

# *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju, an expanding, highly adaptive cyanobacterium: worldwide distribution and review of its ecology

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With 9 figures in the text

## Abstract

Because of its potential toxicity and tendency to form dense blooms that interfere with different kinds of water use, *Cylindrospermopsis raciborskii* has become one of the most notorious blue-green algal species. Its ecological success is attributable to many factors like buoyancy, tolerance of low light, ability to use internal P-sources, high affinity P- and ammonia uptake, N<sub>2</sub>-fixation and resistance to grazing by zooplankton. Existing information about the above factors are discussed. *C. raciborskii* can successfully travel along river courses and, moreover, especially in subtropical temperate lakes, it produces large numbers of resistant akinetes, suitable to dispersal by birds and other chance events. It survives swampy or slightly saline conditions. These make the species a successful invader: during the 20th century it has apparently spread to more and more water bodies all over the world which represent a wide habitat diversity. An analysis of ecological constraints, available floristic data and migrational patterns leads to a hypothesis concerning the origin and the present distribution. Investigations on genetic, biochemical and ecophysiological level in cultured materials deriving from different areas of the world are desirable.

## Introduction

*Cylindrospermopsis raciborskii* was described as *Anabena raciborskii* by WOLOSZYNSKA (1912) from a plankton sample collected in a small pond in Central Java in 1899–1900. The sample was brought to Poland by Prof. RACIBORSKI. Subsequently, the species has been found in the tropical-subtropical regions of each continent and data are accumulating from temperate regions of North America and more prominently of Europe.

Appearance of *C. raciborskii* in natural lakes or in newly built reservoirs has been frequently followed by water blooms during which it has reached peak densities of about 10<sup>8</sup>–10<sup>9</sup> filaments l<sup>-1</sup>. These blooms can seriously jeopardize water use for recreation or as drinking water supply, e.g. Lake Balaton in Hungary and Paranoá Reservoir, Brasília, Brazil.

*C. raciborskii* had been thought to be non-toxic for a long time but in November 1979 an outbreak of hepatoenteritis at Palm Island, Australia involving 148 people, mainly school children, occurred a few days after treatment of Solomon Dam, a drinking water supply for the island, with copper sulphate to control dense algal

bloom (BYTH 1980, BOURKE et al. 1983). Later, the "Palm Island species" was identified by Prof. KOMÁREK, Třeboň, Czech Republic, as *C. raciborskii*. The hepatotoxin, cylindrospermopsin, was isolated and described by OHTANI et al. (1992). Toxic strains are not restricted to Australia: a *C. raciborskii* population developed in the Zámolyi Reservoir, Hungary, proved to be toxic in intraperitoneal mouse tests (T.-KOZMA & MAYER 1988). Literature about toxicity of the species has been increasing (HAWKINS et al. 1985, BAKER & HUMPAGE 1994, HARADA et al. 1994, RUNNEGAR et al. 1994, TERAO et al. 1994, RUNNEGAR et al. 1995, SNIDER & HARVEY 1995, EAGLESHAM 1996, HEINTZELMAN & WEINREB 1996, HAWKINS et al. in press).

*C. raciborskii* appeared in Hungary in the 1970s and was described from different localities by many independent investigators within quite a short time period. The sudden increase of new floristic data in Hungary indicated that this was a new invader. A similar expansion occurred in Central Asia during the 1950s–1960s (VINOGRADSKA 1974).

*C. raciborskii* inhabits very different environments, ranging from the subtropical, oligotrophic Kariba Reservoir in the southern hemisphere, to small, shallow, hypertrophic, temperate ponds in the northern one. Surprisingly, many data are from rivers or other intensively flushed environments and from newly built reservoirs. These localities represent a wide habitat diversity, in terms of both geomorphology and water chemistry, thus indicating a high level of ecophysiological adaptability of the species.

Partly because of the increasingly evident invasive behavior of *C. raciborskii*, partly because of its potential or apparent toxicity, there is a worldwide increase in interest about its ecology. This paper attempts to summarize our existing knowledge concerning taxonomic/morphological aspects, geographic distribution, population dynamics and physiological ecology of this species. Although I have been working with the *Cylindrospermopsis* problem in Balaton for several years, this is not research paper. However, where it is reasonable to do so, I use my unpublished data. The sampling and counting methods are described in the following earlier publications: G.-TÓTH & PADISÁK (1986), PADISÁK (1994, 1995), PADISÁK & ISTVÁNOVICS (in press).

### Taxonomy and morphological variability of *Cylindrospermopsis raciborskii*

The species was originally described as *Anabaena raciborskii* (WOLOSZYNSKA 1912). Following the establishment of the genus *Anabaenopsis* (MILLER 1923) for species with terminal heterocytes *Anabaena raciborskii* was moved to *Anabaenopsis*. Because heterocytes of this species develop in a quite different way from those of other *Anabaenopsis* species (in *Cylindrospermopsis* from terminal cells while in *Anabaenopsis* from pairs of cells in the middle of the filaments thus breaking them into two) *Cylindrospermopsis*, that time a monospecific genus, was separated from *Anabaenopsis* (SEENAYYA & SUBBA RAJU 1972). The validity of this separation, and also its relationship to genera *Cylindrospermum* and *Anabaenopsis* was a matter of some debate (STARMACH 1962, JEEJI BAI et al. 1977) but, finally, especially after the thorough investigations by HORECKÁ & KOMÁREK (1979) and HINDÁK (1988), it became generally accepted. *Cylindrospermopsis* also differs from *Cylindrospermum* in respect to:

- (i) the presence of gas vacuoles that are absent in *Cylindrospermum*;
- (ii) the heterocyte-free end of trichomes have attenuated and pointed ends;
- (iii) the position of akinetes (see HORECKÁ & KOMÁREK 1979 for details).

Synonyms of *C. raciborskii* are listed in HORECKÁ & KOMÁREK (1979) and in KOMÁREK & KLING (1991). Other species of *Cylindrospermopsis* (*C. philippinensis*, *C. africana*, *C. cuspis*, *C. catemaco*, *C. curvispora*) have also been described and these are apparently restricted to the tropical regions (TAILOR 1932, KOMÁREK & KLING 1991, KOMÁRKOVÁ-LEGNEROVÁ & TAVERNA 1996, WATANABE 1995).

Since its taxonomic position has been fairly well clarified, *C. raciborskii*'s field populations are easy to identify, if at least some of the filaments carry heterocytes and/or akinetes, and it remains identifiable in either Lugol- or formaldehyde-preserved samples. The practical problem in identifying the species lies in the fact that the morphology of the trichomes varies during population growth and, in extreme cases, both heterocytes and akinetes are absent. The most pronounced identification is described by BRANCO & SENNA (1991): it took two decades before the dominant alga of the Lago Paranoá, Brasília, Brazil could be confirmed as *C. raciborskii*. Changes in trichome morphology during population growth were noted and described as early as the 1939 (SINGH 1962).

Another future task is to clarify the taxonomic significance of straight-, sigmoid- or curled-filaments. They co-occur in many localities in Australia and intermediate forms are rare. Whether these morphotypes have separate genotypes or are different forms as a result of varying environmental conditions has yet to be answered (FABBRO et al. 1996, BAKER 1996). In laboratory cultures, a tendency for coiled strains to become straight over time has been observed, but not *vica versa* (BAKER 1996).

Morphological descriptions and documentations (drawings and/or micrographs) of the species are available in many publications (WOŁOSZYNSKA 1912, SKUJA 1938, KOGAN 1956, PRESCOTT & ANDREWS 1955, DESIKACHARY 1959, SINGH 1962, HORTOBÁGYI 1969, HILL 1970, SEENAYYA & SUBBA RAJU 1972, HAMAR 1977, SCHMIDT 1978, HORECKÁ & KOMÁREK 1979, LEWIS & RIEHL 1982, ROTT 1983, KOMÁREK 1984, HINDÁK 1988, HINDÁK & MOUSTAKA 1988, TORGAN & GARCIA 1989, PADISÁK 1990–91, BRANCO & SENNA 1991, KOMÁREK & KLING 1991, SANT'ANNA 1991, KOMÁRKOVÁ-LEGNEROVÁ & TAVERA 1996, KRIENITZ & HEGEWALD 1996).

## Geographic distribution

### Far East (Fig. 1)

*Cylindrospermopsis raciborskii* was described from a material collected in Rawa Damangan, Java in 1899–1900 (WOŁOSZYNSKA 1912). During the German Sunda expedition (1928–1929), it was found at many localities in East-, Central- and West Java and Bali (GEITLER & RUTTNER 1936), however, it was not found in Sumatran lakes. GEITLER & RUTTNER (1936) classified *C. raciborskii* as one of the few species occurring exclusively in tropical waters. Later SKUJA (1949) found it in two lakes and characterized the species as typically Indo-Malayan. HOLSINGER's (1955) *Cylindrospermum* sp. from 1949–52 from the Nuwara Wewa tank, Sri Lanka, has usually been accepted as

