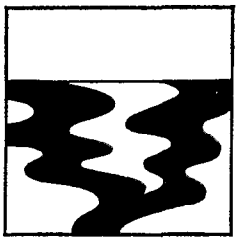

# *Distributional patterns in some neotropical desmid species (Algae, Chlorophyta) in relation to migratory bird routes* (1)

Peter F. M. Coesel (2), Santiago R. Duque (3), Gonzalo Arango (4)

## Abstract

*Based on own investigations in Colombia and literature data, the distribution patterns of a number of neotropical desmid species are discussed in relation to migration routes of waterfowl. Marked differences in the composition of the tropical desmid flora of Central America and western South America as compared to that of the Orinoco-Amazon area suggest that the Andes effectively restrict the exchange of freshwater algae by forming a barrier for migratory lowland waterbirds which function as potential carriers.*

Key words : Biogeography — Migration — Freshwater algae — Desmids — Neotropics — Colombia — South America.

## Résumé

### Répartition de Desmidiées néotropicales (Algae, Chlorophyta) en fonction des voies migratoires des oiseaux

*La discussion est basée sur des échantillonnages réalisés par les auteurs en Colombie, et sur les données de la littérature. Des différences marquées entre la flore des Desmidiées tropicales d'Amérique Centrale et de l'ouest de l'Amérique du Sud, d'une part, et celle des bassins Orénoque-Amazone, d'autre part, suggèrent que les Andes limitent la distribution des algues d'eau douce en étant une barrière aux migrations des oiseaux aquatiques qui en sont les vecteurs potentiels.*

Mots-clés : Biogéographie — Migrations — Eaux douces — Algues — Desmidiées — Colombie — Amérique du Sud.

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(1) Studies on Colombian Cryptogams XXIX.

(2) *Hugo de Vries-Laboratorium, University of Amsterdam, Kruislaan 318, 1098 SM Amsterdam, the Netherlands.*
(3) *Laboratorio de Morfología Vegetal-Investigación, Dpto. Biología, Universidad Nacional, AA 23227 Bogotá, Colombia.*
(4) *Coleccion de Ornitologia, Instituto de Ciencias Naturales, Universidad Nacional, AA 7495 Bogotá, Colombia.*

RESUMEN

TIPÓS DE DISTRIBUCIÓN DE ALGUNAS ESPECIES NEOTROPICALES DE DESMIDIACEAS (ALGAE, CHLOROPHYTA) EN RELACIÓN CON LAS RUTAS DE AVES MIGRATORIAS

*Con base en investigaciones realizadas y una revisión bibliográfica, se discute los patrones de distribución y el número de espécies neotropicales de Desmidiaceas en relación con las rutas migratorias de aves acuáticas. Marcadas diferencias en la composición de la flora tropical de Desmidaceas en América central y la parte occidental de América del Sur fueron comparados con la flora del área del Orinoco-Amazonas, sugiriendo que la región Andina restringe el paso algas de agua dulce, formando entonces una barrera para la migración de aves acuáticas de tierra caliente, las cuales funcionan como transportadores potenciales.*

PALABRAS CLAVE : Biogeografia — Migración — Algas — Agua dulce — Desmidiaceae — Colombia — America del Sur.

