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11. The Indo-Malaysian North-Australian phycogeographical region revised

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Abstract

The present knowledge of the freshwater algal flora in the Indo-Malaysian North Australian region is reviewed. More than 4700 taxa have been recorded from this region. Desmids, diatoms and cyanobacteria are among the better studied groups of organisms, while phytoflagellates have received very little attention. Phytoplankton communities in tropical lakes are generally similar to summer communities of temperate lakes. In addition, there is a large number of typical tropical taxa, including pantropical and regional endemic elements. Local endemism occurs in the old Tertiary lakes of the region. The composition of algal communities changes markedly along an altitudinal gradient, and tropical taxa are gradually replaced by taxa characteristic for cool climatic conditions. Biogeographical distribution patterns are exemplified for the desmids and diatoms. Among the more than 2680 desmids recorded from the Indo-Malaysian North Australian region, about 800 have never been found elsewhere. Dispersal by migratory birds and past climatic changes might explain distribution patterns. Because of incomplete taxonomy and a general lack of understanding of the autoecology, distribution and speciation of freshwater algae, however, there remain serious obstacles for detailed biogeographical analyses.

Introduction

Biogeography has never been very popular among freshwater phycologists. That groups which are distributed by passive dispersal make poor subjects for biogeographical enquiry (Ball, 1975), was a statement which has been vigorously opposed to by workers on freshwater zooplankton, especially by students of rotifers and copepods (e.g. Bayly & Morton, 1978; Dumont, 1980, 1983). Recent studies have shown that among zooplankton clear patterns emerge in the geographic distribution of taxa, which can be related to historical factors such as past climatic conditions, continental drift etc. (e.g. Maly & Bayly, 1991). Why has there not been any recent response from freshwater phycologists?

In the following, I will use the example of the Indo-Malaysian North Australian region to discuss some features of the geographic distribution of tropical freshwater algae and to illustrate some problems related to the interpretation of tropical algal floras. As early as 1902, West & West recognised that the region encompassing the Indian subcontinent, Sri Lanka, tropical south-east Asia and northern Australia shared a number of characteristic desmid species. This was further confirmed by Krieger (1932) who defined the Indo-Malaysian North Australian phycogeographical region, along with nine other phycogeographical provinces, based on the composition of the desmid flora.

Location and general characteristics of the Indo-Malaysian North Australian Region

The Indo-Malaysian North Australian region (IMNAR) (Figure 1) is an extremely diversified region in terms of geology, topography, climate, vegetation, and fauna. It comprises the land masses of the Indian subcontinent, the south-eastern part of the Asian continent, the Indonesian Archipelago, New Guinea and North Australia. The northern margin of the province roughly coincides with the Tropic of Cancer, to the south it is restricted to the more humid regions in the northern part of the Australian continent. The climate ranges from permanently humid and hot in New Guinea and a large part of Indonesia, to the distinct monsoonal climatic conditions at higher latitudes. Temperate and cold climates prevail in mountainous regions such as the central cordillera of New Guinea and Kalimantan. The Indonesian archipelago and New Guinea are important biogeographical boundary zones for the terrestrial fauna and flora, reflecting to a large extent past tectonic and climatic events.

Limnologically, the IMNAR is no less diverse than its terrestrial habitats. There is a wide range of aquatic habitats as regards origin and physical-chemical characteristics, including the numerous tectonic and volcanic lakes of Tertiary and more recent origin, extensive floodplain systems, alpine lakes and man-made lakes and reservoirs. Recent reviews of the limnology in the IMNAR have been published by Chambers (1987), Costa (1994), Giesen (1994), Ho (1994), Khondker (1994), Nontji (1994), and Pearson (1994).

History and nature of phycological research

As for most parts of the world, freshwater algal identification manuals do not exist for the Indo-Malaysian North Australian region. The widely scattered literature in various, often hardly accessible journals, makes it difficult to obtain precise estimates of the amount of work done on this region. We have made a compilation of 330 publications dealing with the systematics and ecology of freshwater algae in the IMNAR (Vyverman, unpubl.). This list is probably not complete but it reflects the amount and nature of the studies done. Despite the considerable number of publications, research in this region still lags considerably behind the better-studied northern temperate regions.

Taxonomic studies of the freshwater algae in the IMNAR started in the middle of last century (Grant, 1842 *cit. in* Suxena & Venkateswarlu, 1966), approximately at the same time when the earliest studies were undertaken in tropical South America and Africa. However, a rapid increase in the number of published studies did not start until the end of the nineteenth century. The large expeditions in the first half of the present century such as the German Sunda expedition (1928–1929) in Indonesia, the Wallacea expedition (1932) in the Philippines, the Sunda islands and Hawaii, have made a major contribution to the knowledge of the ecology and distribution of the freshwater algae in this region. One third of all publications are from India, illustrating the great phycological activity in this region. Indonesia (especially Java, Bali and Sumatra), Bangladesh, Malaysia and Korea are the next best studied regions, in terms of the amount and size of publications. However, in recent years, there have been very few phycological studies in Indonesia, while it was intensively studied earlier in this century. Since the late seventies, there is an increasing number of papers on the algae from Papua New Guinea.

A prerequisite for any biogeographical study is to record species distributions. There have only been few attempts to study the aquatic habitats of the IMNAR in a systematic way (e.g. Ruttner, 1952; Behre, 1956; Hustedt, 1937–1939, 1942; Ling & Tyler, 1986; Vyverman, 1991a, 1991b, 1992a, 1992b, 1992c, 1996). Many of the earlier publications and numerous present studies, rely on samples collected by non-phycologists. Although these publications contain very valuable information, the biogeographically most interesting but often hardly accessible aquatic habitats have only been scarcely studied. In a recent review of the major Indonesian lakes (surface area larger than 1 ha), Giesen (1994) states that among 35 lakes for which limnological data are known, only 14 have been comprehensively studied. The remaining 470 lakes in the archipelago are virtually unknown, illustrating the lack of even basic knowledge of their physical and chemical characteristics, let alone the biological parameters. In Papua New Guinea, the distribution of desmids and diatoms in only 150 of the more than 5000 large and small lakes (surface area larger than 0.1 ha) have been studied (Vyverman, 1992a, 1992b, 1992c); in only about 40 of them complete phytplankton communities have been investigated (Vyverman, subm., unpubl.). These observations are equally applicable for almost any other part of the IMNAR. Consequently, distribution patterns are very incomplete and have to be interpreted with great care as they reflect the distribution of studied localities rather than the geographic distribution of species.

