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5. Biogeography of desmids

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Abstract

Compared with other groups of unicellular freshwater algae, desmids lend themselves well to biogeographical studies since, at species level, identification is often relatively easy, whereas high ecological demands use to curtail their geographical distribution. Considering some ten desmid floral regions as distinguished in the beginning of this century, Indo-Malaysia/Northern Australia, tropical America, and equatorial Africa come to the fore as most pronounced. Also well typified are Eastern Asia, New Zealand/Southern Australia, and North America. Less endemic species are met with in Southern Africa and extratropical South America, whereas temperate Eurasia, with respect to the other continents, is mainly negatively characterized. The so-called arctic-alpine desmid flora may be encountered on all continents, provided that adequate minimum temperatures occur. Its distribution seems to be determined microclimatologically rather than macroclimatologically. Arguments for a tropical origin of the desmids as an algal group are adduced.

Introduction

Consisting of unicellular organisms, members of the freshwater green algal family Desmidiaceae tend to show cosmopolitic distribution patterns, in this respect resembling bacteria rather than, e.g., macroscopic seaweeds. Yet, among freshwater algae desmids are known for a high number of exceptions to this general rule. Already G. S. West (1909) stated that no group of freshwater algae exhibits such marked geographical peculiarities as the Desmidiaceae. West (*loc. cit.*) even suggested that these peculiarities would enable to recognize the rough geographical origin of any desmid collection. Presumable explanations for the particular position of the desmids in this respect are, in the first place, the high number of taxa characterized by a conspicuous cell shape facilitating a ready and reliable identification. Furthermore, since in most desmid species the formation of resistant, wind-transportable spores is a rare phenomenon (Coesel, 1974a), distribution is supposed to be realized mainly as vegetative cells by insects and birds (Brook, 1981: 208). Distances bridged in that way in general will

be rather limited because of the chance of desiccation, or wash out in salt water. Finally, it is well-known that the vast majority of desmid taxa are confined to an oligo(-meso)trophic habitat. Consequently, most desmids may be considered K-strategists (Coesel & Kooijman-Van Blokland, 1991). Compared to r-strategists (like most chlorococcalean green algae) K-strategists make high demands upon their environment, requirements which usually may be only met in limited areas (MacArthur, 1972).

Krieger (1933, 1937) tentatively distinguished some ten desmid floral regions: Temperate Eurasia, The circumpolar regions, Eastern Asia, Indo-Malaysia/Northern Australia, New Zealand/Southern Australia, South Africa, Equatorial Africa, North America, the tropical part of America, and the extratropical part of South America. Although Krieger (*loc. cit.*) advanced that this classification would be refined as inventories intensified, so far nobody made a serious attempt to it. The reasons for this are not hard to find. First of all, the inventory of the various geographical regions is still extremely ill-balanced, so that geographical distribution maps often reflect the inten-

sity of phycological investigations rather than real distribution patterns. Actually, the following statement by Prescott (1948) is still standing: 'The picture is still hazy and lines are not well drawn, partly because the literature is so bulky that summarizing analyses are difficult, whereas many species seem to be characteristic of geographical areas and indeed may be classed as endemic, generalizations are continuously broken down as information increases and as supposed endemics are reported from far away stations'. Another cause of the stagnating development in the discipline of desmid biogeography is in the confusion associated with many taxonomic delimitations. No doubt, there is a lot of synonymy to be cleared up. Since even at genus level taxa have been mixed up – see, e.g., the discussion in Scott & Prescott (1960) concerning the closely allied *Micrasterias moebii* (Borge) W. & G. S. West, and *Euastrum turgidum* Wall. – utmost carefulness is demanded when drawing biogeographical conclusions. As Brook (1981: 211) rightly stated, no real progress in the delimitation of distribution areas may be expected until more knowledge is available about the morphological variability of the taxa in question. Therefore, before trying to refine Krieger's classification it seems recommendable to discuss the different regions mentioned with the help of distribution data of a number of clearcut taxa.

Concise characterization of the main desmid floral regions

Temperate Eurasia

Although better investigated than any other region, Eurasia turns out to have but few species on its own. Considering some possible examples, *Euastrum vigrense* Rypp., known from N. Russia, Poland, Finland, and Sweden (Engels & Handke, 1994) shows a sub-arctic distribution, and *Staurastrum verticillatum* Arch., known from Ireland, Scotland, Norway, S.W. France, and Portugal (Heimans, 1969) a distinct atlantic one. *Cosmarium insigne* Schmidle has been reported from Germany, Switzerland, France, Italy and The Netherlands (Coesel, 1974b). *Cosmarium dilatatum* Lütkem., reported from the Czech Republic, Finland, and The Netherlands (Coesel, 1989b) meanwhile is also known from Poland (A. Oleksowicz, in manuscript), and France (F. Kouwets, pers. comm.).