## INTRODUCTION

Biogeographical studies are mostly concerned with higher plants and animals because these organisms often show a clearly marked distribution area related to climate or migration barriers like seas or mountains chains. Lower forms have received considerably less attention from biogeographers. Reasons for this are frequently complicated taxonomic status linked to problems in identification, gaps in the knowledge concerning distribution patterns, a weaker dependency on climatological factors, or more pronounced long-distance dispersal. Many microorganisms seem to have almost worldwide distributions. The fundamental rule «everything is everywhere, but the environment selects» stated by BAAS-BECKING (1934) on the basis of investigations by the Dutch microbiologist M. W. BEIJERINK was primarily based on results from enrichment cultures. Species of unicellular freshwater algae also usually are supposed to be cosmopolitic (FOTT, 1971 : 458). This general view has occasionally been questioned. Particulary among the desmids (unicellular conjugatophyceous green algae) DONAT (1926) mentions many species with a seemingly characteristic distribution within Europe. He concludes that phytogeographical notions as «atlantic», «arctic-alpine» etc. may be applied to freshwater algal species as well. Considering desmid distribution on a worldwide scale, KRIEGER (1933 a) distinguishes ten floral belts and opposes the view, apparently then in vogue, that most of the freshwater algal species would be cosmopolitic. His view, expressed in his well-known desmid flora (KRIEGER, 1933 b : 109) is that species occur everywhere their ecological demands are met. Climate and geology limit these ecological conditions to one of the 10 desmid floral belts. However, it is questionable to what extent climatological factors play a critical role in the ecology of predominantly asexually reproducing freshwater algae. For instance, many desmid species known as «boreo-alpine» occur in reduced frequency in the temperate lowland. For these species presumably temperature is less limiting than a (hemi-)atmophytical way of life in a more or less pH-neutral habitat (COESEL, 1979). On the other hand a growing number of taxa originally thought to have an exclusively tropical distribution is also met in temperate and even arctic climatic zones. For instance, among taxa considered tropical by DONAT (see KRIEGER 1933 b : 108), *Phymatodocis nordstedtiana* Wolle was found in Canada and New Zealand (CROASDALE *et al.*, 1983), *Pleurotaenium ovatum* Nordst. in Canada (PRESCOTT *et al.*, 1975) and in Japan (HIRANO, 1959), while *Micrasterias foliacea* Bailey ex Ralfs nowadays is also known from e. g. Canada (PRESCOTT *et al.*, 1977), Japan (HIRANO, 1956) and South Africa (CLAASSEN, 1982).

Therefore, a more important factor explaining actual distribution patterns seems to be the potential for long-distance dispersal. Though many freshwater algal species can be transported by wind, this mode of dispersal plays a minor role in desmids (BROWN *et al.*, 1964; SCHLICHTING, 1964). Drought-resistant zygospores are only incidentally formed in this algal group while their vegetative cells in general are sensitive to desiccation (EVANS, 1958; PROCTOR, 1966). On the contrary, vegetative cells of desmids (as well as other aquatic microorganisms) may be carried readily by waterbirds, both on the external surface and in the digestive tract (PROCTOR, 1966). In the latter case cells of several species proved to retain their viability for some four hours, as has been shown in Mallard Ducks (*Anas platyrhynchos*) and Killdeer (*Charadrius vociferus*) by PROCTOR *et al.*, 1967. Therefore some distribution patterns in

desmid species could be explained by the migration activities of their most likely carriers among waterfowl, especially over medium-long distances. The present paper, primarily based on phycological investigations in Colombia, aims at bringing to light such a possible relation.

## STUDY SITES AND METHODS

This study focusses on the tropical clear water lake Laguna Juncal, situated in the Colombian province of Huila some ten kilometers south-west of Neiva, near the Magdalena River (fig. 1). The lake covers an area of c. 3 × 2 km, it has a mean depth of 2 m with a maximum of 3 m. The pH (measured electrometrically) ranges from 7.4 to 8.5, and the conductivity from 70 to 115 μS $cm^{-1}$ (at 25 °C). Originally fed by small oligotrophic tributaries, its trophic status has been raised by input of nutrient-rich water from the Magdalena River since a number of years. This input became necessary, because the tributaries were progressively used for irrigation of surrounding paddy fields. Nowadays the shallow lake is partly filled in with dense vegetations of *Eichhornia, Typha, Ceratophyllum, Utricularia*, and *Nymphaea* species, allowing the development of rich varied tychoplankton assemblies. The predominant role of desmid species in the tychoplankton indicates that the overall water quality is still satisfactory, but the local appearance of neuston films, consisting of *Euglena, Phacus* and *Trachelomonas* species, reflects high nutrient supply by the Magdalena River water (MARGALEF, 1978). The local avifauna is luxurious, among the waterfowl being many ducks, grebes, rails and waders. Next to more or less sedentary species like *Jacana jacana hypomelaena* (Jacanidae), *Oxyura dominica* (Anatidae) and *Podilymbus podiceps* (Podocipedidae), also species with a distinctly migratory way of life *Actitis macularia* (Scolopacidae) and *Anas discors* (Anatidae) can be observed.