Species diversity

Among the studies in our data-base, general accounts on the phytoplankton composition and ecology prevail (38%). The remaining 62% mainly concern systematic accounts of Chlorophyta (34%), especially desmids (22%), followed by Bacillariophyta (12%), Cyanobacteria (6%) and Rhodophyta (5%). Many of the general systematic accounts mainly concern the desmids (e.g., West & West, 1902; Ling & Tyler, 1986), illustrating

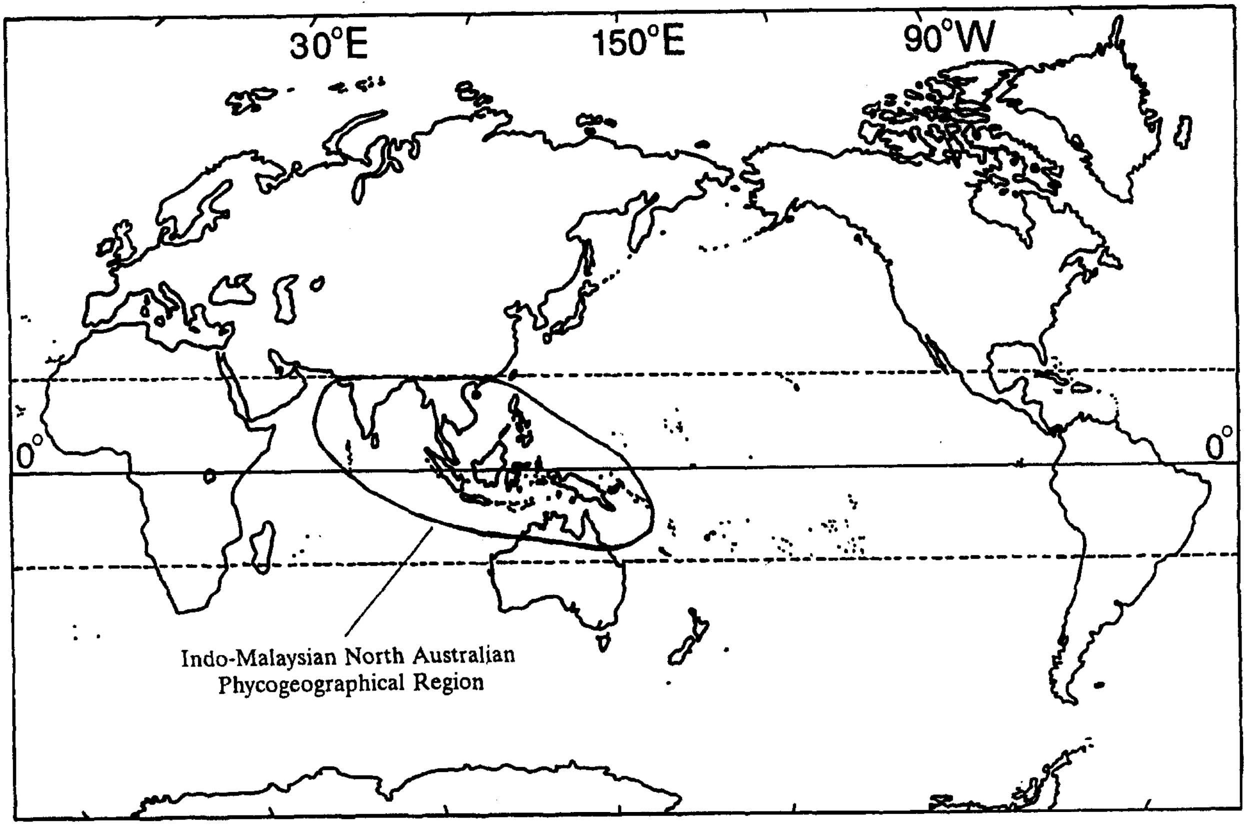

Figure 1. Location of the Indo-Malaysian North Australian phycogeographical region.

the great diversity of this algal group in the INMAR and the scientific preferences of the authors. Phytoflagellates are only poorly studied; studies in Euglenophyta, Cryptophyta, Dinophyta and Chrysophyta comprise only 5% of all studies. The recent discovery in the tropics of a high diversity of silica-scaled chrysophytes (e.g., Cronberg, 1989), formerly believed to be a group of cold-water organisms, confirms that the knowledge of phytoflagellates in tropical waters is still very limited.

It is difficult to estimate the actual number of taxa reported from this region. Not only the literature is widely scattered, but in many cases species lists need taxonomic and nomenclatural revision. With the exception perhaps of the diatoms and desmids, the figures given in Table 1 are only rough approximations of the total number of taxa per major taxonomic group described from the INMAR. We estimate that at least 4700 taxa have been recorded from this region. The overwhelming majority of them are chlorophytes (67%), especially desmids (57%); diatoms (19%) and blue-green algae (6%); whereas there is only a small number of phytoflagellates. New taxa are constantly being described, even in the better known groups such as desmids and diatoms, illustrating the insufficiently known species composition and diversity.

The vast number of taxa and their often incompletely known taxonomy is another great barrier towards a biogeographical analysis of the freshwater algal flora.

Comparison of tropical and temperate algal flora's

Reynolds (1984) gives a general scheme of the composition of phytoplankton assemblages and their seasonal succession in temperate lakes of different trophic status. Tropical lakes represent an equally diverse limnological spectrum as their temperate counterparts; the major factors controlling the wax and wane of algal communities are grossly the same as in temper-

Table 1. The dominant phytoplankton composition in low- and high-altitude lakes of different size and origin in the Indo-Malaysian North Australian region.