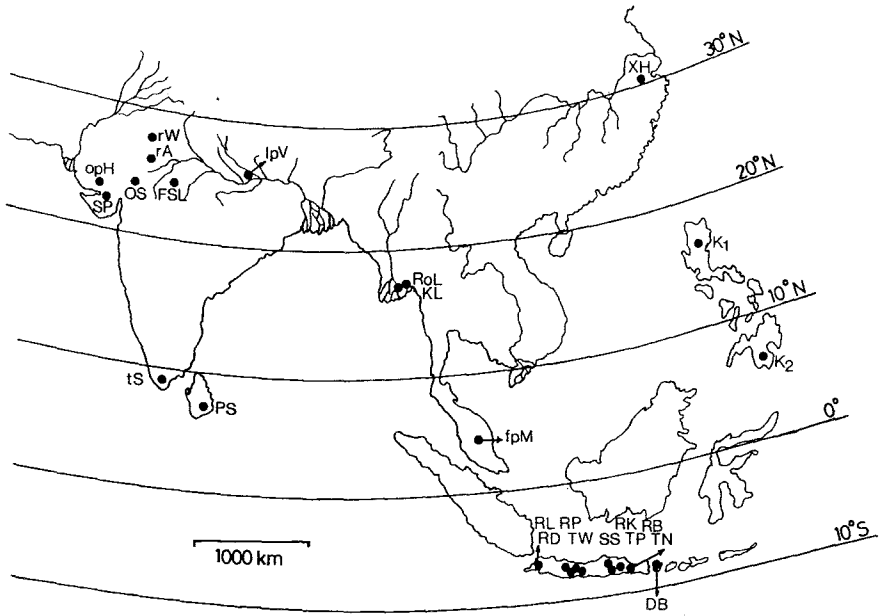


Fig. 1. Occurrence of *Cylindrospermopsis raciborskii* in Far East. Year of observation (when available) is indicated between locality name and source of the record. Abbreviations: DB: Danau Batur, Bali, 1929 (GEITLER & RUTTNER 1936); fpM: fish-ponds in Malaya (FOGG et al. 1973); FSL: Fatehsagar lake, India, 1966 (GUPTA & KUMAR 1968); lpV: local ponds at Varanasi, India, 1939 (SINGH 1962); K<sub>1</sub>, K<sub>2</sub>: from KOMÁREK 1985; KL: Kokine Lakes, Rangoon, Burma, 1935 (SKUJA 1949); opH: old pond at Hyderabad, India, 1964–66 (SEENAYYA & SUBBA RAJU 1972); OS: Osman Sagar lake, India (ZAFAR 1986); PS: Parakrama Samudra, Sri Lanka, 1979–80 (ROTT 1983); rA: reservoir at Agra, India, 1964 (HORTOBÁGYI 1969); RB: Ranu Bedali, East Java, 1928–29 (GEITLER & RUTTNER 1936); RD: Rawa Damangan, Java, 1899–1900 (WOLOSZYNSKA 1912); RK: Ranu Klindungan, East Java, 1928–29 (GEITLER & RUTTNER 1936); RL: Ranu Lamongan, East Java, 1928–29 (GEITLER & RUTTNER 1936); RoL: Royal Lakes, Rangoon, Burma, 1935 (SKUJA 1949); RP: Ranu Pakis, East Java, 1928–29 (GEITLER & RUTTNER 1936); rW: reservoir at Wazirabad, India, 1964 (HORTOBÁGYI 1969); SP: Shatum pond, India, 1964–66 (SEENAYYA 1971); SS: Stautele Sindaglaya, West Java, 1928–29 (GEITLER & RUTTNER 1936); TN: Telaga Ngebel, Central Java, 1928–29 (GEITLER & RUTTNER 1936); TP: Telaga Pasir, Central Java, 1928–29 (GEITLER & RUTTNER 1936); tS: tank at Salem, India (DESIKACHARY 1959); TW: Telaga Warna, West Java, 1928–29 (GEITLER & RUTTNER 1936); XH: Xi-hu, China, latest in 1995 (ILEC, 1995).

*C. raciborskii*, however, it carries more similarities with other recently described *Cylindrospermopsis* species. Nevertheless, *C. raciborskii* does occur in Sri Lanka: ROTT (1983) found it in samples taken from Parakrama Samudra in 1979–1980. A single report reports its occurrence in fishponds of Malaya (FOGG et al. 1973).

The first record in India is from 1939 (SINGH 1962). Since then, data accumulated rapidly during the 1960s. DESIKACHARY (1959) mentioned it in a tank at Salem, and in the period 1964–66 *C. raciborskii* was found at many places in India by different investigators (GUPTA & KUMAR 1968, HORTOBÁGYI 1969, SEEMAYYA 1971a, 1971b; SEENAYYA & SUBBA RAJU 1972). Later ZAFAR (1986) mentioned it from the stratifying Osman Sagar.

The species was recorded in the Xi-hu, China (ILEC 1995). KOMÁREK (1985) indicates two localities in the Philippines where *C. raciborskii* occurs.

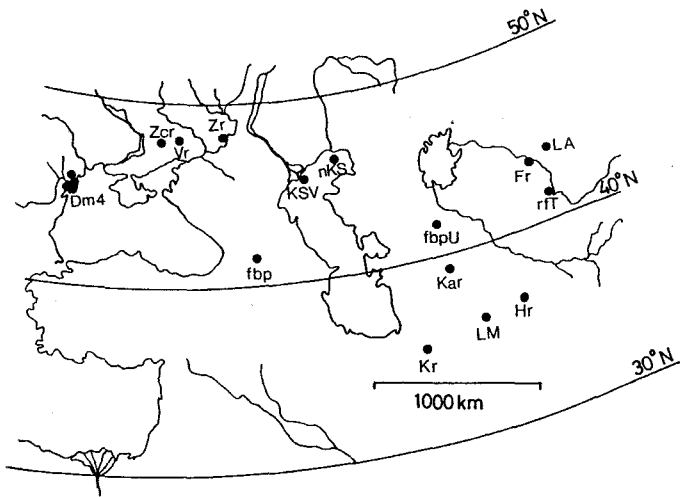


Fig. 2. Occurrence of *Cylindrospermopsis raciborskii* in Central Asia and eastern Europe. Year of observation (when available) is indicated between locality name and source of the record. Abbreviations: Dm4: four localities in the Danube mouth, Moldavia, 1958 (ROLL 1961, KOSTIKOVA 1969); fbp: fish breeding ponds, Gruzia, 1965 (UCHAIZDE 1969); fbpU: fish breeding ponds, Uzbekistan (SAKSENA 1965); Fr: Farkhadskoe Reservoir, Kazakhstan (ERGASHEV 1969); Hr: 3rd Hindukush reservoir, Turkmenia, 1949–1951 (KOGAN 1958); KaR: Kayrakkumskoe Reservoir, Turkmenia (ANDRIEVSKAYA 1969); Kr: Kurtlinskoe Reservoir, Turkmenia (KOGAN & YAZKULIEVA 1968); nKS: northern Caspian Sea, Kazakhstan (USSATCHEV 1938); KSV: Caspian Sea near the mouth of Volga (PROSHKINA-LAWRENKO & MAKAROVA 1968); LA: Lake Akkul, Kazakhstan, 1959 (OBUCHHOVA & KOZENKO 1964); LM: Lake Mordovinko, Turkmenia, 1949 (KOGAN 1955, 1956); rT: rice fields in Tashkent region, Uzbekistan (KUTSHAROVA 1963); Vr: Veselovskoe Reservoir, Russia 1955–58 (MOROZ 1960); ZcR: Zuevskoe cooling Reservoir, Russia, 1966 (VINOGRADSKA 1974); ZR: Zimlianskoe Reservoir, Russia (AKSENOVA 1965).

### From Central Asian areas to Danube mouth in Europe (Fig. 2)

USSATSHEV (1938) found single filaments of *C. raciborskii* in the northern Caspian Sea. After 10–15 years, it had been more and more frequently reported from the region. In 1949 it was found in huge amounts in Lake Mordovinko (KOGAN 1955, 1956) and it built up water blooms both in 1949 and 1951 in the 3rd Hindukush Reservoir (KOGAN 1958). It was found in rice fields in the Tashkent region (KUTSHAROVA 1963), in Lake Akkul, southern Kazakhstan (OBUCHHOVA & KOZENKO 1964), in fish-breeding ponds in Uzbekistan (SAKSHENA 1965), in Kurtlinskoe (KOGAN & YAZKULIEVA 1968), Kayrakkumskoe (ANDRIEVSKAYA 1969) and Farkhadskoe (ERGASHEV 1969) reservoirs. In 1965 *C. raciborskii* bloom was recorded in a fish-breeding farm in Georgia (UCHAIZDE 1969).

In the same period (1954–1964), *C. raciborskii* was found in more northern regions. In 1958 ROLL (1961) found it in the Danube, near Ismail and Reni, in arms and bays Anankiniy, Delukoviy and Chinese. At the latter locality it was also registered by KOSTIKOVA (1969). It was found again in the Caspian Sea near the mouth of the Volga river (PROSHKINA-LAWRENKO & MAKAROVA 1968). *C. raciborskii* was observed in the Veselovskoe reservoir (MOROZ 1960), Zimlianskoe reservoir (AKSENOVA 1965) and in Zuevskoe cooling water reservoir (VINOGRADSKA 1974). MICHEEVA's (1967) observation in Paulskoe lake, Vitebsk region was re-identified as *Anabaenopsis cunningtonii* (HORECKÁ & KOMÁREK 1979).

## Europe

Before the 1970s, there is only one certain record of *C. raciborskii* in Europe, that is SKUJA's (1938) observation in Lake Kastoria, Greece. SZALAI's (1942) record from river Körös, Hungary, cannot be accepted (PADISÁK & KOVÁCS 1997). CLAU's (1961) observation has been usually accepted by taxonomists but, for of several reasons, it is problematic to consider this species as *C. raciborskii*.

These reasons are:

1. Contradictions between the morphological description ("hardly visible cross-walls") and his Fig. 33 (well visible constricted crosswalls, with thickenings);
2. "Pseudanabaena-like" visible chromatoplasma of *C. raciborskii* has not been mentioned by other authors;
3. Complete lack of gas-vacuoles, a major differential feature between *Cylindrospermum* and *Cylindrospermopsis*, that has not been observed in any other *Cylindrospermopsis* population independently from that tropical or temperate;
4. The specimen drawn by CLAU (1961) on Fig. 31/a as *Schizothrix bosniaca* may well be a young stage [with not yet developed heterocytes] of the species on Fig. 33;
5. Close resemblance to *Anabaenopsis raciborskii*/*Cylindrospermum stagnale* in STARMACH's (1962) description that was later confirmed as a *Cylindrospermum* by HORECKÁ & KOMÁREK (1979).