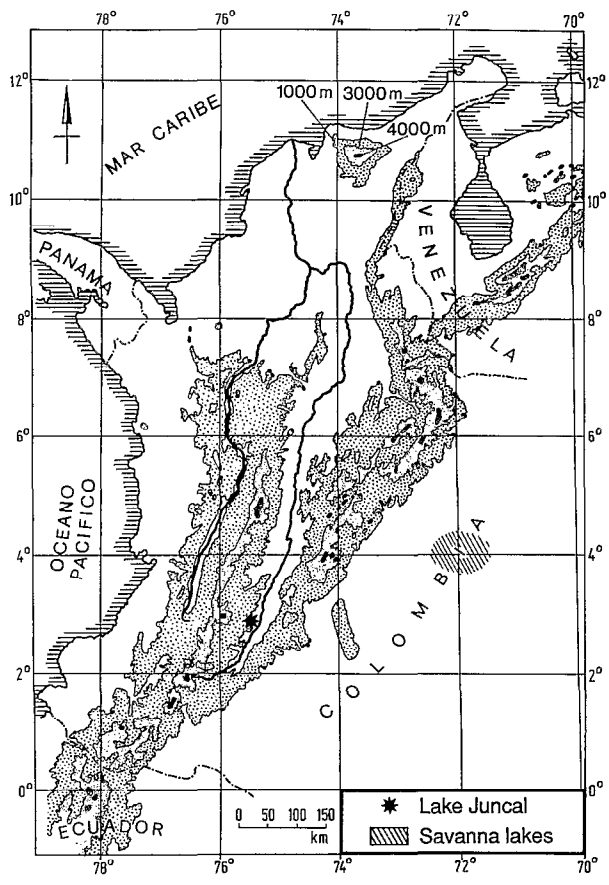


FIG. 1. — Location of the investigated Colombian lowland lakes. *Localisation des lacs échantillonnés et de la barrière montagneuse*

Lake Juncal was compared to a number of lakes situated in the savannas east of the Andes in the province of Meta (fig. 1) : Lake Mateyuca (ca. 20 km south-west of Puerto Lopez), Lake Flor Amarilla (7 km east of Lake Mateyuca) and Lake Rancho Grande (40 km east of Puerto Lopez). Like Lake Juncal these are tropical clear water lakes, with a surface area not larger than some square kilometers and with a depth of only a few meters. In contrast to Lake Juncal they are hydrologically isolated, only fed by rainwater and consequently distinctly oligotrophic. Conductivity ranges between 7 and 14 μS $cm^{-1}$, and pH between 5.4 and 5.6. Along the gently sloping banks dense *Eriocaulon, Isoetes* and *Mayaca* species stands are present, offering an excellent habitat for benthic and tychoplanktonic life-forms. These microcoenoses are marked by numerous desmid species including some very rare and interesting ones (COESEL, 1987). Like Lake Juncal the above mentioned savanna lakes are inhabited by many waterbirds, especially waders as herons and ibises.

Algal samples were collected by means of a plankton net (mesh size 40 μm), or by squeezing out submersed water plants. Samples from the latter three lakes were taken in March 1985, those from Lake Juncal in November 1985.

## RESULTS AND DISCUSSION

The eastern savanna lakes Mateyuca, Flor Amarilla and Rancho Grande have a largely similar desmid flora. Among the numerous taxa (ranging from ca.

