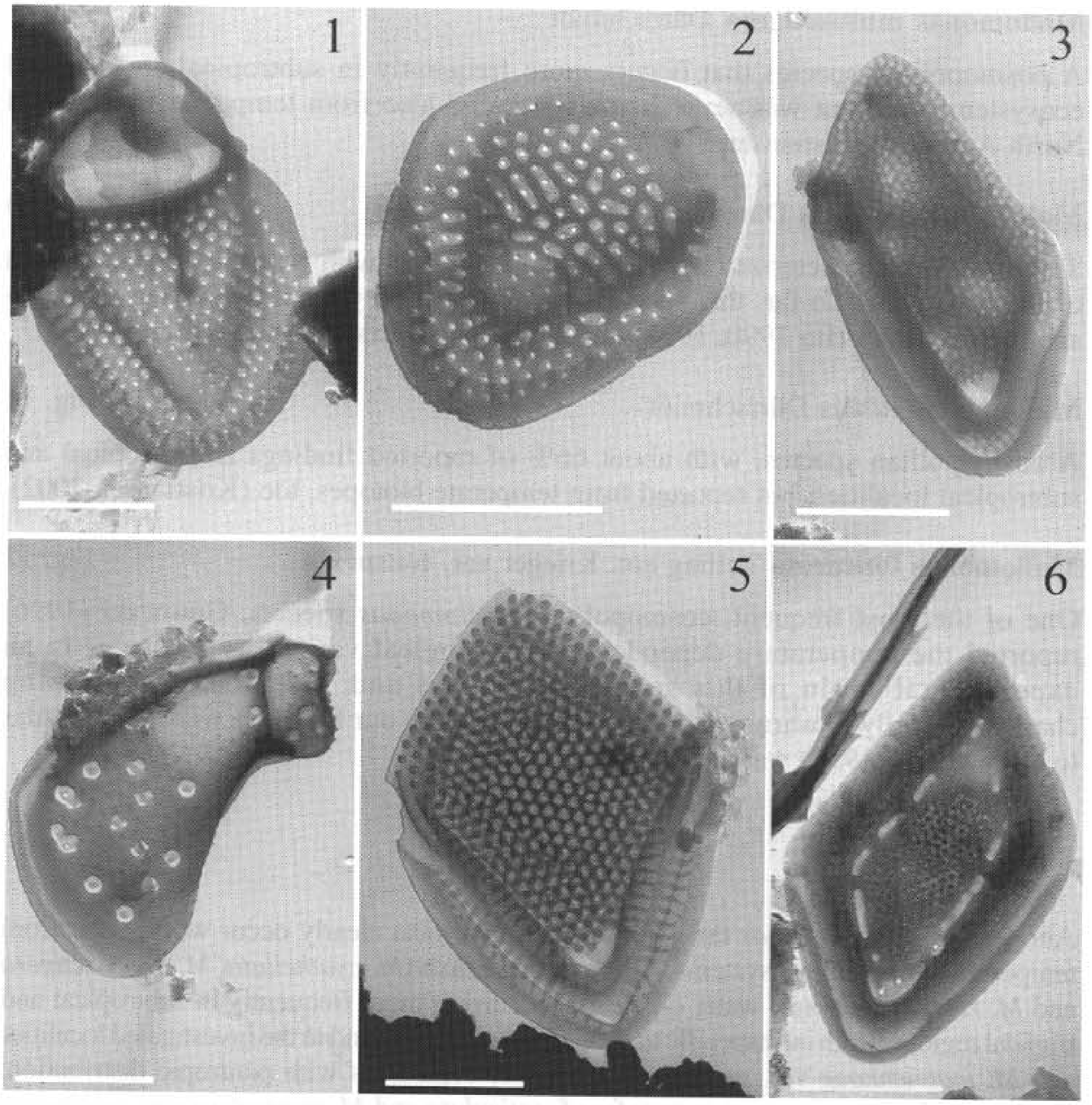
Mallomonas mangofera Harris & Bradley var. **sulcata** Dürrschmidt Fig. 6

This variety of *M. mangofera* is characterized mainly by the presence of grooves along the margin of the shield (Kristiansen 2002).