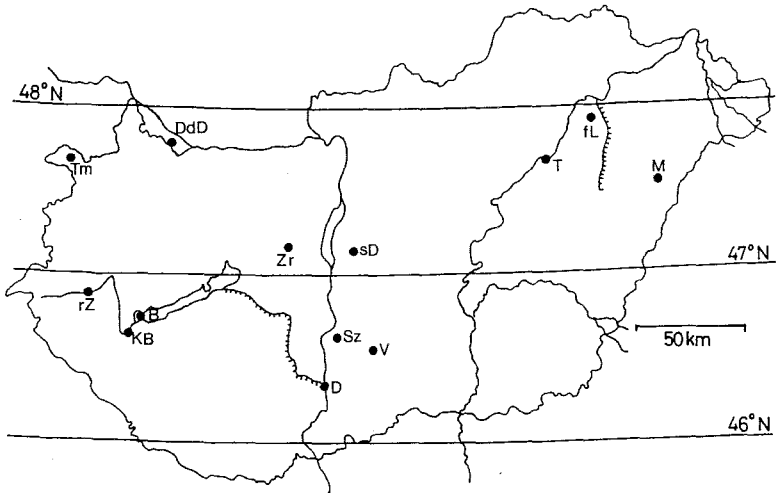


Fig. 3. Occurrence of *Cylindrospermopsis raciborskii* in Hungary. Year of observation (when available) is indicated between locality name and source of the record. Abbreviations: B: Balaton, 1978 (OLÁH et al. 1981); D: Duna, 1982 (SCHMIDT 1987, 1994); DdD: Dunaszegi dead arm of the Danube, 1976–80 (T.-BARTALIS 1987); fL: fishpond at Levelek, 1996, leg. E. ISTVÁNOVIC; KB: Kis-Balaton reservoir, 1993 (PADISÁK 1996); M: Méheskúti pond, 1993 (GRIGORSZKY pers. comm.); rZ: river Zala, 1980s (VÍZKELETI pers. comm.); dD: stream at Dabas (HORECKÁ & KOMÁREK 1979); Sz: Szelidi-tó, 1976 (SCHMIDT 1978); T: river Tisza, 1976 (HAMAR 1977); Zm: Tómalom 1984 (PADISÁK 1990–91); V: Vadkerti-tó, 1990s (SCHMIDT pers. comm.); Zr: Zámolyi Reservoir, 1984 (T.-KOZMA & MAYER 1988).

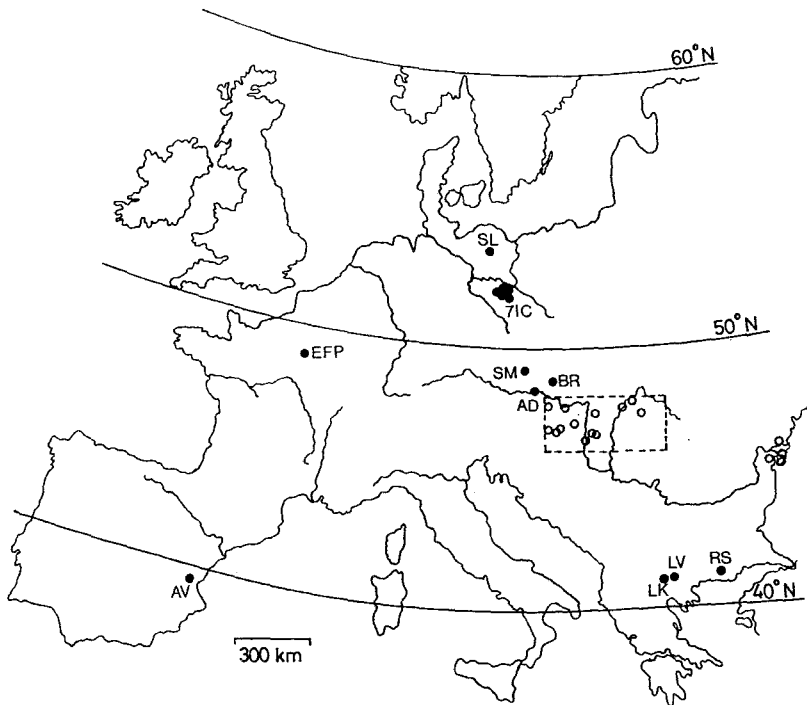


Fig. 4. Occurrence of *Cylindrospermopsis raciborskii* in Europe. Year of observation (when available) is indicated between locality name and source of the record. Abbreviations: AD: Alte Donau, Austria, 1993–1994 (DOKULIL & MAYER 1996); AV: Albufera la Valencia, Spain, 1982–83 (ROMO & MIRACLE 1994); BoR: Boryčki Reservoir, Slovakia, 1970s (HORECKÁ & KOMÁREK 1978); EFP: Etang des Francs Pêcheurs, Paris, France, 1995 (COUTÉ et al. 1997), LK: Lake Kastoria, Greece, 1935 (SKUJA 1938); LV: Lake Volvi, Greece, 1984–85 (HINDÁK & MOUSTAKA 1988); RS: River Strymon, Greece, 1991–1992 (TRYFON et al. 1996); SL: See Lieps, Germany, 1989–1992 (KRIENITZ & HEGEWALD 1996); 71C: seven lakes near Cottbus, Germany, 1990s (WIEDNER pers. comm.). Occurrences in the Danube mouth and Hungary are indicated with open circles, they are listed in detail on Figs. 2–3.

### Hungary (Fig. 3)

Between 1975 and 1980 *C. raciborskii* was found in lake Szelidi-tó (SCHMIDT 1978), river Tisza (HAMAR 1977, BANCSEI et al. 1978), Lake Balaton (OLÁH et al. 1981), Dunaszegi dead-arm of river Danube (T.-BARTALIS 1987) and a fast-flowing artificial stream at Dabas (HORECKÁ & KOMÁREK 1979). During the 1980–1990s, it occurred each year in Lake Balaton (PADISÁK et al. 1984, G.-TÓTH & PADISÁK 1986, PADISÁK 1994, 1995) and was also found in river Danube (SCHMIDT 1987, 1994), Tómalom pond (PADISÁK 1990–91), river Zala (VÍZKELETI, pers. comm.), Zámolyi Reservoir (T.-KOZMA & MAYER 1988), Kis-Balaton Reservoir (PADISÁK 1996), Méheskút pond (GRIGORSZKY, pers. comm.), Vadkerti-tó (SCHMIDT, pers. comm.) and a fish pond at Levelek (leg. ESZTER ISTVÁNOVICS, det. PADISÁK).

### Other countries in Europe (Fig. 4)

*C. raciborskii* was recorded in Boryčki Reservoir, Slovakia (HORECKÁ & KOMÁREK 1979, HINDÁK 1988) and in the urban lake, Alte Donau, in Austria (DOKULIL &

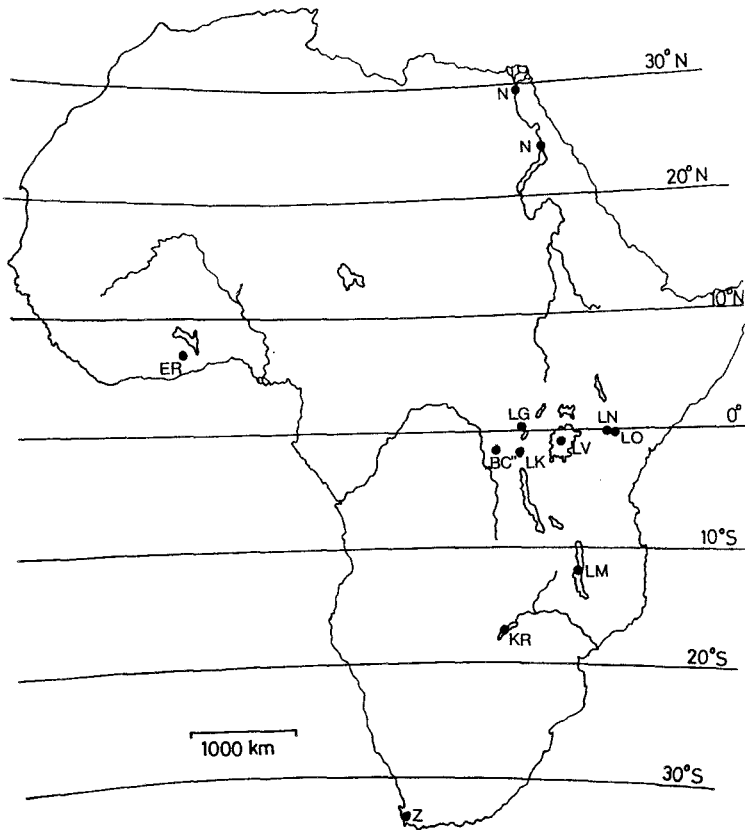


Fig. 5. Occurrence of *Cylindrospermopsis raciborskii* in Africa. Year of observation (when available) is indicated between locality name and source of the record. Abbreviations: "BC": Belgian Congo, West Africa (WOODHEAD & TWEED 1958); ER: Eleyele Reservoir, Nigeria, 1962–1963 (IMEVBORE 1969); KR: Kariba Reservoir, Zambia and Zimbabwe, 1982–1984 (RAMBERG 1984, 1987); LG: Lake George, Uganda, 1967–68 (GANF 1974); LN: Lake Naivasha, Kenya, 1979–1980 (KALFF & WATSON 1986); LO: Lake Oloiden, Kenya, 1979–1980 (KALFF & WATSON 1986); LK: Lake Kivu, Central Africa, 1972 (HECKY & KLING 1987); LM: Lake Malawi, East Africa, 1992 (PATTERSON & KACHINJIKA 1993); LV: Lake Victoria, Uganda, 1988–1990 (KOMÁREK & KLING 1991); N: Nile, 1890s (HUBER-PESTALOZZI 1938 and after KOMÁREK 1985); Z: Zeekoevlei, South Africa, 1992–1993 (HARDING 1996).

JANAUER 1995, DOKULIL & MAYER 1996). KOMÁREK (pers. comm.) found it in southern Moravia. In 1990 *C. raciborskii* was found in See Lieps, northern Germany (KRIENITZ & HEGEWALD 1996) and so far this has been the northernmost record of the species. More recently, it occurred in several lakes (Lebbiner See, Melangsee, Langer See, Petersdorfer See, Storkower See, Kleiner Glubigsee, Springsee) near Cottbus, Germany (CLAUDIA WEIDNER, pers. comm.) and in the small private fishing lake, Étang des Francs Pêcheurs, near Paris, France (COUTÉ et al. 1997). Data from southern European countries are surprisingly scarce: except Lake Volvi, Greece (HINDÁK & MOUSTAKA 1988) River Strymon, Greece (TRYFON et al. 1996) and Albufera la Valencia, Spain (ROMO & MIRACLE 1994), no other data are known. *C. raciborskii* still occurs in Lake Kastoria, Greece (SKUJA 1938; MARIA MOUSTAKA, pers. comm.).