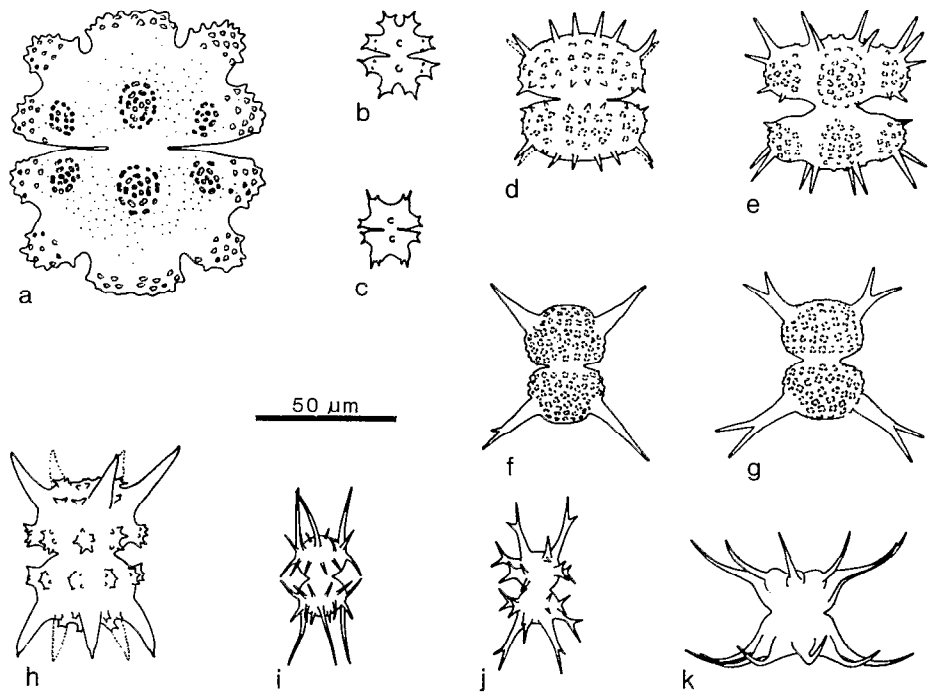


FIG. 2. — Selection of desmid taxa encountered in some Colombian savanna lakes, and characteristic for the Amazon-Orinoco area.
*Quelques Desmidées des lacs de savane de Colombie, caractéristiques de la région Amazone-Orénoque*
*a : Euastrum grandiornatum;* b : *E. cuspidatum* var. *goyazense;* c : *E. foersteri;* d : *Cosmarium horridum;* e : *C. cornigerum;* f, g : *Staurastrum circulus;* h : *S. spiculiferum;* i : *S. lentaculiferum;* j : *S. inaequale* var. *triceps;* k : *Staurodesmus calyxoides* var. *marthae*

100 to 150 per lake) a minority concerns fairly cosmopolitic species. With respect to the remaining part a few species can be characterized as mainly pantropical in their distribution, e. g. *Onychonema laeve* Nordst. (see WEST *et al.*, 1923), *Micrasterias arcuata* Bailey and *M. laticeps* Nordst. (see FÖRSTER, 1982). A much greater number of the taxa is only known from the Americas or even exclusively from tropical South America. In our samples the last mentioned group (tropical S. American) comprises some fifty taxa among which as most frequently occurring ones : *Euastrum cuspidatum* Wolle var. *goyazense* (Först.) Först., *E. fissum* W. & G. S. West var. *brasiliense* Krieg., *E. foersteri* Scott & Croasd. ex Croasd., *E. grandiornatum* (Först.) Först., *E. pirassununguae* Borge, *Cosmarium cornigerum* (Nordst.) Först., *C. dimaziforme* (Grönbl.) Scott & Grönbl. var. *undalatum* Först. ex Först., *C. furcatum* Först, *C. horridum* Borge, *C. pseudomagnificum* Hinode var. *brasiliense* (Forst.) ex Först., *C. redimitum* Borge, *Xanthidium mamillosum* (Grönbl.) Först. var. *nordstedtii* (Grönbl.) Först., *X. regulare* Nordtst., *Staurodesmus calyxoides* (Wolle) Croasd. var. *marthae* (Grönbl.) Teil., *Staurastrum boergesenii* Racib. var. *elegans* Borge, S. *circulus* Grönbl., *S. foersteri* Coesel, *S. inaequale* Nordst., *S. spiculiferum* Borge, *S. stelliferum* Borge, *S. lentaculiferum* Borge and *S. urinator* Smith var. *brasiliense* Grönbl. (see also fig. 2). These taxa were previously recorded from the Amazon region in Brasil (e. g. GRÖNBLAD, 1945; FÖRSTER, 1964, 1969, 1974; SCOTT *et al.*, 1965; THOMASSON, 1971). Many of them are also known from French Guyana (BOURRELLY & COUTÉ, 1982; THÉRÉZIEN, 1985). None of these species was encountered in any of the Colombian mountain lakes sampled in the same period (February-March 1985), nor mentioned in publications of West (1914) and TAYLOR (1935) dealing with algal founds in that Andean region.