The pooriness in endemic species of the temperate Eurasian region at least partly may be ascribed

to the Pleistocene glaciations. Most flora elements characteristic of the tropical climate ruling in a large part of Europe during the Paleocene and Eocene were driven away from the continent during the glacial peaks in the Pleistocene (Frenzel, 1968). Whereas a fair number of land plant taxa could find a refugium in the Mediterranean region, warmth-demanding desmid species probably were doomed to extinction since the dry and often calcareous soils prevailing in the Southern parts of Europe and W. Asia are reputedly inhospitable to this algal group.

The periods of glaciation were also responsible for a considerable lowering of the sea level resulting in the development of temporary land bridges. Biogeographically most important was the Bering connection between N. America and N.E. Asia, explaining the many related flora and fauna elements on both continents (Cox & Moore, 1993). With respect to desmids, a fair number of species may be designated as holarctic, thus restricted in their distribution to Eurasia and N. America. Apart from a series of so-called arctic-alpine taxa (see next section) can be mentioned: *Euastrum insigne* Ralfs, *Eu. verrucosum* Ralfs, *Micrasterias oscitans* Ralfs, *M. verrucosa* Biss., *Cosmarium cyclicum* Lund., *C. perforatum* Lund., *C. protractum* (Näg.) De Bary, *Xanthidium subhastiferum* W. West, *X. brebissonii* Ralfs, *Staurastrum arcticon* (Ralfs) Lund., *S. elongatum* Bark., and *S. ophiura* Lund. (Prescott et al., 1977, 1981, 1982; see also Figure 1).

The circumpolar and high mountain regions

Quite a lot of desmid species are said to show an arctic-alpine distribution pattern. However, a critical perusal learns that but a few of them are strictly confined to these regions. Apart from the mesotaeniaceous snow alga *Ancylonema nordenskioeldii* Berggr., also *Euastrum spetzbergense* (Nordst.) Krieg., *Eu. tetralobum* Nordst., *Cosmarium holmii* Wille, *Staurastrum novae-semiliae* Wille, and *S. petsamoense* Järnef. so far were only found in the arctic parts of Eurasia and North America (Krieger, 1937; Kossinskaja, 1960; Prescott et al., 1981, 1982). Species like *Euastrum aboense* Elfv., *Eu. boldtii* Schmidle, *Eu. dissimile* (Nordst.) Schmidle, *Eu. tuddalense* Ström, *Cosmarium anceps* Lund., *C. caelatum* Ralfs, *C. costatum* Nordst., *C. crenatum* Ralfs, *C. cymatopleurum* Nordst., *C. hexalobum* Nordst., *C. holmiense* Lund., *C. nasutum* Nordst., *C. notabile* Bréb., *C. speciosum* Lund., *C. tatricum* Racib., *C. tetragonum* (Näg.) Arch., *Staurastrum acarides* Nordst., *S. capitulum* Bréb., *S. rhabdophorum* Nordst.,

Figure 1. A selection of holarctic desmid species: a. *Micrasterias oscitans*, b. *Euastrum verrucosum*, c. *Euastrum insigne*, d. *Staurastrum ophiura*, e. *Staurastrum elongatum*, f. *Staurastrum arcticon* (a, b. after Coesel, 1985; c. after West & West, 1905; d–f. after West et al., 1923).

and many others assigned to the group of arctic-alpine species (West & West, 1908, 1912; West et al., 1923; Ružička, 1981; see also Figure 2) are found predominantly under the rough climatic conditions of high latitude or altitude, but to a greater or less extent may be encountered in the temperate lowlands as well. Several authors (e.g. Grönblad, 1933; Krieger, 1937; Coesel, 1979) paid attention to the fact that so-called arctic-alpine species use to live hemi-atmophytically in water-saturated moss layers or on dripping rocks. Thomasson (1956), in a study on arctic and alpine lakes, concluded that among the euplanktic algae hardly any decidedly arctic or alpine forms could be distinguished, such in contradiction to the benthic algae. Obviously, the microclimate generated by the local

Figure 2. A selection of so-called arctic-alpine species: a. *Cosmarium speciosum*, b. *Cosmarium hexalobum*, c. *Cosmarium nasutum*, d. *Staurastrum capitulum*, e. *Staurastrum acarides*, f. *Staurastrum rhabdophorum* (a, c. after West & West, 1908; b. after Nordstedt, in West & West, 1908; d. after West & West, 1912; e. after West et al., 1923; f. after Nordstedt, in West & West, 1912).

environmental conditions to a large extent may compensate for the macroclimate.