Lake	Surface km^2	Altitude m.a.s.	Phytoplankton composition (major taxa)	References
Aman	0.02	?	Eugleno, Chloro, Cyano, *Euglena, Trachelomonas, Ankistrodesmus, Crucigenia, Chlorella, Scenedesmus, Microcystis, Anabaena, Oscillatoria*	Yusoff & Patimah, 1994
Angii	4.5	1780	Chloro, Bacill, Cyano, *Oocystis, Staurastrum, Coelastrum, Surirella, Aulacoseira, Chroococcus*	Vyverman, unpubl. Irian Jaya
Batur	15.9	1031	Bacill, Cyano, Dino, *Nitzschia, Cyclotella, Dactylococcopsis, Anabaena, Lyngbya, Peridinium*	Ruttner, 1952.
Bune	0.1	2200	Chloro, Bacill, Chryso, *Staurastrum, Cosmarium, Aulacoseira, Mallomonas*	Vyverman, unpubl.
Govermas	9.8	40	Cyano, Chloro, Bacill, Dino, *Microcystis, Staurastrum, Cosmarium, Peridinium, Aulacoseira, Rhizosolenia, Eunotia*	Vyverman, subm.
Habbema	0.7	3325	Chryso, Dino, Chloro, *Dinobryon, Peridinium, Ceratium, Cosmarium*	Vyverman, unpubl., Irian Jaya
Imbuando	4.1	20	Eugleno, Cyano, Bacill, Chloro, Chryso, *Euglena, Trachelomonas, Oscillatoria, Aulacoseira, Dictyosphaerium, Mallomonas*	Vyverman, subm.
Keloet	?	1121	Cyano, Bacill, *Anabaena, Surirella*	Huber-Pestalozzi, 1932
Klindungan	1.9	10	Cyano, Dino, *Dactylococcopsis, Anabaenopsis, Lyngbya, Peridinium, Peridiniopsis*	Ruttner, 1952
Kopawunum	0.72	40	Chloro, Cyano, Bacill, Eugleno, Chryso, *Volvox, Dictyosphaerium, Kirchneriella, Oscillatoria, Aulacoseira, Rhizosolenia, Euglena, Trachelomonas, Mallomonas, Dinobryon*	Vijverman, subm.
Kutubu	4.99	808	Chloro, Cyano, *Botryococcus, Staurastrum, Cosmarium, Anabaena*	Bayly et al., 1970, Vyverman, unpubl.
Lamongan	0.34	240	Cyano, Bacill, *Anabaenopsis, Lyngbya, Nitzschia, Melosira, Oocystis, Tetraedron, Scenedesmus*	Ruttner, 1952
Lanao	357	700	Chloro, Cyano, Eugleno, Bacill, Dino, Crypto, *Oocystis, Closterium, Nitzschia, Melosira, Lyngbya, Anabaena, Ceratium, Trachelomonas*	Lewis, 1978
Lau	0.05	2800	Chloro, *Oocystis, Staurastrum*	Vyverman, unpubl.
Mainit	141	27	Cyano, Dino, Crypto, Chloro, *Anabaena, Lyngbya, Peridinium, Gymnodinium, Oocystis, Tetraedron, Rhodomonas*	Lewis, 1973
Merdada	2	2000	Chloro, *Staurastrum, Cosmarium, Scenedesmus*	Huber-Pestalozzi, 1935
Ohoitiel	?	?	Dino, Chloro, *Staurastrum, Arthrodesmus, Peridinium*	Nygaard, 1926
Pansoon Reservoir	130	?	Chloro, Crypto, Bacill, Dino, Chryso, *Euastrum, Staurastrum, Rhodomonas, Cryptomonas, Mallomonas, Dinobryon, Cyclotella, Gonyaulax*	Anton, 1994
Parago	0.9	2350	Dino, Bacill, *Ceratium, Peridinium, Aulacoseira, Cyclotella*	Vyverman, unpubl.
Patengang	?	1600	Chloro, Dino, *Staurastrum, Cosmarium, Ceratium*	Huber-Pestalozzi, 1935
Piunde	0.15	3650	Dino, Chloro, Bacill, *Peridinium, Staurastrum, Rhizosolenia*	Thomasson, 1967, Vyverman, unpubl.
P. Frederik Hendrik	0.2	3	Chloro, Bacill, Cyano, Chryso, Dino, *Staurastrum, Cosmarium, Xanthidium*	Vyverman, in prep.

ate lakes. One major difference, however, is the fairly constant temperature and solar irradiance in tropical lakes.

Pollingher & Berman (1991) state that major differences in the phytoplankton assemblages between lakes of the warm belt and those of other regions are mainly to be seen in large and deep lakes. Previous com-

Table 1. Continued.

Lake	Surface km^2	Altitude m.a.s.	Phytoplankton composition (major taxa)	References
(unnamed lake)			*Euastrum*, *Coelastrum*, *Scenedesmus*, *Dictyosphaerium*, *Kirchneriella* *Aulacoseira*, *Eunotia*, *Peridinium*, *Dinobryon*, *Mallomonas*	
Ranau	126	540	Bacill, Chloro, Synedra, *Nitzschia*, *Oocystis*, *Botryococcus*, *Tetraedron*, *Schroederia*, *Staurastrum*	Ruttner, 1952
Sindanglaja	0.02	1050	Dino, Bacill, Eugleno, *Ceratium*, *Peridinium*, *Cyclotella*, *Melosira*, *Synedra*, *Nitzschia*, *Trachelomonas*	Ruttner, 1952
Tasek Dayang Bunting	0.24	20	Dino, Chloro, Bacill, *Glenodinium*, *Staurastrum*, *Eunotia*	Yadav & Ratnasbapathy, 1974
Telaga Ngebel	1.48	730	Cyano, Chloro, Bacill, *Anabaena*, *Lyngbya*, *Anabaenopsis*, *Botryococcus*, *Oocystis*, *Cosmarium*, *Synedra*, *Cyclotella*	Ruttner, 1952
Titiwangsa	0.46	?	Cyano, Chloro, Dino, Chryso, *Merismopedia*, *Microcystis*, *Staurastrum*, *Eudorina*, *Peridinium*, *Dinobryon*, *Uroglenopsis*	Yusoff & Patimah, 1994
Tjigombong	0.3	500	Dino, Chloro, *Peridinium*, *Ceratium*, *Mallomonas*, *Dinobryon*, *Dactylococcopsis*, *Oocystis*, *Botryococcus*	Ruttner, 1952
Toba	1130	905	Bacill, Chloro, Cyano, *Denticula*, *Synedra*, *Melosira*, *Planctonema*, *Closterium*, *Aphanothece*, *Peridinium*	Ruttner, 1952

parisons of phytoplankton of tropical and temperate lakes (e.g., Lewis, 1978; Pollingher & Berman *op. cit.*) used the complete phytoplankton composition including spring, summer, autumn, and winter assemblages. A comparison of typical summer assemblages in temperate lakes (e.g., Reynolds, 1984) with phytoplankton assemblages from tropical lakes however indicates a greater overlap than when the complete phytoplankton composition is considered. Table 2 summarizes the dominant phytoplankton composition in some lowland and highland lakes in the Indo-Malaysian North Australian region. Although different sampling techniques were used (net plankton, quantitative samples), some general trends can be seen among the larger phytoplankton species. Typically, phytoplankton communities in tropical lakes are dominated by 'cosmopolitan' taxa, along with pantropical taxa in lowland lakes and 'northern-montane' species in highland lakes; while species with a more restricted geographic distribution usually occur in low densities.