The desmid flora of Lake Juncal also comprises dozens of different taxa. With the above discussed eastern savanna lakes, Lake Juncal shares cosmopolitic taxa and also some predominantly pantropical ones (*Onychonema laeve, Micrasterias laticeps).* The group of taxa characteristic for the tropical South American lowland — partly listed above for the savanna lakes — is completely absent from Lake Juncal, which contains a number of species not previously recorded for Colombia. With its peculiar assortment of desmid species Lake Juncal shows a

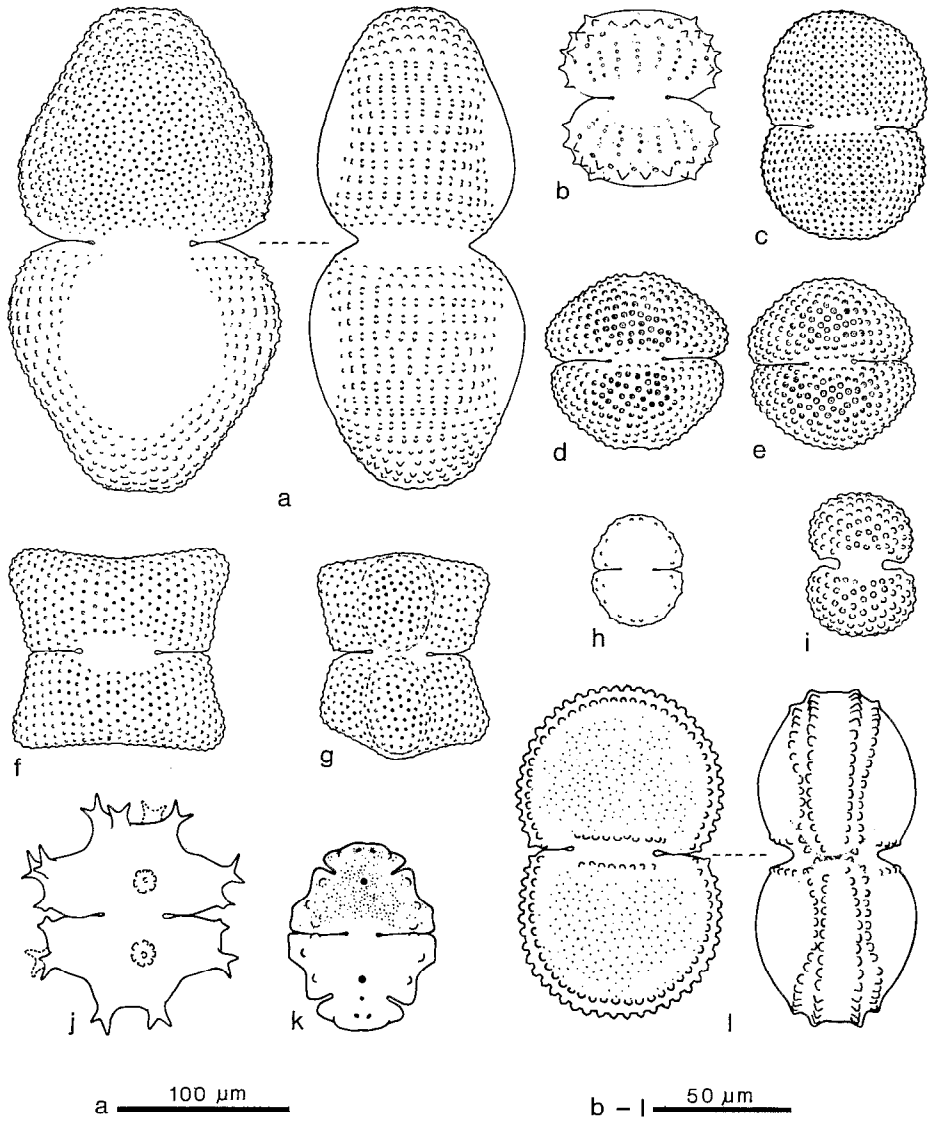


FIG. 3.— Selection of desmid taxa encountered in Lake Juncal, for the most part characterized by a predominantly north-south distribution along the American continent. *Desmidées du lac Juncal, caractérisées pour la plupart par une distribution Nord-Sud dans le continent américain*

*a : Cosmarium splendidum* (cell wall scrobiculation only indicated in frontal view of upper semicell); b : *C. guatemalense;* c : *C. panamense;* d, e : *C. baccalum;* f, g : *C. porrectum* (g : triradiate form); h : *C. corumbense;* i : *C. portianum* var. *brasiliense;* j : *Xanthidium trilobum;* k : *Euastrum subintegrum* var. *brasiliense;* l : *Cosmarium ginzbergeri*

marked resemblance to some Panama lakes. Apart from *Cosmarium splendidum* Borge, an apparently very rare species only known from one locality in Paraguay (BORGE, 1903) and *C. corumbense* Borge known from Corumbá at the Paraguay-Brazil border (BORGE, 1903) and from the western Chilean Lake district (THOMASSON, 1963) all «typical» Lake Juncal taxa illustrated in fig. 3 are also recorded from Panama by PRESCOTT (1966). On these, *Cosmarium porrectum* Nordst. has a rather scattered pantropical distribution (PRESCOTT *et al.*, 1981), but the other ones are exclusively known from the American continent. *Euastrum subintegrum* Nordst. var. *brasiliense* Grönbl. (synonymous with var.