Arctic-alpine species are particularly known from Eurasia and North America, but a number of them have been recorded from cold regions on other continents as well. For instance, from the Japanese Alps: *Cosmarium anceps*, *C. caelatum*, *C. nasutum*, *C. notabile*, *C. tetragonum* (Hirano, 1953), from Mount Wilhelm, in New Guinea: *Cosmarium caelatum*, *C. nasutum*, *Staurastrum capitulum* (Thomasson, 1967), from Mount Kenya, in equatorial Africa: *Cosmarium cymatopleurum*, *C. galeritum* Nordst., *C. garrolense* Roy & Biss. (Kusel-Fetzman, 1968), from Santa Marta Mountains, in Colombia: *Cosmarium caelatum*, *C. holmiense*, *C. nasutum*, *C. tetragonum* (Taylor, 1935), from the subantarctic Kerguelen Islands: *Cosmarium anceps*, *C. crenatum*, *C. holmiense*, *C. speciosum*, *C. tatricum*, *Staurastrum acarides* (Thérézien & Couté, 1977).

In contrast to the arctic regions, the desmid flora of Antarctica is extremely poor. Hirano (1965) in a review paper on Antarctic freshwater algae, mentions the mesotaeniaceous snow alga *Ancylonema nordenskioeldii* and, next to that, only five *Cosmarium* species: *C. crenatum*, *C. curtum* Bréb. (= *Actinotaenium curtum* (Bréb.) Teil.), *C. pseudoconnatum* Nordst., *C. undulatum* Ralfs, and the probably endemic *C.*

antarcticum Gain. In explanation of this poorness in species, Hirano (*loc. cit.*) refers to the strong isolation of Antarctica. Moreover, the absence of warm sea currents such as those operating near the northwesternmost parts of Eurasia and North America results in an almost complete and permanent covering of the Antarctic continent by pack-ice.

Eastern Asia

Although the temperate and colder parts of Eastern Asia have been relatively little searched for desmids a fair number of species seem to be characteristic of this geographical region. Illustrative are the many taxa newly described for Japan, e.g.: *Euastrum ozense* Hirano, *Cosmarium horomuiensis* Hirano, *C. margispinatum* Hirano, *C. pseudoquinarium* Hirano, *Xanthidium japonicum* Hirano, *Staurastrum asoensis* Hirano, *S. karasuensis* Hirano, *S. koidzumii* Hirano (Hirano, 1957, 1959a, 1959b). It is likely that a great deal of these taxa are present in China too. At the time of the Pleistocenic glaciations Japan was connected to China by a land bridge (De Lattin, 1967), and even nowadays the distance to China over sea may be thought to be bridged by migrating waterfowl. Unfortunately, so far only a few reports on desmids from China are known and, consequently, the number of species proper to both of these countries is low, e.g. *Euastrum horikawae* Hinode (Hinode, 1960; Wei, 1991) and *Staurastrum zahlbruckneri* Lütkem. (Lütkemüller, 1900; Hinode, 1977). The many new taxa recently described by Wei (1984, 1993) for some mountain areas in Eastern Asia make us believe that there is still much to be discovered in this geographical region.

Apart from a high number of presumable endemics, the biogeographical region under discussion is also characterized by quite a lot of species having the main point of their distribution in the tropics. Hirano's (1956, 1959a) Japanese desmid flora comprises species as *Ichthyocercus longispinus* (Borge) Krieg., *Pleurotaenium kayei* (Arch.) Rab., *P. ovatum* Nordst., *P. subcoronulatum* (Turn.) W. & G. S. West, *P. trochiscum* W. & G. S. West, *Euastrum gnatophorum* W. & G. S. West, *Eu. turgidum* Wall., all listed in Krieger's flora as tropical. No doubt, this has to do with the fact that, in contrast to the major part of Eurasia, the easternmost region of this continent remained free of pack-ice during the Pleistocenic glaciations (Pielou, 1979), and that there were open migration routes – unhampered by high mountain chains – to the tropical regions. This easy connection also explains the rather gradual transi-

tion between the Eastern Asian desmid region and the Indo-Malaysian/Northern Australian one.

North America

The North American continent is characterized by a rich desmid flora. As noticed already under the section Temperate Eurasia, North America shares a series of species with the European continent, among which quite a lot that seem to be confined to the northern hemisphere. However, in addition to that, the North American desmid flora counts many taxa which have the main point of their distribution in the tropics. Species like *Pleurotaenium ovatum*, *P. verrucosum* Lund., *Euastrum evolutum* (Nordst.) W. & G. S. West, *Micrasterias foliacea* Ralfs, *Staurastrum leptacanthum* Nordst., *S. leptocladum* Nordst., *S. rotula* Nordst. and *Phymatodocis nordstedtiana* Wolle, particularly known from various tropical regions, appear to penetrate into North America as far as Canada, or even Alaska (Prescott et al., 1975, 1977, 1982; Croasdale et al., 1983; see also Figure 3). The occurrence of these tropical elements in the colder parts of North America most probably has to do with the almost continuous series of freshwater bodies connecting tropical America with the northernmost regions (see, e.g., Figure 4 in Hoshaw & McCourt, 1988) and also with the N–S orientation of the main mountain chains, facilitating algal migration by waterfowl during and after the Pleistocenic glaciations.