Table 2. Approximate numbers of species per major algal group in the Indo-Malaysian North Australian region, based on a survey of 330 phycological and limnological publications. Taxonomic and nomenclatural revision is needed for most groups.

Taxonomic group	Taxa	%
Cyanobacteria	300	6.3
Bacilliariophyta	900	19.0
Euglenophyta	150	3.2
Chlorophyta	3200	67.3
Desmidiales	2700	56.7
Others	500	10.6
Chrysophyta	90	1.9
Cryptophyta	10	0.2
Dinophyta	50	1.1
Prymnesiophyta	?	?
Xanthophyta	50	1.1
Total	4750	100.0

In lowland lakes, chlorophytes and cyanobacteria, sometimes together with diatoms, are dominating, a feature which was also observed by Lewis (1978) and Pollingher & Berman (1991). There is no evidence for a decrease in species diversity towards the equator. The diatoms *Rhizosolenia* spp., *Aulacoseira granulata* (Ehr.) Simonsen and especially its var. *angustissima* (O.M.) Simonsen, and many genera of the chlorophytes and cyanobacteria typically also develop during the summer months in temperate lakes. Chrysophytes do not seem to play an important role in large tropical lakes, although Hecky & Kling (1987) found that in Lake Tanganyika a considerable fraction of the phytoplankton biomass is attributable to chrysophytes. In smaller lowland lakes such as the floodplain lakes in

New Guinea, chrysophytes are common (Vyverman & Cronberg, 1993) and quantitatively important, especially the genera *Dinobryon, Synura*, and *Mallomonas*. Other phytoflagellates, including euglenoids *(Euglena, Trachelomonas, Strombomonas)*, Volvocales *(Pandorina, Eudorina, Volvox)*, dinoflagellates *(Peridinium, Glenodinium)*, and unidentified green flagellates, constitute a significant fraction of the phytoplankton biomass in these lakes, especially during periods of mixing (Vyverman, 1996). A similar assemblage, dominated by euglenoids, was reported from Amazonian floodplain lakes (Schmidt & Uherkovich, 1973). This assemblage is also reminiscent of the summer phytoplankton of brown-water lakes in temperate regions, where phytoflagellates play an important role (e.g., Ilmavirta, 1988).

With increasing altitude, the phytoplankton composition changes considerably. Cyanobacteria are less important, and chlorophytes, dinoflagellates, diatoms and chrysophytes dominate. This altitudinal zonation in algal communities in tropical lakes is also obvious when benthic assemblages are considered. In Papua New Guinea, a highly significant relation was found between the composition of littoral diatom assemblages and altitude (Vyverman, 1992b; Vyverman & Sabbe, 1995), suggesting a strong effect of temperature and related factors on the composition of algal communities.

Despite the overall similarities in the structure of tropical and temperate phytoplankton communities, tropical lakes show striking some floristic differences with high-latitude lakes. To our knowledge, *Asterionella formosa* Hassal has never been reported from the IMNAR, but it is a common and often dominant species in the spring and summer phytoplankton communities in temperate lakes in the northern and southern hemisphere. In some tropical lakes, the genus *Surirella* is abundant in the plankton (Hustedt 1937–1939), while most temperate species of this genus are benthic. In other, often more eutrophic lowland lakes, *Synedra* and *Nitzschia* spp. may dominate the phytoplankton. The dinoflagellate genus *Peridinium* seems to replace the genus *Ceratium* towards the equator while *Ceratium hirundinella* (O.F. Müller) Dujardin, a very common and dominant species in temperate lakes, is rare; to our knowledge it has never been reported in typical lowland lakes of the INMAR. Whereas we have never found this species in the highland lakes of New Guinea, there are several reports from mountain lakes in Indonesia. In the New Guinea highland lakes the closely related species *C. brachyceros* Daday and *C. cornutum* (Ehr.) Claparède & Lachmann are common (Vyverman & Compère, 1991; Vyverman, unpubl.). It would be interesting to see whether the former reports of *C. hirundinella* agree with the typical forms from the temperate lakes or with *C. brachyceros*, or represent other species of this genus.

In the tropics, phytoplankton studies have mainly focussed on large lakes, whereas there is very little information on phytoplankton communities and species succession in smaller lakes. Other discrepancies between tropical and temperate lakes may be found after careful analysis and further studies of the algal communities in tropical lakes.

Geographic distribution patterns of freshwater algae

A large portion of the algal taxa in tropical lakes appears to have a world-wide distribution. Estimations of the cosmopolitan element in tropical phytoplankton communities invariably quote 50–80% of taxa with a world-wide distribution (e.g., Compère & Iltis, 1983). Only very few freshwater algal genera have a restricted geographic distribution. Among the desmids, the genera *Amscottia, Phymatodocis, Streptonema, Apriscottia*, and *Allorgeia* are confined to tropical regions. The diatom genera *Terpsinoë* and *Hydrosera* have their main distribution in the tropics, although there are some records from temperate regions (Round et al., 1990).

Although the geographic distribution of most algal species is badly known, there is little doubt that the high degree in cosmopolitanism to a large extent is true. However there are some difficulties related to the term 'cosmopolitan'. First, identification of tropical phytoplankton is mostly done using identification manuals or other publications from temperate regions, and the often slight differences in the morphological characteristics are neglected or interpreted as intraspecific variation. There are very few studies dealing with the morphological variation of these cosmopolitan species, using material from both tropical and temperate locations. In addition, there may be ecological or genetic differences between tropical and temperate populations of the same species, but this has not yet been studied in much detail. Finally, species are often referred to as cosmopolitan, but examination of their distribution patterns in the tropics shows that they mainly occur in high-altitude lakes.

The remaining 20 to 50% of the species in phytoplankton assemblages from tropical regions have more restricted distributions. They can be classified as pantropical 'northern-montane or northern hemispheric'. 'southern-montane or southern hemispheric', or 'local and regional endemic' taxa.