*poriferum* Prescott), *Xanthidium trilobum* Nordst. and *Cosmarium ginzbergeri* Grönbl. have been recorded from both Central and South America, *C. panamense* Prescott from Central America and the southern United States, while *C. guatemalense* Taylor (better to be considered as a variety or forma of *C. paraguayense* Borge, see TAYLOR, 1939) was only found in Central America. The two remaining forms illustrated in fig. 3 have an uncertain taxonomic status. The form identified as *C. portianum* Arch. var. *brasiliense* Wille (according to PRESCOTT *et al.*, 1981, known from some sites in both South and North America) almost certainly is identical with the one recorded by THOMASSON (1963) from the western Chilean Lake district under the name *C. portianum* var. *maius* Scott & Prescott, and presumably also with those diagnosted simply as *C. portianum* by TAYLOR (1939) and PRESCOTT (1966) from Guatemala and Panama respectively. Finally, the form labeled as *C. baccatum* Scott & Grönbl., up to then only known from the southern United States (PRESCOTT *et al.*, 1981) may well be the same as the one figured by PRESCOTT (1966, t. 5 : 15) as a forma of *C. botrytis* (Menegh.) Ralfs var. *tumidum* Wolle.

In summary, most of the characteristic species of Lake Juncal (by which it is distinguished from shallow, tropical clear lakes east of the Andes) show a predominantly north-south distribution along the American continent, with a concentration of records in the isthmus of Panama. This feature suggests that Lake Juncal is situated on a north-south migration route of waterfowl. Indeed the lake harbours a rich and diversified avifauna, among which there are typical migratory species. One of the migrants is the Blue-winged Teal (*Anas discors discors*), observed in large numbers by the third author in November 1979. The feeding habits of this dabbling duck make it a likely potential vector of algae. It breeds in North America and winters from the southern United States to central Argentina and Uruguay (RIDGELY, 1976). RIDGELY (loc. cit. : 53) mentions this species «though a migrant, easily the most numerous and widespread duck in Panama». WETMORE (1965) reports the main flight from the north arriving in Panama in the latter half of October and returning in March-April. As one of the numerous residences of this species in Panama he states Gatun Lake in the Canal Zone, the same locality from where PRESCOTT (1966) collected the algal samples under discussion. In Colombia *Anas discors discors* can be encountered in tropical to temperate zones (MEYER de SCHAUENSEE, 1964), apparently it avoids the high mountain lakes of the Andes. Judging from a distribution map in BLAKE (1977) the species does not seem to occur in the region east of the Andes.

## BIOGEOGRAPHIC CONSIDERATIONS

It is a remarkable fact that on the American continent many desmid species with a predominantly (sub)tropical distribution are able to penetrate up to high latitudes, but that such is not the case for desmid species originating from (sub)tropical Africa on the European continent. For instance, more or less pantropical species (at least occurring in both tropical America and Africa) like *Micrasterias foliacea* Bailey ex Ralfs, *Pleurotaenium verrucosum* (Bailey) Lundell, *P. subcoronulatum* (Turner) W. & G. S. West, *Euastrum evolutum* (Nordst.) W. & G. S. West and *Staurastrum rotula* Nordst. are known from the northern United States and Canada while these taxa were never recorded from mid and western Europe. Apparently means of dispersal, rather than temperature, limit the spread of these species in the old world. It is obvious that dispersal of freshwater algae by waterfowl from tropical regions northward will be much easier in America than in Africa. In America migrating birds may meet almost continuous series of freshwater bodies. On the other hand in northern Africa and to a lesser extent also in southern Europe extensive arid areas force the birds either to long continuous flights which drastically reduce the survival chances of transported algal cells, or to select coastal routes including estuarine waters in which desmid cells can not survive.