Compared with Europe, the North American desmid flora not only is rich in tropical elements but also in endemic taxa. Of these latter, *Euastrum wollei* Lagerh., *Micrasterias muricata* Ralfs, *M. nordstedtiana* Wolle, *Cosmarium dentatum* Wolle, *C. eloiseanum* Wolle, and *Spinocosmarium quadridens* (Wood) Presc. & Scott are widely distributed throughout the United States and Canada (Prescott et al., 1977, 1981, 1982; see also Figure 4).

Tropical South and Central America

The geologically only recent (ca 3 million years ago) connection between Central and South America is well reflected in their respective desmid floras. Although treated as one geographical region by Krieger (1933), numerous taxa of common occurrence in tropical South America are unknown for Central America, e.g.: *Euastrum foersteri* Scott & Croasdale, *Eu. grandior natum* (Först.) Först., *Eu. pirassunungae* Borge, *Cosmarium cornigerum* (Nordst.) Först., *C. furcatum* Först.,

Figure 3. Desmid species with predominantly tropical distribution: a. *Staurastrum leptacanthum*, b. *Staurastrum rotula*, c. *Staurastrum leptocladum*, d. *Micrasterias foliacea*, e. *Phymatodocis nordstedtiana* (a. after Smith, in Prescott et al., 1982; b. after Förster, in Prescott et al., 1982; c. after Irénée-Marie, in Prescott et al., 1982; d. after Prescott et al., 1977; e. after Scott & Prescott, in Croasdale et al., 1983).

C. horridum Borge, *C. redimitum* Borge, *Xanthidium regulare* Nordst., *Staurastrum circulus* Grönb., *S. foersteri* Coes., *S. spiculiferum* Borge (Förster, 1982; Coesel et al., 1988; see also Figure 5).

No doubt, the high number of endemic taxa in tropical South America has to do with the long period of isolation of this continent, from the Middle Cretaceous up to the Late Pliocene (Cox & Moore, 1993), whereas the absence of these taxa in the likewise tropical water bodies in nearby Central America could be explained by the upheaval of the Andean mountains in about the same period that the Panama land bridge was formed. Most probably, the Andes, by forming a barrier for migrating waterfowl, effectively restricts the exchange of freshwater algae between the above-mentioned tropical areas (Coesel et al., 1988).

Figure 4. Some North American desmid species: a. *Micrasterias nordstedtiana*, b. *Micrasterias muricata*, c. *Euastrum wollei*, d. *Spinocosmarium quadridens* (a–c. after Prescott et al., 1977; d. after Prescott et al., 1982).

Extratropical South America

The richness in endemic taxa in tropical South America is in distinct contrast to the rather poor and trivial desmid flora encountered in the cool-temperate parts of this continent. Thomasson (1963), who studied the plankton in a large number of Northern Patagonian lakes, did not find an obvious relationship between the desmid flora of these lakes and that of tropical South America. He ascribed this to the elimination of many biota during the quaternary glaciations when ice covered a large part of Northern Patagonia. Recolonization from tropical South American regions would be hampered by the Andean mountain chain and the deserts in between. Tell (1980) stated that, on the American continent, many tropical desmid species reach their southern distribution limits in Northeastern Argentina (province of Corrientes).

Some desmid species, e.g. *Cosmarium andinum* Couté & Iltis (1988), *C. araucarense* Thomasson (1963), *C. magdalenense* Taylor (1935), and *Staurastrum mayori* G. S. West (1914) are exclusively known from cool-temperate areas in South America notably from the Andean mountains, it is true, but as long as these taxa are only known from a single locality they

Figure 5. Some species characteristic of the Neotropics: a. *Euastrum grandior natum*, b. *Euastrum foersteri*, c. *Cosmarium redimitum*, d. *Cosmarium cornigerum*, e. *Staurastrum circulus* (a–d. after Förster, 1982; e. after Coesel et al., 1988).

are hardly to be considered characteristic of the region under discussion.

The discrepancy between the Central American and the South American desmid flora as signalized in the previous section of course does not imply an absolute partition. A few taxa might be considered American endemics, occurring on both the Southern and the Northern continent, but their number seems to be very limited, e.g.: *Staurastrum minnesotense* Wolle, and *S. novae-caesareae* Wolle (Förster, 1969; Couté & Tell, 1981; Prescott et al., 1982).

Indo-Malaysia/Northern Australia

The rich, tropical desmid floras of Indo-Malaysia and Northern Australia are closely related as has already pointed out by West & West (1902) and later on by e.g. Krieger (1933), Scott & Prescott (1958) and Thomasson (1986). Characteristic species of this regions are, e.g., *Triploceras splendens* Prowse, *Euastrum asperum* Borge, *Eu. moebii* (Borge) Scott & Presc., *Micras-*

Figure 6. Some species characteristic of the Indo-Malaysian/Northern Australian region: a. *Micrasterias anomala*, b. *Micrasterias ceratofera*, c. *Staurastrum tauphorum*, d. *Staurastrum freemanii* (a–d. after Scott & Prescott, 1961).

terias anomala Turn., *M. ceratofera* Josh., *Staurastrum freemanii* W. & G. S. West, *S. tauphorum* W. & G. S. West, and *Streptonema trilobatum* Wall. (Krieger, 1933; Scott & Prescott, 1961; Thomasson, 1986; Ling & Tyler, 1986; see also Figure 6).