The varieties and forms of *M. mangofera* belong to the most frequently reported *Mallomonas* taxa from the tropics. However, it has also been found in the summer season in several temperate localities. *Mallomonas mangofera* var. *mangofera* f. *reticulata* was reported in seven studies from South America, Africa and Asia (Kristiansen 2002). So far, *M. mangofera* var. *sulcata* was reported in three studies from subtropical Japan and South America (Dürrschmidt 1983, Ito 1990, 1991).

Mallomonas matvienkoae (Matvienko) Asmund & Kristiansen var. **matvienkoae** f. **matvienkoae** Fig. 7

One of the most common, cosmopolitan *Mallomonas* species occurring in tropical to subarctic ecosystems.



Figs 1-2. *Mallomonas cyathellata*. Fig. 1. Body scale, Fig. 2. Rear scale. Scale bars = 1 µm. Figs 3-4. *Mallomonas grata*. Fig. 3. Body scale. Scale bar = 1 µm. Fig. 4. Collar scale. Scale bar = 2 µm. Fig. 5. *Mallomonas mangofera* var. *mangofera* f. *reticulata*. Body scale. Scale bar = 2 µm. Fig. 6. *Mallomonas mangofera* var. *sulcata*. Body scale. Scale bar = 2 µm.

Mallomonas matvienkoae (Matvienko) Asmund & Kristiansen var. **grandis** Dürrschmidt & Cronberg Fig. 8

This variety is characteristic by the presence of large subcircular pores on the proximal area of the scales and by larger scale dimensions. So far, this taxon was reported in 18 studies from tropical ecosystems world-wide (Kristiansen 2002, Franceschini & Kristiansen 2004, Wujek & Dziedzic 2005).

Mallomonas multisetigera Dürrschmidt Fig. 9

A cosmopolitan species that occurs more frequently in subtropical and tropical ecosystems, but that was several times reported also from temperate Europe and North America (Kristiansen 2002).

Mallomonas ocellata Dürrschmidt & Croome Fig. 10

The scales are characterized by the large eye-like pits with centrally thickened area of the base plate. So far, this species was reported only from two Asian regions - subtropical Japan (Ito 1990, 1991) and Malaysia (Dürrschmidt & Croome 1985).

Mallomonas rasilis Dürrschmidt Fig. 11

A cosmopolitan species, with about 66% of reported findings from tropical and subtropical localities, but reported from temperate biotopes, too (Kristiansen 2002).

Mallomonas tonsurata Teiling em. Krieger var. **tonsurata** Fig. 12

One of the most frequent, cosmopolitan *Mallomonas* species. Gutowski (1996) reported the temperature dependent morphological variability of scales in an experimental strain of this species with short and wide scales developing characteristically in warm water. The scales found in our localities were very similar to Gutowski's (1996) warm water morphotypes.

Discussion

Altogether 10 *Mallomonas* taxa were found. Five taxa clearly occur world-wide from temperate to tropical ecosystems. Three of these taxa (*M. cyathellata*, *M. multi-setigera* and *M. rasilis*) are warm water organisms occurring more frequently in subtropical and tropical regions. Both infraspecific taxa of *M. mangofera* found in the investigated localities and *M. matvienkoae* var. *grandis* are probably organisms with pantropic distribution. However, *M. mangofera* var. *mangofera* f. *reticulata* and *M. mangofera* var. *sulcata* are very rare taxa and, in addition, their taxonomic status is still unclear. *Mallomonas matvienkoae* var. *grandis*, with frequent reports from tropical regions of Central and South America, Africa and Asia, is a typical tropical taxon and its scales can be used as bioindicators of tropical climate in palaeoecological investigations.

Two species (*M. grata* and *M. ocellata*) seem to be geographically restricted and therefore are of special interest in the context of evaluation of the neutral dispersal model in synurophytes. So far, both these species have been found only in Asian localities. *Mallomonas ocellata* was only reported from subtropical and tropical localities. In total, there are now 74 floristic studies from all types of freshwater localities in subtropical or tropical ecosystems world-wide (Kristiansen 2002, Wujek et al. 2002, Wujek & Ogundipe 2003, Franceschini & Kristiansen 2004, Wujek et al. 2004, Wujek & Dziedzic 2005). From these floristic investigations, 18 studies were carried out in Asia. *Mallomonas ocellata* was found in four independent studies (including this paper) (Kristiansen 2002).