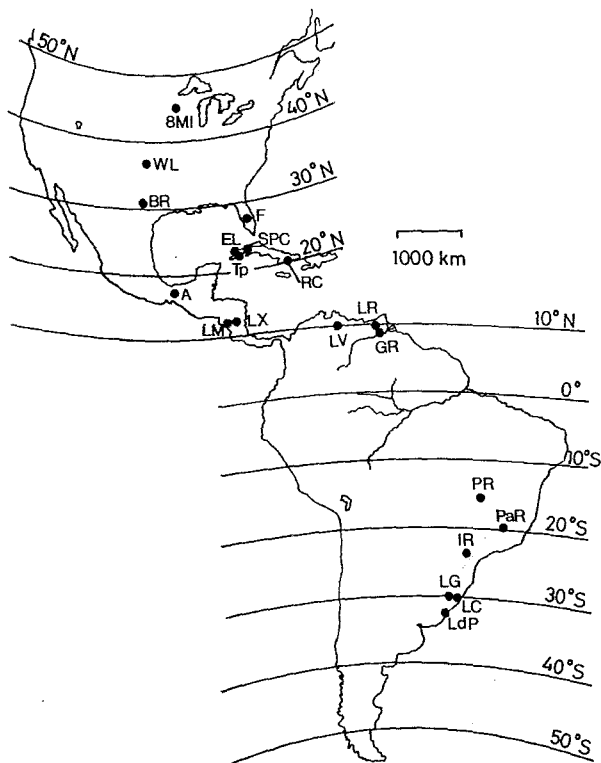


Fig. 6. Occurrence of *Cylindrospermopsis raciborskii* in America. Year of observation (when available) is indicated between locality name and source of the record. Abbreviations: A: Asmolapan, Mexico (KOMÁRKOVÁ-LEGNEROVÁ & TAVERA 1996); BR: Belton Reservoir, Texas (LIND 1984); GR: Gunapito Reservoir, Venezuela, 1974 (LEWIS & WEIBEZAHN 1976); EL: El Laguito, Habana, Cuba, 1964 (KOMÁREK 1984); F: 5 lakes in Florida (CHAPMAN & SCHELSKE 1997); LC: lago Chines, Brasília, 1986–87 (FRANCESCHINI 1991); IR: Itaipu Reservoir (TUNDISI); LdP: Laguna dos Patos, Brasília, 1986 (TORGAN & GARCIA 1989); LG: lago Gaucho, Brasília, 1986–87 (FRANCESCHINI 1991); LR: Lagartijo Reservoir, Venezuela, 1966–68 (LEWIS & WEIBEZAHN 1976); LV: Lake Valencia, Venezuela, 1977–1981 (LEWIS 1986); LM: Lake Masaya, Nicaragua (HOOKER et al. 1993); LX: Lake Xolotlán, Nicaragua, 1986–87 (HOOKER et al. 1991); PaR: Pampulha Reservoir, Brasília, 1984–85 (GIANI 1994); PR: Paranoá Reservoir, Brasília, approx. 1965 (BRANCO & SENNA 1991, 1994); RC: Represa Chalons, Santiago de Cuba, Cuba, 1964 (KOMÁREK 1964); SPC: lagoons at San Pedro de Cacaocum, 1964 (KOMÁREK 1984); Tp: *Tilapia* pond at San Luis, Cuba, 1980 (KOMÁREK 1984); WL: Wooster Lake, Kansas, 1951 (PRESCOTT & ANDREWS 1955); 8MI: Eight lakes in Minnesota, 1966–69 (HILL 1969–70).

**Africa (Fig. 5)**

HUBER-PESTALOZZI (1938) describes the species *Cylindrospermum kaufmannii* (SCHMIDLE) HUBER-PESTALOZZI that coloured the water of the Nile in June of each year at the end of the 19th century (KAUFMANN 1897; BRUNNTHALER 1914, both in lit. loc. cit.). JEEJI-BAI et al. (1977) conclude that *C. kaufmannii* has to be included in "*Anabaenopsis*" *raciborskii* and they refer to personal communication with Prof. KOMÁREK, who examined the alga in a plankton sample from that locality and came to the same conclusion. Therefore, the world's earliest floristic record of occurrence of *C. raciborskii* is probably that from the Nile.

*C. raciborskii* is included in the checklist of tropical West African algae (WOODHEAD & TWEED 1958) as occurring in "Belgian Congo". Next, it was reported from the

Eleiyele Reservoir, Ibadan, Nigeria (IMEVBORE 1969). GANF (1974) found it in 1967–68 in the shallow Lake George where KLING (pers. comm.) found it again in 1995. The species was recorded in lakes Naivasha and Oloiden, Kenya (KALFF & WATSON 1986), in Lake Kariba (RAMBERG 1984, 1987) in Lake Victoria (KOMÁREK & KLING 1991), in Lake Edward (KLING, pers. comm.) and in the Zeekoevlei, South Africa (HARDING 1996). Among other *Cylindrospermopsis* spp., it probably occurs in Lake Kivu (HECKY & KLING 1987) and Lake Malawi (PATTERSON & KACHINJIKA 1993).

### North America (Fig. 6)

*C. raciborskii* was first found in North America in Wooster lake, Kansas (PRESCOTT & ANDREWS 1955) and this remained a solitary record for a long time. In the period 1966–1969 HILL (1970) found it in eight small, nearby lakes in Minnesota. LIND (1984) published about the species from the Belton Reservoir, Texas. The species was recently reported from five hypertrophic lakes in Florida (CHAPMAN & SCHELSKE 1997). KOMÁRKOVÁ-LEGNEROVÁ & TAVERA (1996) mentions the occurrence of *C. raciborskii* in the small lake Asmolapan situated in the vicinity of Lake Catemaco, Veracruz, Mexico.

### Central and South America (Fig. 6)

*C. raciborskii* was found in some localities in Cuba during the 1960s (KOMÁREK 1984). It appeared in the Paranoá Reservoir, Brasil, probably very quickly after it was built, also in the late 1960s (BRANCO & SENNA 1991, 1994). During the 1970's the species was found in the Gunapito and Lagartio reservoirs (LEWIS & WEIBEZAHN 1976) and in Lake Valencia, Venezuela (LEWIS 1986). It was found in two in Nicaraguan lakes, Lake Masaja (HOOKER et al. 1993) and Lake Xolotlán (HOOKER et al. 1991). More recently, *C. raciborskii* was found in the following Brazilian waters: Laguna dos Patos (TORGAN & GARCIA 1989), Lago Chines (FRANCESCHINI 1991), Represa de Serraria (SANT'ANNA 1991), Pampulha (GIANI 1994) and Itaipu Reservoirs (ANDRADE et al. 1995). According to KOMÁREK (pers. comm.), the species occurs in the Amazonian region, too.

### Australia (Fig. 7)

The first floristic evidence for occurrence of *C. raciborskii* in Australia appeared as late as 1979 (HAWKINS et al. 1985). It was found in the drinking water reservoir Solomon Dam, Palm Island, Queensland, where artificial breakdown of a cyanobacterium bloom by copper sulphate resulted in the "Palm Island mystery disease". A subsequent floristic survey (BAKER 1991) indicated that *C. raciborskii* occurs widely in eastern Australia. Precise data are available from Lake Cargelligo (BOWLING 1994), North Pine Dam (HARRIS & BAXTER 1996), Fitzroy River (FABBRO & DUIVENVOORDEN 1996), Oatley pond (HAWKINS et al. in press), Lake Julius (BAKER 1996), Lake Alexandrina (BAKER 1996). Numerous sporadic data report on the overall occurrence of the species in Central Queensland (FABBRO et al. 1996), western New South Wales and northern Victoria (BAKER 1996). A thorough survey in 1990–1993 in the Murray Darling River Basin evidenced the occurrence of the species in no less than 72 sampling stations

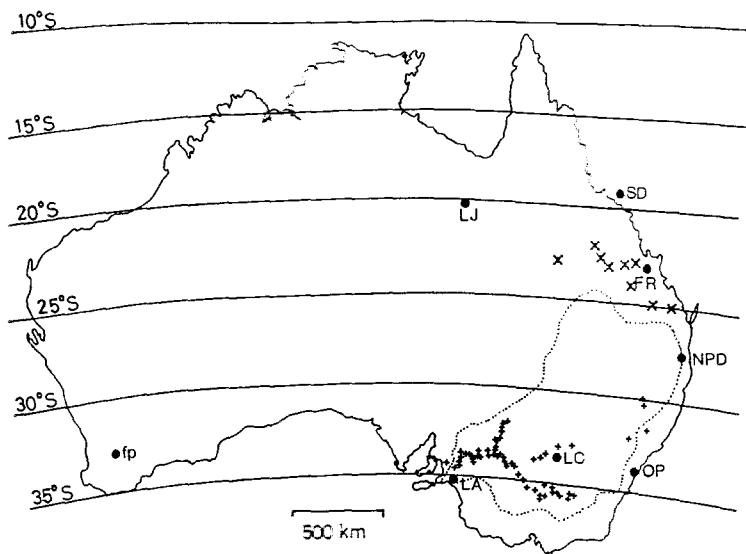


Fig. 7. Occurrence of *Cylindrospermopsis raciborskii* in Australia. Year of observation (when available) is indicated between locality name and source of the record. Abbreviations: fp: farm pond in SW Australia (BAKER pers. comm. 1996); FR: Fitzroy River, 1992 (FABBRO & DUIVENVOORDEN 1996); LA: Lake Alexandrina (BAKER 1996); LC: Lake Cargelligo, 1988–91 (BOWLING 1994); LJ: Lake Julius (BAKER 1996); NP: North Pine Dam, 1977–1994 (HARRIS & BAXTER 1996); OP: Oatley Pond, 1995 (HAWKINS et al. in press); SD: Solomon Dam, 1979 (HAWKINS et al. 1985); +: P. BAKER's unpublished *C. raciborskii* data from the Murray Darling Basin (dotted line) from 1995–1996; x: L. FABBRO's unpublished data from the period 1993–1996 in Queensland.

including main courses of rivers, swamps and lakes (BAKER et al. 1993, BAKER, pers. comm.). FABBRO (pers. comm.) found it at nine localities (dams, river impoundments, rivers) in Queensland which are not among those mentioned earlier.