The high degree of resemblance between the desmid flora of Indo-Malaysia and that of Northern Australia is not surprising in view of the fact that the Australian continental plate, as a result of continental drift, contacted the Asian one already some 5 million years ago (Cox & Moore, 1993). The resulting formation of the closely packed Indonesian island archipelago will have considerably facilitated the exchange of freshwater algae between these two continents. Nevertheless, a number of desmid species described from Northern Australia so far have not been encountered in S.E. Asia, so they might be endemic of Australia: *Pleurotaenium australium* (Borge) Scott, *Cosmarium securiforme* Borge, *Xanthidium multicornae* Borge, and *Staurastrum elegans* Borge (Thomasson, 1986).

Southern Australia and New Zealand

Although West (1909) stated that the Australian desmid flora is largely tropical in character, 'even as far as Victoria', acknowledged tropical elements in the desmid flora so far described from Southern Australia are hardly known. Maybe, *Staurastrum sagittarium* Nordst. can be designated as such, being reported from tropical Africa (Bourrelly, 1957; Grönblad et al., 1958; Thomasson, 1965; Couté & Rousselin, 1975) and tropical Northern Australia (Scott & Prescott, 1958; Ling & Tyler, 1986), but also from Southern Australia (West, 1909; Prescott & Scott, 1952) as well as New Zealand from which the species originally was described (Nordstedt, 1888).

Rather than by pronounced tropical species the South Australian desmid flora is characterized by a number of (supposed) Australian endemics, such as *Micrasterias hardyi* G. S. West, *Cosmarium murrayi* Playf., *Staurastrum assurgens* Nordst., and *S. victoriense* G. S. West (West, 1909; Thomasson & Tyler, 1971; Thomasson, 1980; Ling & Tyler, 1986; Tyler & Wickham, 1988). However, these endemics are not at all common and in the southern part of Australia thrown into the shade by species widely distributed in temperate regions all over the world. The quite distinct character of the South Australian desmid flora as compared with the North Australian one probably has not only to do with a difference in climate but also with the absence of interconnecting series of suitable freshwater bodies, most of the land in between even being a desert.

The predominantly cosmopolitic character shown by the South Australian desmid flora is even more pronounced in the flora described from New Zealand, particularly where planktic habitats are concerned (e.g. Thomasson, 1973). Yet, a number of taxa may be designated as linking this island biogeographically to the Australian continent; e.g.: *Euastrum longicolle* Nordst., *Eu. sphyroides* Nordst., *Xanthidium octonarium* Nordst. (Croasdale & Flint, 1986, 1988), *Staurastrum rosei* Playf. (Thomasson, 1972), *S. sagittarium*, and *S. victoriense* (see above).

Although New Zealand, together with Southern Australia, originally made part of the Southern Gondwana province, it is unlikely that the distribution of the above-mentioned taxa argues a relict area. For New Zealand was split off from Gondwana already some 70 million years ago and since then has been isolated (Cox & Moore, 1993). Regarding the above-mentioned taxa, the close morphological resemblance between

specimens from Australia and from New Zealand is indicative of a much more recent geographical contact. Moreover, if it does concern relict areas one would also expect one or more of the taxa under discussion in the southern part of South America which proceeded from Southern Gondwana too. However, in the phytoplankton of North Patagonian lakes no elements have been found indicating such a transantarctic connection (Thomasson, 1963).

In view of the long period of isolation it is not astonishing either that the New Zealand desmid flora is characterized by a fair number of taxa of its own. Some examples: *Euastrum euteles* Skuja, *Eu. haplos* Skuja, *Eu. lagynion* Skuja, *Cosmarium subcyclicum* Mask., *C. turnerianum* Mask., *Xanthidium multigibberum* (Nordst.) Skuja (Croasdale & Flint, 1986, 1988).