The desmid inventory data presented in this paper suggest that a similar restriction of dispersal of desmids by water fowl may influence their South American distribution. Particularly the high mountain chains of the Andes could restrict an east-west exchange and thereby cut off the connection with Central (and North) America for many species. The avifauna of South America is known as extremely rich, and a substantial proportion of it is narrowly endemic. CRACRAFT (1985) postulates no fewer than 33 areas of endemism, resulting from the high ecological and climatological differentiation and the many physiographic barriers on this continent. HAFFER (1985) confining himself to the tropical lowlands distinguishes 22 such areas. Contributors to avian zoogeography of S. America habitually mention the Andes as an effective barrier for tropical species, splitting up the continent in a western or Pacific area (including the Andes) and an eastern or Amazonian area (CHAPMAN, 1917). Lake Juncal is located in the western area, in a faunal region specified as the «Upper Magdalena Valley» while the lakes Mateyuca, Flor Amarilla and Rancho Grande are situated in the eastern area, i. e. the savannas of the Orinoco region. Both regions are characterized by semi-arid conditions, comprising but few scatte-

red bodies of permanent, stagnant water (MEYER de SCHAUENSEE, 1964). Regular migratory birds usually ignore the boundaries of areas of endemism, but in this case the steep mountain chain of the Eastern Cordillera (2000-5000 m in altitude, and continuing northward up to the Carribbean Sea) that separates the two tropical lowland areas under discussion, may be considered a substantial barrier that is overcome only by some specialized flyers. In general, migrating lowlands waterbirds are forced either to follow the inter-Andine valleys or to select a Caribbean coastal route eastward. In the latter case the migrating birds concerned no longer can contribute to the dispersal of desmidiaceous algae because these can not survive in saline waters. This may explain why the Amazon and Orinoco areas (including our eastern savanna lakes) are characterized by a number of desmid taxa never encountered in Central and North America. In this they differ from the desmid flora of the inter-Andine Lake Juncal that agrees to a large extent with those in Central American lakes. The South American continent was connected with North America not earlier than in the late Pliocene (VAN DER HAMMEN, 1974). Before that time an exchange of desmid taxa was excluded. The principal upheaval of the Cordillera also took place in the later stages of the Pliocene (VAN DER HAMMEN, *loc. cit.*). The fact that there is still an assortment of desmid taxa widely distributed in the Amazon and Orinoco region but unknown from Central and North America could be attributed to the effective barrier that is formed by the Andean mountain chain. The apparent lack of the Amazon-Orinoco group of desmid taxa west of the Cordillera also suggests a rather recent evolutionary development of those taxa presumably not earlier than the Pleistocene.

Unfortunately this interpretation of neotropical desmid distribution cannot be supported by a larger number of observations. There are few suitable desmid sites in the tropical Colombian lowland. As already mentioned both the inter-Andine valleys and the savannas east of the Andes have a semi-arid climate. In these regions most lakes containing permanent water are in some way connected with river systems. The rivers concerned originate in the Andean mountains and are rich in dissolved nutrients and suspended solids («whitewater rivers» sensu SIOLI, 1984). The turbid water in these rivers and connected lakes («cienagas») renders them unsuitable for harbouring a diversified desmid flora (COESEL, 1983). So, for rich desmid floras one is committed to the few sites where the periodical (oligotrophic) precipitation is draining into hydrologically isolated permanent lakes or pools. Comparing the relatively high pH and conductivity values of Lake Juncal with the relatively low values measured in lakes Matyuca, Flor Amarilla and Rancho Grande we can not exclude the possibility that the differences between the respective desmid floras are based on local ecological parameters rather than biogeographical history. Arguing against an ecological explanation, however, is the acid character (pH 6.2-6.8) of the back waters of the Panama Canal (PRESCOTT, 1966) which waterbodies markedly resemble the alkaline Lake Juncal in their desmid flora. Moreover, the Panama Canal desmid flora is strongly different from that of Amazonian waters with partly comparable pH values (i. e. up to 6.7, see FÖRSTER, 1969). Also the fact in general that so many species frequently found in the Amazon-Orinoco region have never been recorded for Central and North America calls for a biogeographical rather than an ecological explanation. It strongly supports the idea of HEIMANS (1969) that the factor «accessibility» plays an important role in distribution patterns of desmid taxa, a view usually neglected by phycologists, presumably owing to the lack of convincing data.

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