Medically, the Palm Island intoxication can be distinguished from other kinds of intoxications or infections by its distinctive symptoms (HAYMAN 1992). Based on this feature and after a careful examination of medical literature HAYMAN (1992) concluded that the Palm Island case was identical with the disease known as "Belyando fever", "Barcoo fever", "Barcoo spews", "Barcoo sickness" or simply "the Barcoo" in Australia. During an intensive literature survey he found four appropriate medical descriptions (BAKER 1887, STIRLING 1894, WATSON 1905, CLELAND 1911) that can be diagnosed as Barcoo fever. The commonness of the Barcoo fever in Australia is perhaps best supported by its appearance in historical descriptions (JOUNQUAY 1975) and biographies (DURACK 1991).

Despite the lateness of floristic surveys from Australia, medical evidence and epidemiological behavior that fit very well to the species' tolerance of lotic environment, accumulating diseases in summers, association to drought periods, etc., it is very likely *C. raciborskii* has become originally wide-spread in Australia.

### Locality classification, temperature demand, seasonality

*Cylindrospermopsis raciborskii* occurs in a wide range of freshwaters. In the tropical-subtropical region it characteristically occurs in deep, stratified lakes while it inhabits

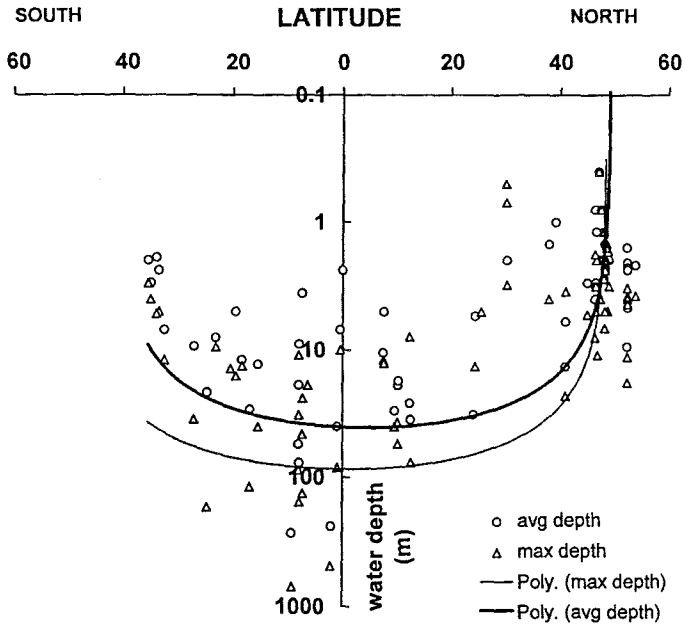


Fig. 8. Average and maximal depths of lakes with *Cylindrospermopsis raciborskii* at different latitudes. Polynomial regressions as trendlines are also given.

shallow waters in temperate regions (Fig. 8). The northernmost stratified (June–August) lake where *C. raciborskii* occurs is most likely Lake Volvi, Greece (41°N, HINDÁK & MOUSTAKA 1988).

Independently from latitude, *C. raciborskii* populations grow and increase only in warm (> 25 °C) water. Consequently, it can maintain large populations in permanently warm waters (Paranoá Lake, Brazil 15° 48' S, BRANCO & SENNA 1994; Lake Oloiden, Kenya 0° 45' S, KALFF & WATSON 1986) all over the year while its appearance is restricted to shorter and shorter summer periods towards higher latitudes. At the northernmost limits of its presently known geographic distribution (Europe, N-America), *C. raciborskii* builds up large populations only in exceptionally warm years while in others only single filaments appear, if at all, late summers. The best known example is Lake Balaton (Hungary, 46° 52' N, G.-TÓTH & PADISÁK 1986, PADISÁK in press), however the phenomenon was observed as early as the 1960s: HILL (1970) found a plenty of filaments in Pond 1 (USA, Minnesota, ~ 46°N) in 1967, but it was not found there at all in 1969. This interannual variability can make *C. raciborskii* a good indicator species of global climate change for temperate regions (PADISÁK in press).

The high temperature requirement of *C. raciborskii* is partly related to the high temperature optimum of akinete germination. Laboratory experiments with akinetes deriving from Lake Balaton showed that high percent of germination occurs only in the temperature range of 22–23.5 °C, while this range for three other heterocytic blue-green algal species was 18–25 °C (GORZÓ 1987). A sediment temperature of about 22 °C can occur in shallow waters only in the temperate region. This is perhaps the main reason why the species has not been recorded in temperate deep lakes. Based on this observation the northern (southern) margin of distribution of *C. raciborskii* can be drawn as the

isocline for a minimum of 21–22 °C summer sediment temperature. Nevertheless, the gradual evolutionary adaptation to colder temperatures in the European waters cannot be excluded, especially because maximum biomass development of a *C. raciborskii* dominated association coincided with temperatures of only 15–18 °C in Alte Donau, Austria (DOKULIL & MAYER 1996). There has been no other observation about growth at such relatively low temperatures. The recent occurrence in Springsee (Germany: having average and mean depths of 9.5 m and 18.1 m) underlines this indication. The highest growth rate ( $\mu = 1.6 \text{ d}^{-1}$ ) of the ACT-9502 strain isolated from Lake Balaton, Hungary was observed at 30 °C (SHAFIK et al. 1997).

At the biochemical level, the association of the vegetative populations of the species with high temperatures can be explained by membrane properties. According to FARKAS'S (1996) ongoing investigations, lipid composition and membrane fluidity of the ACT 9502 strain of *C. raciborskii*, unlike almost any cells of other organisms from human erythrocytes to other blue-green algae, was very similar at 15 °C and 35 °C and this indicates the complete inability of the species to adapt to changing temperatures.

*C. raciborskii* has been recorded many times from in lotic waters from large lowland rivers such as Nile (Egypt; HUBER-PESTALOZZI 1938), Volga (Russia; PROSCHKINA-LAWRENKO & MAKAROVA 1938), Danube, Tisza (Hungary; SCHMIDT 1994, HAMAR 1977), Murray, Darling and Lachlan rivers (Australia, BAKER et al. 1993, BAKER 1996) through small rivers (River Strymon, Greece, TRYFON et al. 1996; Zala, Hungary, VÍZKELETI, pers. comm.) to a fast-flowing artificial stream (Hungary; HORECKÁ & KOMÁREK 1979). As a matter of fact, rivers gave their names to the disease that later proved to be cylindrospermopsin intoxication ("Barcoo" of "Belyando" fever, both are rivers; HAYMAN 1992). The Barcoo river rises in Central Queensland, Australia and flows toward the southern coasts of Australia. In drought conditions the river is reduced to series of water holes or dries up altogether, but in wet seasons, it floods hectares of fields. The literary descriptions (JOUNQUAY 1975, DURACK 1991) of the Barcoo fever are also associated with excursions or stays along rivers courses.

As argued in REYNOLDS et al. (1994), riverine flora is recruited from shallows (and *vice versa*: the river inoculates the adjacent areas) along the river course (STOYNEVA 1994) and from many other waters in the tributaries, as a consequence of which very "unlikely" species, for example scaled chrysophytes (KISS & KRISTIANSEN 1994), can occur in river flora. Based on present knowledge on the ecology of *C. raciborskii*, it is not clear how successfully it can, if at all, grow in river courses. Nevertheless, observations on Danube and Tisza (Hungary) and its almost invariant occurrence along the Murray-Darling system exemplify that if once drifted in, it is very successful in tolerating riverine conditions and can travel far. According to HAMAR (1977), the *C. raciborskii* population was discharged to the river Tisza, Hungary through the Lónyai channel at about 550 rkm and filaments were still found in quantitative samples 400 km downstreams. The *C. raciborskii* population that was found by SCHMIDT (1987) at the mouth (1496 rkm of Danube) of the Sió canal (approx. length: 100 km) had certainly originated from Lake Balaton, where it bloomed that year (G.-TÓTH & PADISÁK 1986).

*C. raciborskii* has been frequently found in artificial reservoirs and river impoundments. Some of them are ancient, like Parakrama Samudra in Sri Lanka, but many of

them were constructed a short time before the species was first recorded. The best examples are from Central Asia, South America and Australia.

Another unique feature of the species is that it seems to tolerate swamp conditions better than other related species do. It was found in rice fields twice (KUTSHAROVA 1963, ROMO & MIRACLE 1994), moreover it was the only blue-green alga that was found at each investigated localities of the swamp-area of the Kis-Balaton Reservoir, Hungary that connects the open-water pre-reservoir and Lake Balaton (PADISÁK 1996).

### Seasonality, sensitivity to water column stability

Although *C. raciborskii* is one of the species that can dominate yearlong or almost yearlong in tropical regions, continuous dominance is more the exception than the rule. Association of *C. raciborskii* population maxima to the annual stratification pattern in most of the tropical lakes indicate that other factors than temperature are also important. In these lakes, the species occurs during stratified periods characterized by high environmental constancy (Lake Naivasha, KALFF & WATSON 1986; Eleiyele Reservoir, IMEBORE 1969; Lake Victoria, and Lake Kivu, KOMÁREK & KLING 1991; Kariba Reservoir, RAMBERG 1984, 1987; North Pine Dam, HARRIS & BAXTER 1996; Lagartijo Reservoir, LEWIS & WEIBEZAHN 1976; Lake Valencia, LEWIS 1986). In a view of the great differences in short-term as well as yearly nutrient supply rates, mixing regimes, residence times and morphological differences of tropical lakes (KALFF & WATSON 1986), however, it is difficult to get a generalized conclusion about the timing of *C. raciborskii* maxima.

In stratified lakes, the populations peak at various depths strictly within the epilimnion. The available data do not permit generalizations about vertical movements or preferred depths in terms of light regime (GEITLER & RUTTNER 1936, FABBRO & DUIVENVOORDEN 1996). In Lake Julius, Australia (SAKER 1996), *C. raciborskii* growth was favored by conditions resistant to vertical mixing (measured as Brunt-Väsälä frequency number), moreover the highest density was recorded at the depth of 2 m (euphotic zone: 0–4.5 m, mixing depth: 6 m). In Solomon Dam, Australia the peaks of *C. raciborskii* coincided invariably with increases in thermal stability after deep-mixing events and the water column stability proved to be a useful predictor of bloom occurrence (HAWKINS 1996).