Equatorial Africa

Like those in Indo-Malaysia/Northern Australia and in Central-South America, the desmid flora in tropical Africa is highly varied and rich in peculiar forms. Among the species characteristic of the African continent, *Staurastrum fuelebornii* Schmidle probably is most widely distributed (e.g. Schmidle, 1902; Rich, 1932; Grönblad et al., 1958; Thomasson, 1960; Compère, 1967; Lind, 1971; Couté & Rousselin, 1975). Other prominent representatives of the African desmid flora are: *Allorgeia incredibilis* (Grönbl. & Scott) Thom., *Micrasterias ambadiensis* (Grönbl. & Scott) Thom., *M. cunningtonii* G. S. West, *M. sudanensis* Grönbl., Prowse & Scott, and *Staurastrum rzoskiae* Grönbl. & Scott (Grönblad et al., 1958; Thomasson, 1960, 1966; Lind, 1971; see also Figure 7). The conspicuously shaped *Xanthidium calcarato-aculeatum* Hieron. and *X. sansibarensense* Schmidle, originally described from Zanzibar (Schmidle, 1898), not only appear to occur in many a tropical African country (e.g. Bourrelly, 1957; Grönblad et al., 1958; Thomasson, 1960, 1966; Lind, 1971) but also in the Indo-Malaysian/Northern Australian region (Scott & Prescott, 1961; Ling & Tyler, 1986) suggesting them to be a typical element of the Old World tropics. On the other hand there seem to be species exclusively in common with the Neotropics, like *Xanthidium mucronulatum* (Nordst.) Först. (= *Arthrodesmus mucronulatus* Nordst.), see Nordstedt (1869), West & West (1895), Grönblad (1945), Bourrelly (1957), Grönblad et al. (1958), Lind (1971), Bicudo (1975), Coesel (1992).

Figure 7. Some taxa characteristic of the equatorial African region: a. *Allorgeia incredibilis*, b. *Micrasterias sudanensis*, c. *Staurastrum rhoskae*, d. *Staurastrum fuellebornii* var. *evolutum* (a–d. after Grönblad et al., 1958).

In biogeographical considerations, the island of Madagascar uses to be dealt with as a separate unit because of the high degree of endemism in its flora and fauna. Also with respect to desmids a fair number of species are exclusively known from this region, e.g.: *Cosmarium allorgei* Bourr. & Couté, *C. anax* W. & G. S. West, *C. baronii* W. & G. S. West, *C. beatum* W. & G. S. West, *C. elaboratum* W. & G. S. West, *C. notochondrum* W. & G. S. West, *Bambusina madagascariensis* Bourr. & Couté (West & West, 1895; Bourrelly & Couté, 1991). However, almost all reports refer to incidental observations at a single locality. So as yet it seems somewhat premature to class them as endemics. Of special interest is also the occurrence of *Haplozyga armata* (Nordst.) Racib. (see Bourrelly & Couté, 1991), a species admittedly known from tropical South America (Nordsted, 1889; Raciborski, 1895; Förster, 1966).

South Africa

The presentation by Krieger (1933) of South Africa as a separate biogeographical region presumably is co-inspired by the extremely high percentage of endemics in its macrophyte flora. However, with respect to desmids, the flora of Southern Africa rather has to be considered a depauperate variant of that in Equatorial Africa.

Fritsch and Rich (e.g. Fritsch & Rich, 1937) described a number of new species from South Africa, it is true, but later on part of these appeared to be distributed in tropical Africa or even on other continents as well, e.g.: *Euastrum subhypochondrum* Fritsch & Rich (Bourrelly, 1957; Thomasson, 1960; Scott & Prescott, 1961), *Cosmarium salisburyi* Fritsch & Rich (Grönblad et al., 1958; Lind, 1967; Gerrath & Denny, 1988), *Xanthidium decoratum* Fritsch & Rich (Thomasson, 1960, 1966; Lind, 1971; Bourrelly & Couté, 1991). Species not encountered elsewhere, like *Euastrum biceps* Fritsch & Rich, *Cosmarium multiberculatum* Fritsch & Rich, *C. subhumile* Rich (Rich, 1935), as far as known were not found again in southern Africa either, so they can hardly be presented as endemics for this region. Just as in Australia, the weak relationship of the southern African desmid flora with its equatorial counterpart could be explained by the position of a vast desert area in between, hampering an easy exchange of aquatic organisms.

Geographical distribution of some selected genera

Illustrative of a possible radiation from a tropical region of origin is the actual distribution of a number of less-known, more or less related genera, i.e.: *Ichthyodontum* Scott & Presc., *Ichthyocercus* W. & G. S. West, *Triplastrum* Iyeng. & Raman., and *Triploceras* Bail. (Figure 8). Of these, *Ichthyodontum* so far has only been reported from the tropical Indo-Malaysian/Northern Australian region (Scott & Prescott, 1956, 1961; Ling & Tyler, 1986).

Ichthyocercus, obviously has a wider distribution, to be characterized as pantropical, i.e.: Indonesia (Krieger, 1933; Scott & Prescott, 1961; Lenzenweger, 1974), Northern Australia (Playfair, 1907; Croasdale & Scott, 1976), Equatorial Africa (West & West, 1897; Gauthier-Lièvre, 1960) and Equatorial South America (Borge, 1899; Förster, 1969; Couté & Tell, 1981; Thérézien, 1985). However, in addition to that, there are also reports from Southern Japan (Hirano, 1956), Madagascar (Bourrelly & Leboime, 1946; Bourrelly & Couté, 1991) and Northern Argentina (Tell, 1979).