A large number of the non-cosmopolitan species can be considered as pantropical and occur widespread over the tropics. Pantropical species are found among all major taxonomic groups (Table 3); their distribution suggests a strict dependence on high and more or less constant temperature regimes (polythermic or warm stenothermic taxa). Some species seem to be more polythermic than others, the latter also occur in subtropical regions. Typical summer species in temperate lakes, such as *Aulacoseira granulata* var. *angustissima*, might also be regarded as warm-water taxa. The present knowledge of the autecology of most species is however too scant to allow more detailed conclusions about the influence of temperature on their occurrence and distribution. We do not know how and to which extent the growth of polythermic species is controlled by temperature, including the frequency and duration of 'cold-water' periods; or if other factors such as the ability to form resting spores, changing competitional strength, or niche availability also play a role. These observations also apply to the numerous 'northern-montane' species and to the increasing number of species described from cool climatic regions in the southern hemisphere, which can be regarded as 'southern-montane' taxa. In tropical high-altitude waters, there is a considerable number of species considered to be oligothermic (= cold stenothermic, in the literature often referred to as temperate- or northern-montane taxa). Again there appears to be a more or less continuous range from cold-stenothermic to poikilothermic species. Round (1981) argues that many of these oligothermic species have much wider distributions but, because of habitat loss, are becoming restricted to the generally less polluted mountainous and high-latitude waters. This may be true to some extent, but the striking similarity of diatom communities in tropical high-altitude lakes (e.g., Servant-Vildary et al., 1990; Vyverman, 1992a) with similar temperate habitats indicates that there is a large number of species confined to cool climatic conditions.

Table 3. Some examples of pantropical freshwater algae.

Cyanobacteria
Anabaena sphaerica Born. & Flah. var. *tenuis* G. S. West
Oscillatoria articulata Gardner
Trichodesmium iwanoffianum Nygaard

Bacillariophyta
Aulacoseira agassizii (Ostenfeld) Simonsen
Aulacoseira ikapoensis (O. Müller) Simonsen
Caloneis incognita Hustedt
Eunotia didyma Grunow
Gomphonema brasiliense Grunow
Navicula perrottetii Grunow
Pinnularia schweinfurthii (A. Schmidt) Hustedt
Pinnularia tropica Hustedt

Euglenophyta
Lepocinclis nayali Conrad
Strombomonas ensifera (Daday) Defl.
Trachelomonas armata (Ehr.) Stein var. *duplex* Playf.
Trachelomonas conica Playf. f. *punctata* Defl.

Chlorophyta
Ankistrodesmus bernardii Komarek
Coelastrum indicum Turner
Schroederia indica Philipose
Cosmarium ordinatum (Borges.) West & West
Euastrum praemorsum (Nordst.) Schmidle
Micrasterias foliacea Bailey ex Ralfs var. *ornata* Nordst.
Micrasterias radians Turn.
Pleurotaenium ovatum (Nordst.) Nordst.

Chrysophyta
Mallomonas bangladeshica (Takah. & Hayak.) Nicholls
Mallomonas bronchartiana Compère
Mallomonas tropica Dürrschmidt & Croome
Synura australiensis Playf.

Dinophyta
Ceratium brachyceros Daday
Peridinium gutwinskii Wolosz.

In addition to the numerous species which have a distinct latitudinal distribution there is a number of clear-cut species restricted to a certain geographic region. It is possible to distinguish between 'local endemics' which are only known from one locality such as geologically old lakes or from a particular ecological habitat, and 'regional endemics' which are confined to a larger geographic region. Regional endemic species can be found in most geographic regions. In Lake Tanganyika for example, 8% (30 taxa) of the diatom flora can be considered as local endemic species, while there are only few known endemic species in Lake Malawi and Lake Victoria (Cocquyt et al., 1993; Cocquyt & Vyverman, 1994). Regional endemic species, confined to the African continent, however, account for about 25% of the total algal flora in these lakes. Uherkovich (1984) estimates that about 390 taxa have been described from the Amazonas region which have never been found elsewhere. Equally, there are several well-defined species of algae which are endemic to Australia (Tyler, this volume).

In the following section I will give some examples of biogeographical distribution types from the INMAR. It is as yet not possible to present a complete analysis of the biogeographical relationships to other tropical regions. Furthermore, as I consider our current knowledge of most major algal groups to be too scant, I will mainly focus on the desmids and diatoms. There is however little doubt that further studies will demonstrate an Indo-Malaysian North Australian element in the other algal groups, such as *Peridinium baliense* Lindeman, *P. lingii* Thomasson and *Trachelomonas mediospina* Vyverman.

Examples of geographic distribution patterns of algae in the Indo-Malaysian North Australian region.

The Tertiary lakes in the Indo-Malaysian North Australian region have a number of endemic diatoms, which can be considered as local endemics and are either confined to one lake or to a number of lakes in the same area. The majority of them belong to the genus *Surirella* and many of them were described from lakes in Sulawesi and Sumatra (Hustedt, 1937–1939, 1942) (Figure 2). As with the African endemic *Surirella* species, they are often found in the plankton, but little more is known of their autecology. Stratigraphic records show that the genus *Surirella* is relatively young, which might be a reason for the large degree of endemism in this genus (Krammer & Lange-Bertalot, 1988). However, as they add, their planctonic life form in large lakes with a characteristic ecology, may prevent rapid dispersal as similar habitats are rare. Although local endemism among freshwater algae certainly exists, it is a rare phenomenon and has to be interpreted with care.

A much larger number of desmids and diatoms can be regarded as regional endemics. These include species which are confined to the INMAR, species which have their main distribution in the INMAR but also occur further to the north and/or south; and species which also occur on the African continent. The latter species are considered as palaeotropical elements.

We prepared a data-base of the desmids from the Indo-Malaysian North Australian region, resulting in about 2700 species, varieties and forms (Vyverman, in prep.). More than 800 of them (31%) have never been found elsewhere (Table 4). A data-base of the diatoms is in preparation, but at present it is taxonomically too incomplete to be used in a similar analysis. Even among the desmids, many taxa, especially the numerous infraspecific taxa, require further taxonomic investigations. Some typical Indo-Malaysian North Australian desmid species are shown in Figure 3, the geographic distribution of a number of them is shown in Figure 4a,b. Although the number of localities where these taxa have been found is rather small, there is little doubt that they also occur in many other suitable habitats in this region. Typically, they are rare in samples although in some lakes they may be abundant, such as e.g., *Staurastrum freemanii* West & West in Lake Birip (Brook & Hine, 1966; Vyverman, 1991b), and *Cosmarium mikron* Skuja in Lake Kopawunum (Vyverman, 1996).

Table 4. Numbers of desmid taxa per major genus and their number of regional endemic taxa recorded from the Indo-Malaysian North Australian region.