In temperate regions, the species occurs exclusively in the warmest periods of the year. In these lakes *C. raciborskii* is sensitive to meteorological conditions. This is due to at least two factors. One is that cold summers may prevent the germination of akinetes, and if so, the alga either does not occur at all or only in small amounts. The second is that it seems to be sensitive to wind-induced physical disturbances (Balaton, PADISÁK 1995; Alte Donau, DOKULIL & MAYER 1996) which is an important factor since all these lakes are shallow and polymictic. *C. raciborskii* growth could be prevented by artificial destratification (aeration) as described by HAWKINS & GRIFFITHS (1993). FABBRO & DUIVENVOORDEN's (1996) observation somewhat contradicts: a dense population  $30 \cdot 10^6$  filaments  $l^{-1}$ ) developed in an impoundment of Fitzroy River while thunderstorms and winds stronger than normal occurred.

## pH, conductivity

*C. raciborskii* characteristically occurs in lakes with pH of 8.0–8.7. Average for available records (29 data) is 8.35. The lowest range (7.3–7.8) occurs in Lake Cargeilligo (BOWLING 1994) while the highest (9.2–9.3) in Lake Xolotlán (HOOKER et al. 1991). The highest annual pH variation (6.0–10.0) of lakes with *C. raciborskii* occurs in Paranoá Reservoir, Brasil (BRANCO & SENNA 1994). As it is true of many other blue-green algae, the species does not occur in acidic waters at all (FOGG et al. 1973).

The highest conductivities were recorded in Lake Valencia, Venezuela (1900–2100  $\mu\text{S cm}^{-1}$ , LEWIS 1986) and Albufera la Valencia, Spain (1780  $\mu\text{S cm}^{-1}$ , ROMO & MIRACLE 1994) while the lowest ones in the Kariba (80–120  $\mu\text{S cm}^{-1}$ , RAMBERG 1984), Paranoá Reservoir (80–120  $\mu\text{S cm}^{-1}$ , BRANCO & SENNA 1994) and Itaipu reservoirs (45  $\mu\text{S cm}^{-1}$ , ANDRADE et al. 1995). All other lakes have conductivities between 161–660  $\mu\text{S cm}^{-1}$ .

No relationship was found between the ionic composition of lake waters and the occurrence of *C. raciborskii*. The species is apparently able to tolerate high salinities for some time since it has been recorded twice in the Northern Kaspean Sea at salinities of 1.5–2‰. In the Murray-Darling river system conductivity ranges between 500 and 4000  $\mu\text{S cm}^{-1}$  (BAKER 1996). *C. raciborskii* was found in the period 1991–1995 at Goolwa (Lake Alexandrina) subjected to seawater ingress at high tide when conductivities ranged from 585 to 4200  $\mu\text{S cm}^{-1}$ . Because groundwater in the Murray Valley, Australia, is rendered saline by residual marine sediments and the effect of irrigation has led to widespread salinization of water resources (WALKER 1992) it is likely that many of the unnamed localities where *C. raciborskii* occurs is at least slightly saline.

## Nitrogen

Being a heterocytic blue-green alga, *C. raciborskii* dominance is often attributed to the ability to fix atmospheric nitrogen to overcome N-deficiency. Since the role of N-deficiency in triggering heterocyte differentiation is known (OGAWA & CARR 1969) their appearance can be used as an indicator to fix N. The Paranoá Reservoir is rich in inorganic N-forms, especially in ammonia (1461  $\mu\text{g l}^{-1}$  in the dry- and 527  $\mu\text{g l}^{-1}$  in the wet season; BRANCO & SENNA 1994). Heterocytes were observed only in 8% of the samples and even in these ones only few trichomes possessed them. Moreover, heterocytes appeared only in months when the lowest level of ammonium was registered. In the oligotrophic Kariba Reservoir almost every filament of the dominant *C. raciborskii* population had heterocytes in the period when inorganic nitrogen in the water was low (RAMBERG 1987) and it was so in Lake Venezuela (LEWIS & RIEHL 1982) where phytoplankton growth is primarily limited by very low inorganic N levels (LEWIS 1986) and it was the case in the Parakrama Samudra, too (ROTT 1983, GUNATILAKA & SENARATNA 1981). Appearance and/or dominance of *C. raciborskii* was attributed to low inorganic nitrogen levels in other tropical and subtropical lakes, like Lake Kivu (HECKY & KLING 1987), Lake Victoria (KOMÁREK & KLING 1991), Lake George (GANF 1974) and Lake Malawi (PATTERSON & KACHINJIKA 1993). Dominance of *C. raciborskii* and *Anabaenopsis* spp. in the North Pine Dam, Australia was attributed to N-limitation because the N/P loading ratios were well below the Redfield proportions (HARRIS & BAXTER 1996).

The above cases, also TALLING's (1965) observation that tropical deep lakes tend to be frequently N-limited support the supposition that N deficiency is indeed a major cause leading to dominance of heterocytic blue-green algae in tropical waters, among them *C. raciborskii*.

In temperate shallow lakes, the ability to fix atmospheric N is probably not a priori but, if at all, an additional reason that leads to *C. raciborskii* dominance. During the 1994 bloom of *C. raciborskii* in Lake Balaton, N<sub>2</sub>-fixation and <sup>15</sup>N-labelled ammonium and nitrate uptake of phytoplankton was measured at two sampling sites (PRÉSING et al. 1996). Nitrate-uptake was insignificant in both basins despite its ambient concentrations were similar to that of ammonia. In the less eutrophic eastern basin of the lake N-fixation contributed 10 % while ammonia uptake 80 % to N-supply at the peak of the bloom. In the western basin N<sub>2</sub>-fixation contributed 49 % to the N-demand. According to PRÉSING et al. (1996), heterocytic blue greens first took advantage of their ability to assimilate ammonium at low ambient concentrations and only when inorganic sources are exhausted and their amounts are not sufficient to support further increase of population does N<sub>2</sub>-fixation play more important role. According to the author's own data during the 1994 bloom 96 % of the heterocytic blue-green algal biomass was attributable to *C. raciborskii* in the eastern basin of the lake while only 73 % in the western one. In the eastern basin of the lake, close negative correlations were found between ambient ammonium concentrations and the biomass of heterocytic blue-green algae (PADISÁK & ISTVÁNOVICS in press). Inverse relationship with population density and ammonium was also found by FABBRO & DUIVENVOORDEN (1996). Morphological observations on the preceding *Aphanizomenon klebahnii* and *C. raciborskii* populations in 1992 and 1994 in Balaton showed that of the *Aphanizomenon* biomass, 5.1 % was found in heterocytes in both years. The biomass that could be attributed to *C. raciborskii* heterocytes was 1 % in 1992 and 1.4 % in 1994 (PADISÁK & ISTVÁNOVICS in press). N<sub>2</sub>-fixation as a factor leading to *C. raciborskii* dominance in Alte Donau, Austria was ruled out because of the low frequency of heterocytes (DOKULIL & MAYER 1996).

The above data from temperate shallow lakes show that N-deficiency is not a priori reason for the development of *C. raciborskii* blooms and N<sub>2</sub>-fixing ability becomes important only when other sources are exhausted. The data allow us to suppose that the threshold concentration of ammonium uptake of *C. raciborskii* is probably lower than that of other blue-green algae which can be a major competitive advantage during development of blooms because N<sub>2</sub>-fixation only enables further increase when other species are already outcompeted.

## Phosphorus

Inorganic phosphorus content as well as total phosphorus concentrations vary within a wide range in the lakes where *C. raciborskii* occurs in large amounts. Comparisons of growth to ambient P concentrations revealed no clear relationships or were independent in many cases (SAKER 1996, DOKULIL & MAYER 1996, PADISÁK & ISTVÁNOVICS in press). According to BRANCO & SENNA (1994), the species' ability to rapidly absorb phosphate



even at low concentrations and the migration to nutrient rich deeper waters can be of importance in Paranoá Reservoir.

In chemostat experiments with the ACT 9502 *C. raciborskii* strain (ISTVÁNOVICS 1997) half-saturation constants ( $K_m$ ) of 1.5–2.5  $\mu\text{g P l}^{-1}$  were found which are relatively low values as compared to other algae, however, they are not extremely low. The threshold concentration was 0.3  $\mu\text{g P} [\mu\text{g chl } a]^{-1}$  or 2.5  $\mu\text{g P} [\text{mg C}]^{-1}$ , which are, again, relatively but not exceptionally low values. P-storage capacity of *C. raciborskii* (within quasi-steady state conditions 12 times higher, if P-supply is pulsed 24 times higher cell quota than the minimal) allows the population to divide 5 times on expense of the stored P (ISTVÁNOVICS 1997).

The field data from Lake Balaton (PADISÁK & ISTVÁNOVICS in press) allow the supposition that P-storage does play an important role in development of blooms. *C. raciborskii* blooms in Lake Balaton (eastern basin) developed when SRP concentrations were both below the analytically detectable level and the threshold, and no external P-source was available while the sediments of the lake were relatively rich in P. Based on numerous indirect evidences it can be supposed that P-pool akinetes is also essential in development of *C. raciborskii* blooms in the lake. Thus, the species can be a key organism in the internal P-load of shallow lakes. There are observations from other lakes that seem to support this view. In the Parakrama Samundra, Sri Lanka low dissolved nutrient concentrations in the water are combined with exceptionally high concentrations in the sediment (GUNATILAKA & SENARATNA 1981). In Lake George dominance of *C. raciborskii* was related to the internal P-load (GANF 1974). Based on observations in an old pond, in Hyderabad, India. SEENAYYA & SUBBA RAJU (1972) noted that paucity of P may lead to akinete production. Akinetes were also produced in quantities well exceeding the amount necessary for perennation in Lake Balaton, Hungary, too (PADISÁK & ISTVÁNOVICS, in press).