The distribution of *Triplastrum* – as far as known limited to the Old World – shows a rather scattered pattern, but still with an accent on warmer climatic regions: Equatorial Africa (Gauthier-Lièvre, 1960; Couté & Rousselin, 1975), South Africa (Claassen, 1977), Southwestern France (Allorge, 1924; Capde-

Figure 8. Four genera with a mainly tropical distribution, radiating to different extent into colder climatic regions. a. *Ichthyodontum* (*I. sachlanii*), b. *Ichthyocercus* (*I. longispinus*), c. *Triplloceras* (*T. verticillatum* var. *minor*), d. *Triplastrum* (*T. spinulosum* var. *africanum*) (a. after Scott & Prescott, 1956; b–d. after Gauthier-Lièvre, 1960).

vielle, 1978), Turkestan (Krieger, 1937), India (Iyengar & Ramanathan, 1942), Japan (Hinode, 1952).

Finally, of the four taxa under discussion, *Triplloceras* is the most widely distributed and also the most successful in penetrating into colder climatic regions. Being a common taxon in all tropical regions (Krieger, 1937), it is also known from, e.g., Labrador (Prescott et al., 1975), New Zealand (Croasdale & Flint, 1986) and Northern Eurasia (Kossinskaja, 1960). On last-mentioned continent it seems to reach its western limit in the Baltic States and Finnish Lapland (Kossinskaja, 1960; Wasylik, 1961). It has never been reported from Western Europe but probably its appearance is only a question of time, for its potential distribution area seems to be cosmopolitan.

Discussion

Because of their unique way of sexual reproduction, the conjugatophyceean group of green algae, comprising the unicellular desmids, is hypothesized to have its evolutionary origin in an environment that may be characterized as terrestrial rather than aquatic (Stebbins & Hill, 1980). That their occurrence, nowadays, in

aquatic habitats is likely to be considered a secondary adaptation is supported by the fact that the vast majority of the desmid taxa still have a benthic or tychoplanktic way of life. Euplanktic species (which are hardly or never encountered in a sexual stage) are relatively scarce (Brook, 1981). As already stated in the Introduction section, in addition to that, most desmid taxa are confined to a low nutrient state of the habitat. It is worth mentioning that euplanktic desmid taxa, particularly those from eutrophic waters, biogeographically show much less differentiation than benthic, oligomesotrophic taxa (Thomasson, 1955; Coesel, 1992). This might be indicative of a more efficient dispersal and a more successful distribution.

Presumably, the desmids as an algal group – recently estimated at some 3000 species (Gerrath, 1993) – have their evolutionary origin in the tropics. In the discipline of biogeography it is customary to consider the area richest in species or morphological diversity as the area of evolutionary origin of a given taxonomic group (e.g. Banareescu, 1990). Roughly speaking, from poles to equator there is a gradual increase in the number of desmid taxa (both species and genera), culminating into a morphologically highly diversified tropical flora. Bizarre forms as found in the asymmetrical genera *Allorgeia* Gauthier-Lièvre and *Amscottia* Grönb. are confined to the equatorial zone, whereas in (sub)polar regions most taxa are characterized by simple, compact cell shapes (compare Figures 2 and 7). Also when regarding their contribution to the total algal biomass, desmids seem to play a more important role in tropical aquatic ecosystems than in cold-temperate ones. In temperate climatic regions, desmids are well-known for the high number of species, relative to other phytoplankton groups, in oligotrophic waters (Hutchinson, 1967). However, their quantitative contribution (in terms of cell numbers, or biomass) seems to be so small that they are not figuring in any plankton typology based on that criterion (Reynolds, 1984). In contrast to that, there are several authors reporting desmids as the quantitatively dominant group of primary producers in tropical aquatic ecosystems (e.g. Hegewald et al., 1976; Khan & Ejike, 1984; Biswas, 1984, 1992; Anton, 1994).

Finally, the hypothesis of a tropical origin of the desmidiaceous algae is also supported by the high optimum temperatures as experimentally determined in a series of planktic species isolated from Western Europe. Coesel & Wardenaar (1990) found optima ranging from 25 to 30 °C, whereas hardly any growth was measured at temperatures lower than 10 °C. These

optimum temperatures are higher than in most other phytoplankton groups (Reynolds, 1984). In this light it is not amazing that Hirano (1965) reported only 8 desmid species from the Antarctic continent, as against 68 species of diatoms, which, in general, show distinctly lower temperature optima (Reynolds, *loc. cit.*). Accordingly, potential geographical distribution patterns of desmid species will be determined by minimum, rather than maximum temperatures in a given region. For even in arctic and high mountain regions, in summer period the water temperature in shallow pools may rise to over 25 °C at day time (Messikommer, 1942; Thomasson, 1956). In this context it is interesting to note that, as already discussed in a previous section, 'typical' arctic-alpine species are particularly encountered in thin water films covering bare rocks and moss vegetations: a substrate that readily will be frozen at night. Obviously, the species in question can well stand periodical (and also lengthened) freezing. Since these environmental conditions are also operating in temperate lowlands in winter time, it may explain the local occurrence of arctic-alpine species there, but only in such hemi-atmophytic habitats where they will be in competitive advantage over freezing-sensitive species. In bigger water bodies, desmid taxa not withstanding freezing may survive near the relatively warm mud bottom or in the thermally stable (4 °C) hypolimnion zone of deep lakes.