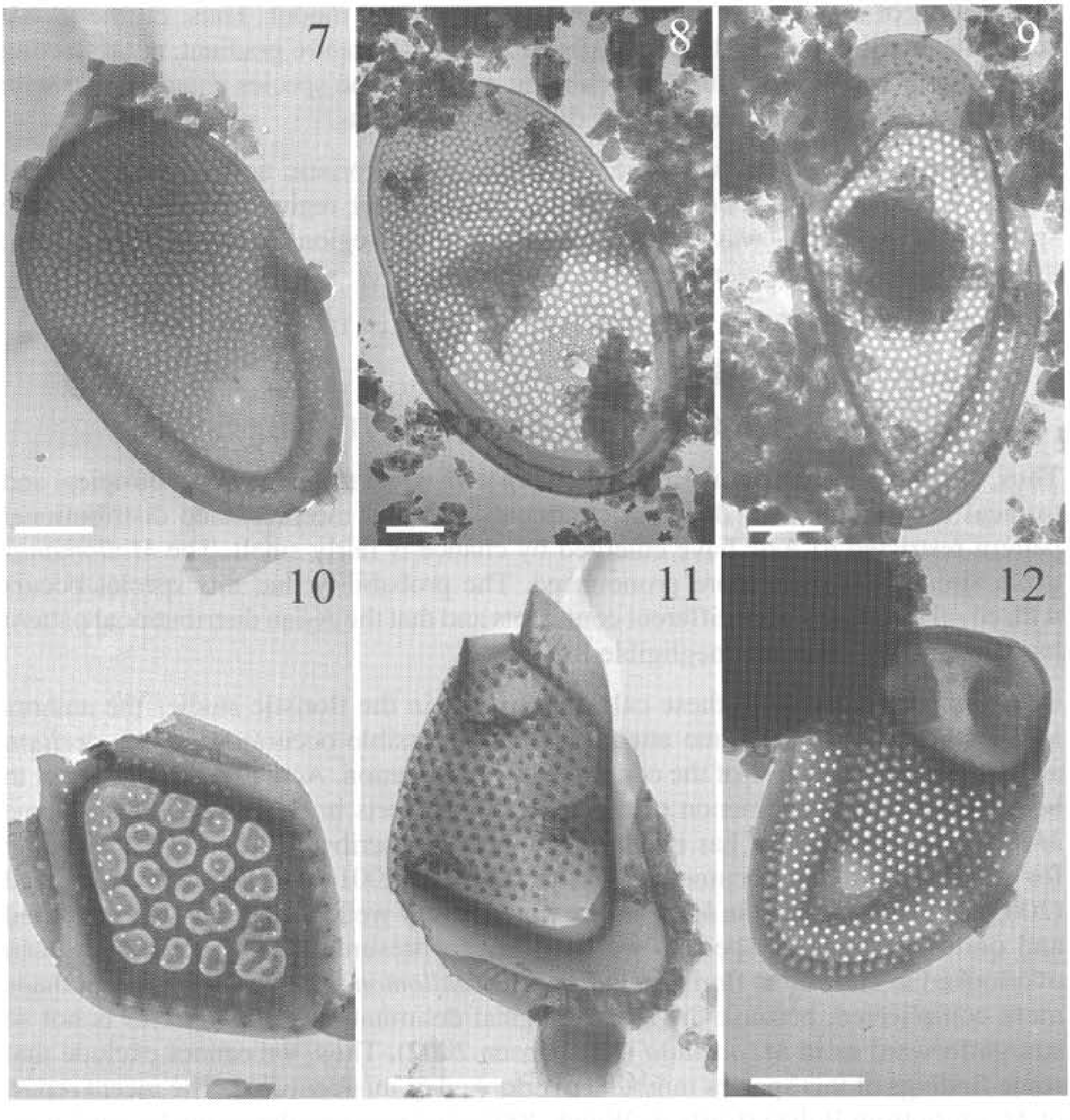


Fig. 7. *Mallomonas matvienkoae* var. *matvienkoae* f. *matvienkoae*. Body scale. Scale bar = 1 µm. Fig. 8. *Mallomonas matvienkoae* var. *grandis*. Body scale. Scale bar = 1 µm. Fig. 9. *Mallomonas multisetigera*. Body scale. Scale bar = 1 µm. Fig. 10. *Mallomonas ocellata*. Body scale. Scale bar = 1 µm. Fig. 11. *Mallomonas rasilis*. Apical scale. Scale bar = 1 µm. Fig. 12. *Mallomonas tonsurata* var. *tonsurata*. Body scale. Scale bar = 1 µm.