### Blooms, bouyancy

Blooms of *C. raciborskii* have been observed by many investigators. The maximal observed densities are about  $10^8$ – $10^9$  filaments  $\text{l}^{-1}$ , that corresponds roughly 30–50  $\mu\text{g l}^{-1}$  in terms of biomass freshweight (HAWKINS & GRIFFITHS 1993, BRANCO & SENNA 1994, DOKULIL & MAYER 1996, PADISÁK & ISTVÁNOVICS in press). Such blooms are more frequently reported in temperate lakes than in subtropical and especially in tropical ones (KOGAN 1955, 1956, PRESCOTT & ANDREWS 1955, DOKULIL & MAYER 1996, PADISÁK & ISTVÁNOVICS in press). Similar densities or blooms from lower latitudes were found exclusively in newly created reservoirs or river impoundments (HAWKINS et al. 1985, BRANCO & SENNA 1994, GIANI 1994, FABBRO & DUIVENVOORDEN 1996). Maximal densities in natural tropical lakes are at least five times smaller than in man-made tropical or different kinds of temperate lakes.

A single observation (FABBRO & DUIVENVOORDEN 1996) reports a change in water colour during a *C. raciborskii* bloom. In the Fitzroy River, Australia water colour turned reddish in the initial phase of population increase. By the time the peak developed, a green colour was apparent. Red and green coloured populations were also found in FABBRO's (pers. comm.) cultured materials and they behaved differently:

green filaments tended to form a scum on the surface while red ones sank to the bottom of the culture flasks.

The only description of development of surface scum under natural circumstances is by PRESCOTT & ANDREWS (1955) from the Wooster Lake: "... a thick surface scum ... endured for two days and then disintegrated, coloring the water greenish-yellow." Greenish-yellow coloration was observed by other investigators, too. HAWKINS et al. (in press) when isolating *C. raciborskii* from the Oatley pond let ... "the buoyant cyanobacterial cells ... first concentrate ... by standing overnight ... [then] filaments [are] harvested from the surface." Except these observations no report about development of surface scums is described even at very high densities. HAWKINS et al.'s (in press) other observation (... "The isolate grew without aggregation or sedimentation in batch cultures, so no agitation was necessary." ...) also supports that the species have extremely good floating abilities. The ability of buoyancy regulation was considered to be an important selective advantage in the tropical oligotrophic Lake Kariba (RAMBERG 1987) that enables to species to utilize the richer nutrient resources of the deeper water layers. It can be attributed to the good floating ability of *C. raciborskii* that dense population do not collapse suddenly; net increase and net decrease rates are very similar (G.-TÓTH & PADISÁK 1986, PADISÁK & ISTVÁNOVICS in press; DOKULIL & MAYER 1996). Maximal net increase rates under field conditions expressed as population doubling time vary between 2.9 and 7 days (4.1 d, Balaton 1982, 2.9 d, Balaton 1992, PADISÁK 1994; 3 d Fitzroy River, FABBRO & DUIVENVOORDEN 1996; 7 d, Alte Donau DOKULIL & MAYER 1996). In laboratory cultures the species grows quicker. HAWKINS (1996) experienced a growth rate of 1.7 divisions per day at 25 °C while no growth was recorded under 20 °C which means that *C. raciborskii* under optimal conditions can increase from detection limit to bloom amounts in 7 days.

### Light conditions

The fact that *C. raciborskii* can persist in very dense populations without sudden collapses implies that it tolerates low light due to self shading. Secchi-disc readings of 30 cm are characteristic during *C. raciborskii* blooms. There has been only one study in the extended literature that attributes the success of the species primarily to its shade tolerance, it is by DOKULIL & MAYER (1996). They observed that chlorophyll-specific photosynthetic rates became light saturated at photon flux densities of 30–60  $\mu\text{E m}^{-2} \text{s}^{-1}$  similarly to cultured *Limnithrix redekei*. The data indicated that the community was low-light adapted and the high light efficiency may be a consequence of chromatic adaptation.

SHAFIK et al.'s (1997) experiments with the ACT-9502 *C. raciborskii* strain from Lake Balaton have shown that maximal growth occurred at 120  $\mu\text{Mol m}^{-2} \text{s}^{-1}$ . Photon fluxes higher than 200  $\mu\text{E m}^{-2} \text{s}^{-1}$  inhibited growth and photoadaptational parameter ( $I_k$ ) was very low: 20  $\mu\text{E m}^{-2} \text{s}^{-1}$ . These data also support the view that *C. raciborskii* can, indeed, grow at very low light intensities. Similarly low values are characteristic exclusively for low-light adapted species like the blue-green algae *Planktothrix agardhii*, *P. rubescens*, deep-layer maximum forming picoalgal *Synechococcus* sp. (PETERSEN 1991,

ZEVENBOOM & MUR 1980, MUR & BEJSDORF 1978) or even the freshwater, deep-layer moss *Chilocyphus rivularis* (FARMER et al. 1988).

Several questions arise in relation to the high light efficiency of the species. In the tropical deep lakes where *C. raciborskii* most probably evolved (see later) it does not occur at bloom densities and these waters are not exceptionally turbid (Secchi transparency between 1.5 and 6 m). No record of *C. raciborskii* is known about its occurrence in deep layer maxima. If so, why and where did the species become adapted to low light?

### Perennation

i) In deep tropical lakes *C. raciborskii* filaments with akinetes are not or only very rarely reported. In the material of the Sunda expedition (GEITLER & RUTTNER 1936) from Java and Bali one single akinete was found only. The lack of akinetes is reported from many deep, tropical lakes of other continents, too (BRANCO & SENNA 1994; RAMBERG 1987, KOMÁREK & KLING 1991). Akinetes of some other *Cylindrospermopsis* species have been still undescribed. In tropical environments, the species perennates in a physiological resting stage like many other phytoplankton species in other lakes (PADISÁK 1992).

ii) In subtropical and temperate regions, *C. raciborskii* exhibits a characteristic morphological series during annual population dynamics as described by SINGH (1962) in detail. Akinetes appear late in the population cycle; usually after the population peaked. In Lake Balaton, this species produced many more akinetes than other heterocytic blue-green algae (PADISÁK & ISTVÁNOVICS in press) that may be connected with P-metabolism. Microscopic observations showed that in the decreasing phase of population growth, appearance of akinetes were paralleled by a continuous fading of common filament cells that provides an impression that all the material of common cells would be transported to the akinetes. By the end of the process akinetes appear as glowing, elongated pearls on hardly visible filaments (personal observation). Later the akinetes sink to the sediment from where they can be germinated under laboratory conditions (GORZÓ 1985).

iii) FABBRO's observation (pers. comm.) that red coloured filaments sink to bottom may also indicate a form of perennation, however, its importance, especially in natural populations, has been unclear.

### Relationships with higher trophic levels

The ecological success of *C. raciborskii* is attributed, at least partly, to its low predation by zooplankton (BRANCO & SENNA 1994).

The earliest observation on edibility of *C. raciborskii* is by SEENAYYA (1971a, b) who noted that peaks of zooplankton preceded those of phytoplankton in a shallow pond in India and the development of zooplankton received a setback when blue-greens, particularly *C. raciborskii* and *Lyngbya mucicola* dominated. An inverse relationship between *C. raciborskii* biomass and Cladocera abundance was described in Solomon Dam, Australia (HAWKINS 1988). The zooplankton of the Paranoá Reservoir, Brasil was generally considered being unable to consume *C. raciborskii* that occurs permanently in high densities (PINTO-COELHO 1983).

Zooplankton investigations during the 1982 *C. raciborskii* bloom in Lake Balaton, Hungary, reported on a qualitative change within the crustacean community: filter feeders of bigger body sizes (*Daphnia*, *Eudiaptomus*) practically disappeared and being replaced by cyclopoids and clearance rate decreased significantly (ZÁNKAI 1985). *C. raciborskii* filaments were found to interfere with the process of food collection of three *Daphnia* species (*D. pulicaria*, *D. hyalina* and *D. cucullata*; GLIWICZ & LAMPERT 1990). Filtering rates of the same three *Daphnia* species of different body sizes were reduced in the presence of *C. raciborskii* under experimental conditions (HAWKINS & LAMPERT 1989) and larger species were more affected than smaller ones.

The straight and rigid filaments of *C. raciborskii* were not ingested by the rotifer, *Brachionus rubens*, in ROTHAUPT'S (1991) experiments, moreover, their presence reduced the ingestion of algae offered simultaneously. The soft filaments of *Anabaena flos-aquae* were ingested at a moderate rate and they did not reduce the ingestion of other algae. During a *C. raciborskii* bloom in Fitzroy River, Australia, *Brachionus angularis* was observed ingesting straight trichomes of *C. raciborskii* while grazing on the dominant coiled filaments were not recorded (FABBRO & DUIVENVOORDEN 1996).

In enclosure experiments (STARLING & ROCHA 1990) three species of facultative planktivorous fishes enhanced the growth of *C. raciborskii* while the obligate planktivorous *Hypophthalmichthys molitrix* reduced its density; the authors conclude therefore that top-down control can be a promising tool in bloom control.

## Predictions

Success of *C. raciborskii* in the world's lakes can be attributed to multiple reasons, especially

- good floating ability that allows on one hand diurnal migration between nutrient rich lower strata and euphotic upper layers and on the other hand to avoid surface accumulation during which many of the filaments would be damaged physiologically;
- superior shade tolerance that allows it to build up large populations before self-shading would prevent further growth;
- high affinity ammonia uptake that allows *C. raciborskii* to utilize the cheapest N-source while other heterocytic species have to fix atmospheric N;
- N-fixation, when no other N-sources are available;
- relatively high affinity P-uptake combined with relatively low thresholds and high P-storage capacity;
- ability to mobilize internal P sources and
- resistance to grazing.

In most lakes a combined action of some of the above features lead to its dominance. Consequently, generalized predictions about its appearance are impossible to outline, investigators have to develop individual explanations with individually weighted reasons for different lakes. However, some generalized predictions are possible.