If the potential area of desmid taxa would be paramountly determined by minimum temperatures indeed, likely but three main geographical regions may be distinguished: tropical, cool-temperate and arctic-alpine. In that case, a further differentiation as shown by actual geographical distribution patterns has to be ascribed to migrational barriers (seas, arid areas, mountain chains) met with in the course of evolutionary development. The distribution of the genera *Ichthyodontum*, *Ichthyocercus*, *Triplastrum* and *Triploceras* as discussed in a previous section, could give an impression of various degrees of unfurling from a tropical region of origin. However, it is quite obscure whether the actual distribution patterns in question have to do with different times of origin at a phylogenetic tree, differences in ecophysiology determining their potential distribution area, or a different success in dispersal. A similar problem is raised by the question whether the occurrence of so-called alpine desmid taxa in high mountain areas in (sub)tropical regions is exogenic (long-distance dispersal from similar habitats elsewhere), or endogenic (evolutionary adaptation of related taxa in nearby lowlands) in origin, or the result of a drastic

climatic change (relict area). Considering the above-discussed high upper limit of the temperature range in arctic-alpine species, and also in view of the remarkable morphological uniformity in many of these taxa, incompatible with a long period of geographical isolation, the first option seems to be the most likely.

However, it is not to be excluded that small differences in morphology as illustrated in certain desmid taxa along altitudinal gradients are caused by temperature. Such differences originally could be phenotypical in nature, but later on genotypically fixed. See, e.g., the length of cell processes in *Staurostrum leptacanthum* Nordst. from different altitudes in Colombia (Coesel, 1992), and in *Micrasterias crux-melitensis* Ralfs versus *M. radians* Turn. described from higher and lower altitudes in Papua New Guinea respectively (Vyverman, 1991).

In biogeography, one of the main indications of the splitting up of an originally connected distribution area is the occurrence of vicariant species. Because of the poor knowledge of the morphological variability of most desmid taxa it is quite a problem to designate such pairs of vicariant species. A possible example might be *Xanthidium trilobum* Nordst. and *X. subtrilobum* W. & G. S. West. So far, *S. trilobum* has only been reported from South and Central America (e.g., Nordstedt, 1869; Grönblad, 1945; Förster, 1964; Prescott, 1966; Thomasson, 1971; Couté & Tell, 1981; Thérézien, 1985; Coesel, 1992), whereas *X. subtrilobum* is known from Africa, S.E. Asia, and N. Australia (e.g., West & West, 1897; Rich, 1935; Jao, 1949; Skuja, 1949; Grönblad et al., 1958; Thomasson, 1960; Scott & Prescott, 1961; Couté & Rousselin, 1975; Croasdale & Scott, 1976; Islam & Haroon, 1980; Ling & Tyler, 1986). It has to be noted, however, that the differences in morphology between *X. trilobum* and *X. subtrilobum* seem far too small to render its plausible that the period of separate evolutionary development started already ca. 100 million years ago (i.e., the presumable extension of the Atlantic Ocean, see Pielou, 1979). So, more likely, the supposed allopatric speciation under discussion is to be described by the dispersal model (colonization) rather than by the vicariance model (fragmentation), see Craw (1988). In general, such desmid sister taxa will be detected more readily at infraspecific level since their mutual relationship is more obvious. A still higher degree of differentiation may be expected at submicroscopic level. Slight differences in genome structure whether or not bound up with a geographical isolation not necessarily need to be expressed in cell morphology but may result into sexual incompat-

ibility, see the biological entities distinguished within *Closterium ehrenbergii* Ralfs (Ichimura, 1985; Coesel, 1989a). However, as yet, for getting a better insight into the main features of desmid biogeography a critical investigation of the morphological variability and geographical distribution of traditional taxa seems to have priority.

When trying to come to a very first, rough evaluation of Krieger's desmid floral regions as discussed in this paper we may conclude that Indo-Malaysia/Northern Australia, tropical America, and equatorial Africa are the most pronounced regions. Also well typified are Eastern Asia, New Zealand/Southern Australia, and North America. Less endemic species are met with in Southern Africa and extratropical South America, whereas temperate Eurasia, with respect to the other continents, is mainly negatively characterized. Finally, the so-called arctic-alpine desmid flora may be encountered on all continents, provided that adequate minimum water temperatures occur. Its distribution seems to be determined microclimatologically rather than macroclimatologically.

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