Genus	Total number	% total	IMNAR	% genus
Actinotaenium	41	1.5	8	19.5
Arthrodesmus	18	0.7	7	38.9
Bambusina	14	0.5	--	--
Closterium	321	11.9	45	14.0
Cosmarium	1041	38.8	310	29.8
Cylindrocystis	11	0.4	4	36.4
Desmidium	45	1.7	9	20.0
Docidium	22	0.8	8	36.4
Euastrum	413	15.4	146	35.4
Hyalotheca	11	0.4	4	36.4
Micrasterias	89	3.3	32	35.9
Penium	39	1.5	13	33.3
Pleurotaenium	84	3.1	31	36.9
Spondylosium	12	0.4	4	33.3
Staurastrum	310	11.5	147	47.4
Staurodesmus	86	3.2	15	17.4
Xanthidium	66	2.5	29	43.9
Other genera	71	2.6	11	15.5
Total	2684	100	823	30.7

Why is the distribution of these species restricted to the Indo-Malaysian North Australian region? Like the pantropical algae, the Indo-Malaysian North Australian flora element seems to be restricted in its distribution by temperature limits, both along latitudinal and altitudinal gradients. A study of the altitudinal distribution of non-cosmoplitan desmids and diatoms

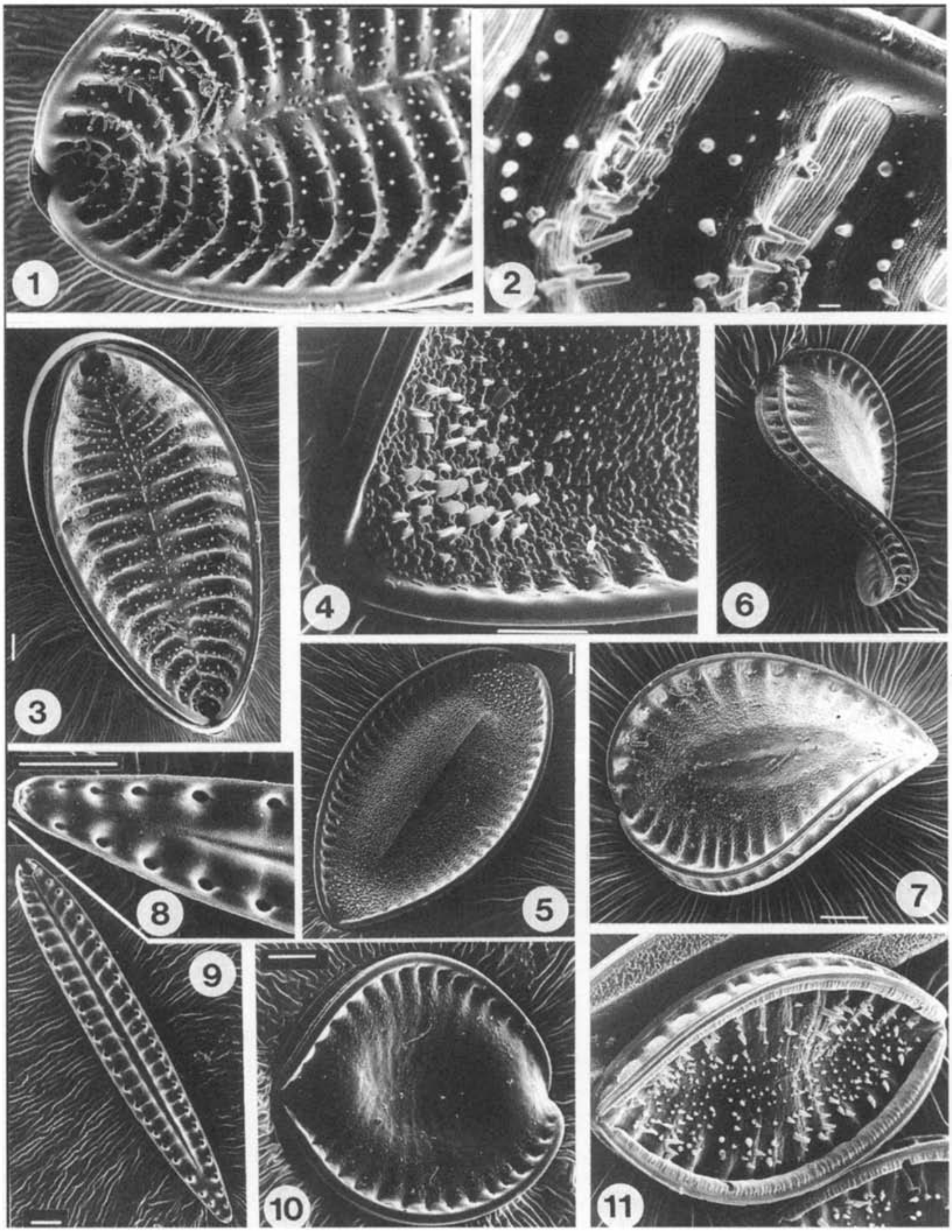

Figure 2. Endemic *Surirella* species from the Indo-Malaysian North Australian region. Figure 2.1–3. *Surirella robusta* Ehr. var. *armata* Hustedt, regional endemic, needs revision; Figure 2.4–5. *Surirella cataractarum* Hustedt; Figure 2.6–7. *Surirella pseudovalis* Hustedt, local endemic in lakes of Sulawesi; Figure 2.8–9. *Surirella excellens* Hustedt, local endemic in Lake Matano, Sulawesi; Figure 2.10. *Surirella woltereckii* Hustedt, local endemic in lakes of Sulawesi; Figure 2.11. *Surirella spinosa* Hustedt. Scale bar = 10 μm.