The second species, *Mallomonas grata*, was reported in 11 independent investigations from Asian localities ranging from typical temperate (winter phytoplankton in north China - Kristiansen 1989) to subtropical and tropical climate (India - Wujek & Saha 1996). In total, there are now 177 studies from these climatic zones world-wide (27 of them are from Asia). On the basis of these data, we can ask for the probability that these seemingly geographically restricted patterns of distribution in both species have emerged by chance. In other words, we ask for the probability that the distribution of a particular species follows the neutral model. Thus, on the global scale, the distribution should be based mostly on temperature gradient, not reflecting any geographic barriers within the climatic zone and the species should occur with approximately equal frequency over different continents.

In *Mallomonas ocellata*, we have 74 independent floristic accounts (*A*). Out of them, 18 studies were conducted in Asia - a particular region of interest (*Z*). The species - *M. ocellata* - was found four times (*x*) in a region *Z*. The probability that this pattern have emerged merely by chance is:

$$p = [Z/A] \; . \; [(Z\text{-}1)/(A\text{-}1)] \; . \; \ldots \; . \; [(Z\text{-}(x\text{-}1))/(A\text{-}(x\text{-}1))],$$

in *Mallomonas ocellata* it is:

$$p = (18/74) \; . \; (17/73) \; . \; (16/72) \; . \; (15/71) = 0.0026$$

Thus, the probability that this species occurs with equal frequency in subtropical and tropical ecosystems over different continents and that the presumed distributional pattern restricted to Asia have emerged by chance is fairly small. The *Mallomonas grata* situation is even more pronounced. The probability that this species occurs with equal frequency over different continents and that the Asian distributional pattern has emerged by chance is negligible 8.8×10^{-10}.

Of course, we suppose in these calculations that in the floristic studies the authors look with generally the same attention for the possible occurrence of *M. ocellata* and *M. grata* irrespective of the continent of investigation. Actually, this needs not to be the case. The phenomenon of more frequent reports in floristic studies of some *Mallomonas* species that has either been recently described or reported as endemic for some region was documented by Kristiansen (2001) and Kristiansen & Lind (2005). However, at least in *M. ocellata*, which is very well morphologically delimited and quite conspicuous species, we need not to presume that it could have been overlooked in non-Asian floristic studies. The *Mallomonas grata* situation is perhaps more complicated, because the morphological delimitation of the species is not so straightforward as in *M. ocellata* (Kristiansen 2002). Thus, we cannot exclude that some findings of this species might be overlooked or misidentified. The recent report of *M. grata* from Belize (Carty & Wujek 2003) that we consider as unclear and non-convincing on the basis of published data serves as an example of the somewhat complicated taxonomic status of this species.

However, on the basis of recent knowledge both *Mallomonas ocellata* and *Mallomonas grata* can be suspected as true Asian endemics. Their geographic distribution probably could contravene the neutral dispersal model and may be geographically restricted across different climatic zones in a single continent. We can now pose the question - which factors can restrict their distribution? In general, we can hypothesize about ecological or evolutionary factors. Either these organisms have significantly lower dispersal abilities than other freshwater microalgae (e.g. lower cyst survival rates than other synurophytes) or they can be young species from an evolutionary point of view that were not yet able to colonize the suitable biotopes elsewhere in the world. Ecophysiological culture studies and molecular phylogenetic data should be of much use in future investigations of this topic. Molecular phylogenetic data should only be acquired from identified cultured material. However, no strains of these species are available so far. Thus, the isolation and cultivation of such geographically restricted species should be of crucial importance for future research progress in this field. At the same time, the further floristic data on distribution of *Mallomonas* flagellates in freshwater localities - especially in the tropics - will be very useful for our understanding of real biogeographic patterns of these organisms.

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