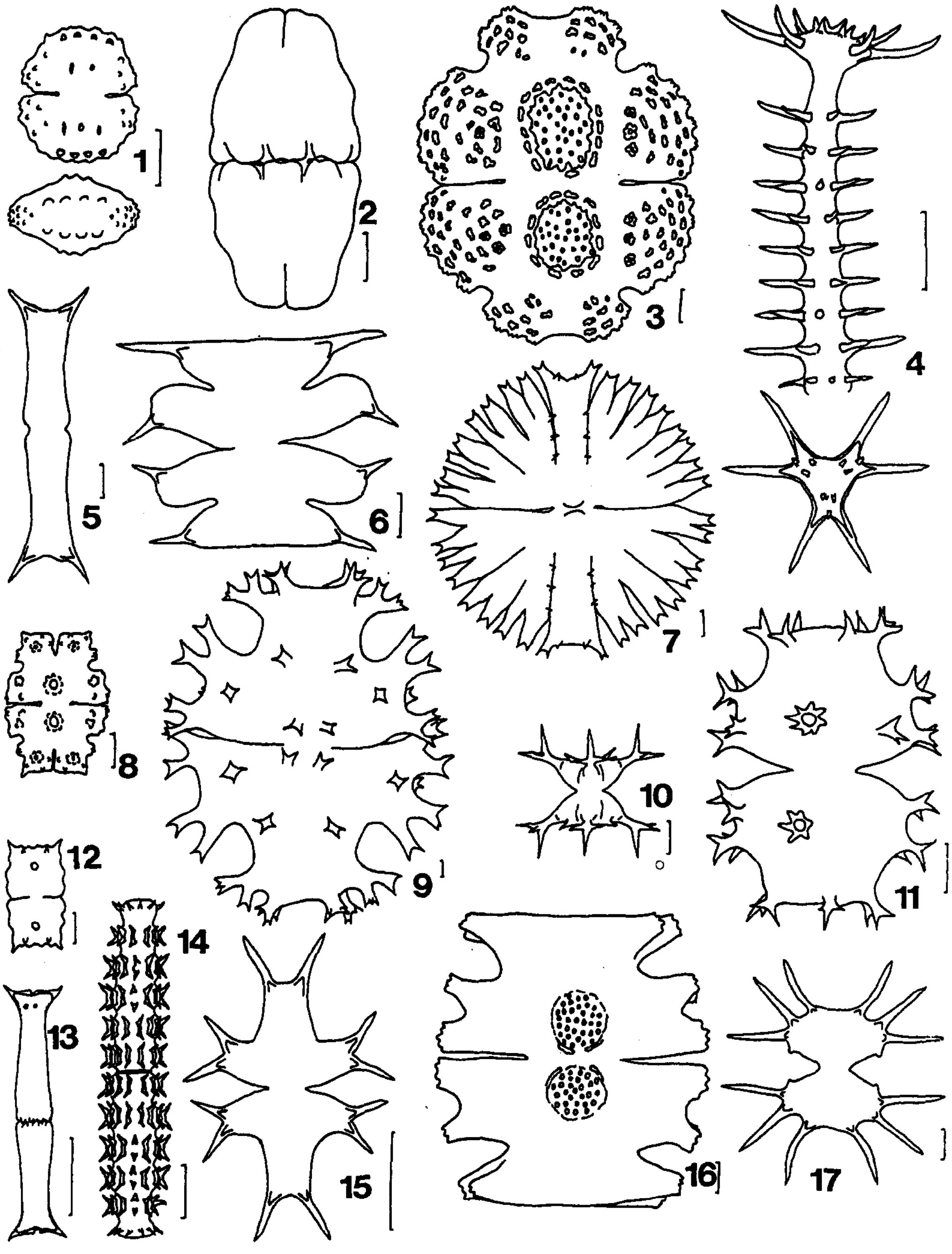

Figure 3. Some characteristic desmids from the Indo-Malaysian North Australian region. Figure 3.1. *Cosmarium ceylanicum* West & West; Figure 3.2. *Euastrum gnatophorum* West & West; Figure 3.3. *Euastrum horikawae* Hinode; Figure 3.4. *Triploceras splendens* Prowse; Figure 3.5. *Ichthyocercus longispinus* (Borge) Krieger; Figure 3.6. *Micrasterias zeylanica* Fritsch; Figure 3.7. *Micrasterias lux* Joshua; Figure 3.8. *Euastrum coralloides* Joshua var. *trigibberum* Lagerh.; Figure 3.9. *Micrasterias anomala* Turner var. *reducta* Scott & Prescott; Figure 3.10. *Staurastrum freemanii* West & West; Figure 3.11. *Xanthidium armatum* (Bréb.) Rabenh. var. *anguliferum* Krieger; Figure 3.12. *Euastrum exile* Joshua; Figure 3.13. *Ichthyodontum sachlanii* Scott & Prescott; Figure 3.14. *Pleurotaenium kayei* (Archer) Rabenh.; Figure 3.15. *Micrasterias ceratofera* Joshua; Figure 3.16. *Euastrum moebii* (Borge) Scott & Prescott var. *burmense* West & West; Figure 3.17. *Xanthidium sexmamillatum* West & West var. *pulneyense* Iyengar & Bai. Figures 3.8, 12, 14: redrawn after Scott & Prescott, 1961; Figures 3.4, 10, 13: redrawn after Ling & Tyler, 1986; Figures 3.1–3, 5–7, 9, 11, 15–17: original. Scale bar = 10 μm in all figures except for Figures 3.4, 14 where scale bar = 50 μm.

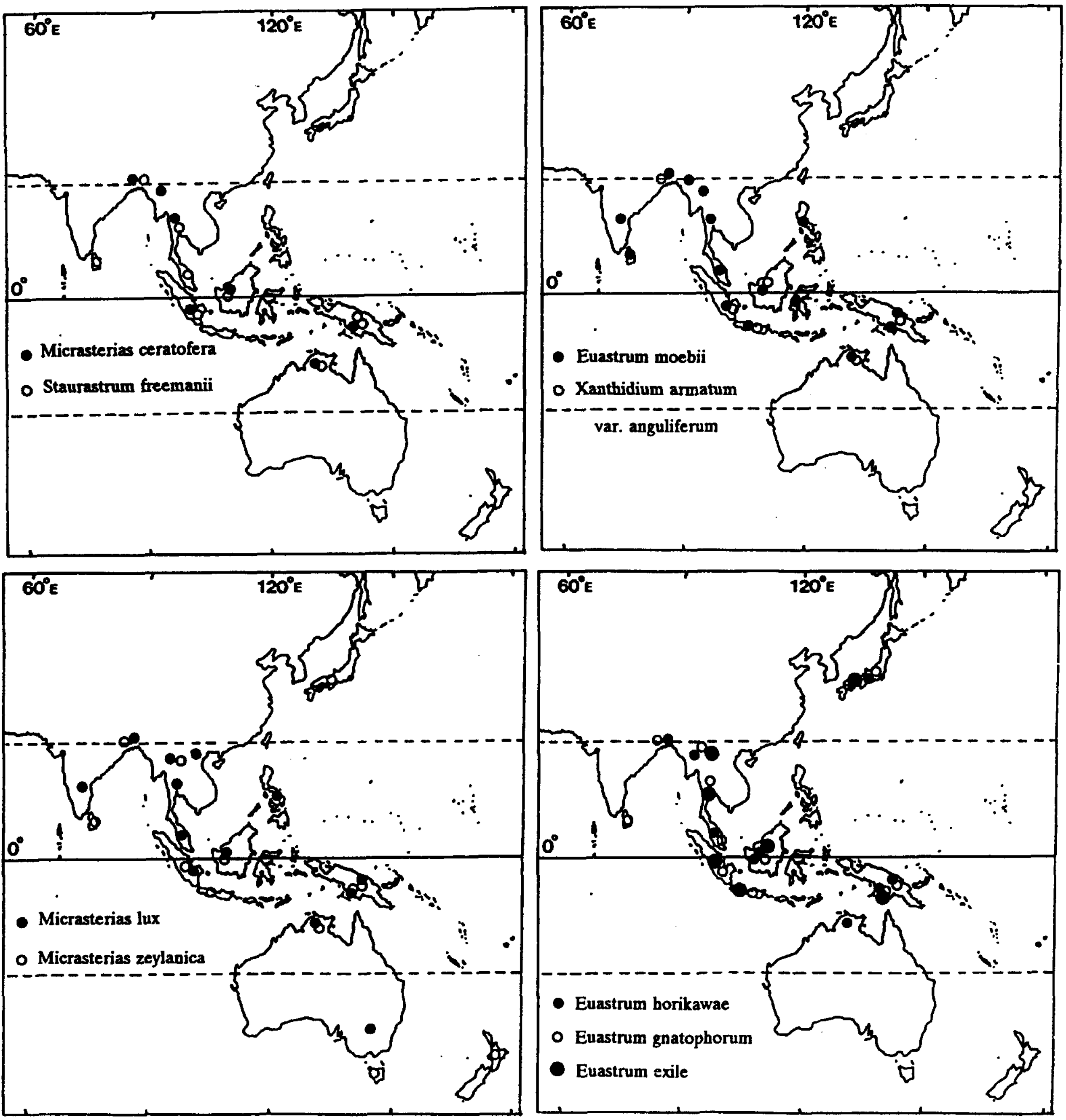

Figure 4. Some typical distribution patterns of desmids endemic to the Indo-Malaysian North Australian region. Figures 4.1–2: species restricted to the IMNAR; Figures 4.3–4: Species with a main distribution in the IMNAR, but also occurring further to the north and south. *Micrasterias zeylanica* also occurs in Africa.

(Vyverman, 1992b) has shown a gradual decrease in the proportion of pantropical, palaeotropical and Indo-Malaysian North Australian taxa along an altitudinal gradient in Papua New Guinea. Similarly, temperate-montane taxa replace the tropical element along higher altitudes. About 20% of the diatoms and 27% of the desmids in this study have a non-cosmopolitan distribution. The zone between 1700 and 2500 m seems to be the transition zone between typical lowland and highland algal floras, which is in agreement with the distribution patterns observed among aquatic macrophytes (Chambers et al., 1987).

There are some aparent differences between the composition of the non-cosmopolitan element in the desmids and diatoms. Among the diatoms, the pantropical element is considerably higher than among the desmids, which have a larger number of typical Indo-Malaysian North Australian species. It was postulated (Vyverman, 1992b) that this may be related to different dispersal capacities and/or speciation rates of diatoms and desmids.

Interestingly, several taxa which have their main distribution in the Indo-Malaysian North Australian region, also occur further to the north and to the south. Examples are *Euastrum horikawae* Hinode, *E. gnatophorum* West & West and *E. exile* Joshua, which occur to the north as far as Japan; and *Micrasterias zeylanica* Fritsch (which is also found in Africa) and *M. lux* Joshua which have been found in south-eastern Australia, Tasmania and New Zealand (Figure 4c,d). Similar distribution patterns were observed in the neotropics (Coesel et al., 1988). A possible explanation for these distribution patterns is passive dispersal by birds along the main north-south orientated migrating routes in the American and Asian/Australian regions. Although this is a plausible hypothesis, no research has yet been undertaken to obtain further evidence.

Palaeotropical species include the above-mentioned *Micrasterias zeylanica* but there are others as well such as *Micrasterias doveri* Biswas var. *africana* Bourrelly and *M. apiculata* (Ehr.) Meneghini ex Ralfs var. *lacerata* Turner. About 3% of the diatoms and 4% of the desmids of Papua New Guinea can be considered as palaeotropical taxa (Vyverman, 1992b). We estimate that for the complete desmid and diatom flora of the IMNAR, comparable or even higher figures will be found. Similar palaeotropical distribution patterns also exist for rotifers (Dumont, 1980) and have been explained by Pleistocene climatic events, allowing dispersal along the near East. In the case of the algae, such distribution patterns need to be further studied, but they indicate that dispersal routes for freshwater algae and rotifers follow similar patterns.

Sometimes, related species show distinct or partly overlapping geographic distributions. *Micrasterias crux-melitensis* (Ehr.) Hassall ex Ralfs and *M. radians* Turner can be used as a good example. Both species are closely related, the former has its main distribution in temperate regions, while the latter has a pantropical distribution. In New Guinea, *M. crux-melitensis* is distributed in some oligotrophic highland lakes, while *M. radians* is widespread in dystrophic lowland lakes and swamps. At medium altitudes, intermediate forms between the two species can be observed (Vyverman & Viane, 1995). *Eunotia serra* Ehr. is another example of a widespread diatom in oligotrophic waters in temperate regions, while related tropical species are *E. serrata* Hustedt, *E. tropica* Hustedt, *E. muelleri* Hustedt, and *E. subrobusta* Hustedt.

Conclusions

The majority of the freshwater lakes on Earth are of relatively young geological age. Most of them are of Pleistocene origin, and have since then been subject to climatic and ecological changes. Variations in water temperature are much smaller than in terrestrial habitats in a similar climatological and topographical setting. From an evolutionary viewpoint, a great dispersal capacity would be of prime importance to freshwater algae, which would contribute to their prevailing cosmopolitan distribution.

The example of the Indo-Malaysian North Australian region shows that, despite the considerable amount of research done, there are still large gaps in our knowledge of species diversity, taxonomy, ecology, and geographic distribution of tropical freshwater algae. This is a serious obstacle for any detailed biogeographical studies. World-wide monographic revisions, supported by modern taxonomic tools such as isozyme characterisation and genetic compatibility studies, combined with autecological studies focussing e.g. on dispersal capacities and on the effect of temperature-dependent processes on growth and survival, would be a first step towards a better understanding of distribution patterns of algae.

There can however be little doubt that freshwater algae do have a biogeography. In addition to a large cluster of pantropical and temperate-montane species with representatives in all major taxonomic groups, there are large numbers of taxa endemic to each of the different tropical regions. This shows that, although the composition and distribution of algal communities within a given region to a large extent is controlled by ecological factors, historical factors must play a role in the origin of regional endemism. At present however, any statement on the origin of such regional centres of endemism would be highly speculative as there is no information on speciation rate nor on the origin of these taxa.

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