Yearlong occurrence of *C. raciborskii* is expected exclusively in tropical-subtropical (25°N–25°S) waters with continuously high temperatures (> 20 °C) and a high level of

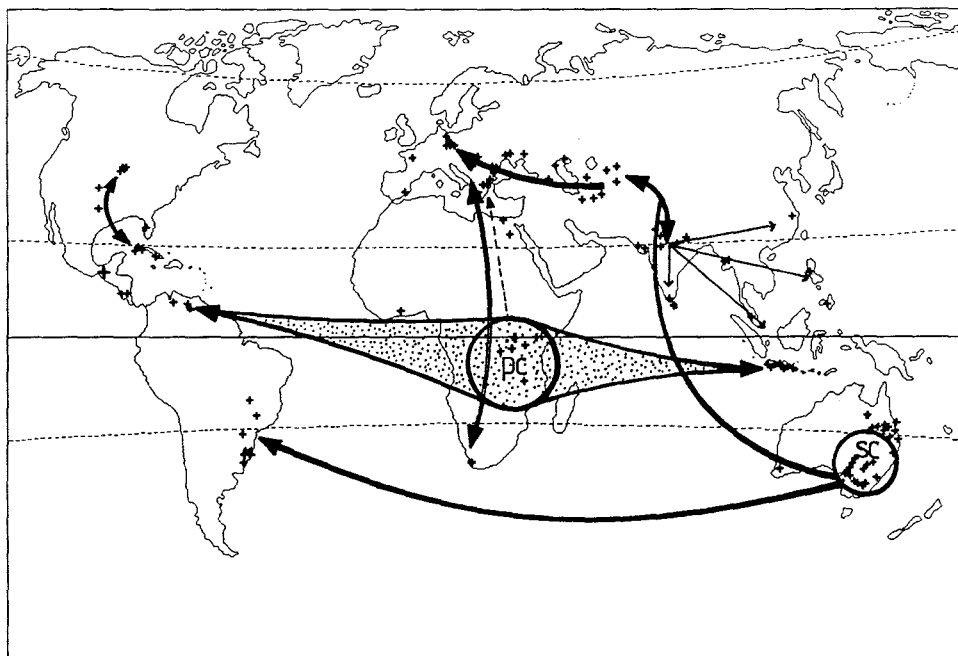


Fig. 9. Occurrences and possible routes of dispersal of *Cylindrospermopsis raciborskii*. pc: primary evolutionary center in the tropical Africa; possible routes of dispersal are indicated with dotted arrow area and dotted line. sc: secondary center in Australia, supposed dispersal routes are indicated with black arrows.

environmental (climatic and hydrological) constancy. These waters usually offer high nutrient levels (for example, Paranoá Reservoir).

Seasonal occurrence in tropical waters is expected if nutrient (either N or P) limitation prevails seasonally. In these lakes it occurs in periods characterized by a high level of environmental constancy (stratification). Phytoplankton growth in these waters is frequently limited by the availability of nitrogen.

In the temperate region, *C. raciborskii* is restricted to the warm season, when lake temperatures exceed 23–25 °C for at least for several weeks. In higher latitudes the species occurs exclusively in shallow, polymictic lakes where sediments warm up to at least 21–22 °C that is necessary for germination of akinetes. Population growth is limited to short periods in late summer especially in those waters where P availability is poor. In P rich waters high population maxima are expanded for longer periods. Evolutionary adaptation to colder temperatures is, probably, going on recently.

Fluctuations in meteorological conditions in different years make the appearance of *C. raciborskii* quite variable. The best example is Lake Balaton (PADISÁK in press), and similar phenomena have been described in Minnesota lakes (HILL 1970) in the subtropical North Pine Dam (HARRIS & BAXTER 1996) and Pampulha reservoir (GIANI 1994).

From the pattern and timing of dispersal within Europe it can be forecasted that *C. raciborskii* will increasingly inhabit European shallow lakes within the next 10–20 years. Depending upon the speed of more and more apparent cold adaptation its occurrence in deeper temperate lakes is also possible.

## Phytogeography, dispersal and evolution of *C. raciborskii*

Across the world there is a prevailing view that freshwater algae are cosmopolitan. This notion has seldom been tested and is unlikely to be true especially in terms of genetics (TYLER 1996).

*C. raciborskii* had been considered as typical Indo-Malayan flora element for a long time. Later, the distributional type was indicated as "pantropical" and this view has been so widespread that despite the increasing number reports from temperate regions some recent authors still cite *C. raciborskii* as example of pantropical distribution (HOFFMANN 1996). In the view of the floristic data summarized in this paper it is evident that *C. raciborskii* cannot be considered as an exclusively tropical or subtropical species, as a matter of fact its northernmost occurrences overlap with southernmost localities of northern circumpolar species, like *Cyclotella tripartita* (SCHEFFLER & PADISÁK 1977).

Biogeography of freshwater algae is of increasing interest (KRISTIANSEN 1996b) and difficulties are also increasingly recognized. In many cases, it is problematic to say that a species is non-existent in a given area since we, almost always, have to consider the insufficiency of historical searches. Species associated with some extreme of environmental factors (hotspring species, snow algae, species occurring at extreme acidities, etc.) are relatively easy to map, difficulties increase tremendously in case of species having "average" demands and wide distributions. It is also increasingly documented that widespread "morphological species" may exhibit different ecophysiological adaptations; ecotypes do exist. The occurrence of so many common freshwater algae throughout the world is a reflection of ease of transport, yet, for the majority, there is no information about transport mechanisms (ROUND 1981). Different dispersal agents have recently been reviewed by KRISTIANSEN (1996a).

My own conviction is that careful analysis of floristic data combined with appreciation of ecological and ecophysiological demands of species can lead to a better understanding of geographic distribution, and can provide a deeper insight to evolution and dispersal of freshwater algal species. In the following sections I try to put together the "*C. raciborskii* puzzle" in a way that can provide at least a hypothetical answer to its evolution and recent and future dispersal.

The high temperature demand and the inability of *C. raciborskii* to adapt to temperature fluctuations indicate that it evolved in tropical lakes (Fig. 9). The fact that diversity of *Cylindrospermopsis* genus is the highest in Africa carries the message that the primary evolutionary center can be placed to the deep lakes in tropical Africa. Limnological characteristics of these lakes show that *C. raciborskii* could have adapted there to low nutrients (ammonia and P), could have taken an advantage from N<sub>2</sub>-fixing ability, and could have developed good floating abilities especially that temperature, therefore density gradient in these lakes is much smaller than in temperate ones. From the primary center in Africa it could have spread over the equatorial region, especially to crater lakes in Indonesia and some lakes in Central America. In all probability, a population originating from this, not very invasive strain was found by SKUJA (1938) in 1935 in Lake Kastoria, Greece which lake lies along one of the most prominent bird migratory route, the "Eastern European Flyway" (PÉTERFI & MOMEU 1996). Occurrence of *C. raciborskii* in Lake Kastoria remained a solitary point for almost 40 years,

however, it cannot be ruled out that this strain populated the nearby Lake Volvi (HINDÁK & MOUSTAKA 1988), the northernmost stratified lake where the species occurs.

To explain the ongoing invasion of *C. raciborskii* both in tropical, subtropical and temperate regions a secondary center has to be supposed because, as it was pointed out previously, superior shade tolerance is not very likely to be selected in tropical lakes. Apart from naturally hypertrophic lakes (which were far less numerous in the past than they are recently) and deep layers of lakes or seas there are two kinds of "low light" aquatic environments: lakes with high inorganic turbidity and rivers. Such environments, lake or river, do not differ essentially from the point of view of phytoplankton adaptation (REYNOLDS et al. 1994). Not only the early epidemiological records help us to recognize the first wide-spread occurrence but as well the hydrological circumstances and its primarily subtropical position indicate that the supposed secondary evolutionary center can be located in Australia. Water discharge, even in the large river systems of the continent fluctuates within a wide range: from complete dry-out to large floods leaving temporary, natural reservoirs behind. Dispersal is going on by river flows whilst the main flow is enriched by inocula from sediments of temporal impoundments as it is nicely described in FABBRO & DUIVENVOORDEN (1996). Both environments are turbid, originally because the inorganic particles drifted by the river secondarily because of mass-production of algae. Salinity tolerance of *C. raciborskii* supports this view; this feature could also be evolved in Australia.

Thus supposition can explain both the high light efficiency of *C. raciborskii* and the fact that it can travel long in river courses. High akinete production, that is not at all necessary in tropical deep lakes, becomes essential: under such circumstances the species cannot perennate in scarce populations, akinetes are necessary to survive in dry periods. Akinetes are important from another aspect of dispersal: they are more likely to survive long travels in the guts of migratory birds (cf. ATKINSON 1972, 1980) than common filaments.

Accepting Australia as a secondary evolutionary center where the shade tolerant, invasive strain was selected, two kinds of dispersal can be recognized. One is the dispersal by birds or other "chance events" of primarily human origin. These are the most likely dispersal agents to South American reservoirs and temperate North American lakes (HILL [1969–70] attributed the occurrence of *C. raciborskii* in Minnesota lakes to shipments of tropical fish). The other is a continental route that can be easily recognized and connects Australia and northern Germany. As a first step the invasive strain had to be carried (probably by birds) either to India (SINGH 1972) or to the catchment area of rivers opening to the northern Caspian Sea (USSATSHEV 1938) some time in the 1930s. From the locality it was introduced first (it is impossible to say which of the above two was the first, however the Caspian region carries more similarities [aridity, temporary rivers with reservoirs, tendency of higher salinities] with hydrological conditions in Australia), it was carried to the other and in both regions it became widespread during the 1950s–1960s. Locally migrating birds and rivers as dispersal factors are increasingly important. From the Central Asian Republics it reached the Danube mouth, then Hungary (1970s) and spread further to northern Germany by the 1990s. Its occurrence in a small lake near Paris indicated that the dispersal route turned south within Europe. It is possible to predict that *C. raciborskii* will populate more and

more waters in France, Italy, Spain and Portugal, maybe enter the waters of Denmark and England. The only known locality in southern Europe (Albufera de la Valencia, Spain) can be considered point-like.

Concerning occurrences in shallower subtropical and tropical lakes in Africa a “back migration” from Europe can be of importance: in European shallow lakes *C. raciborskii* peaks and produces many akinetes in September, just when migrating birds start to fly south.

As a consequence of poor phycological documentation of phytoplankton papers from North America reconstruction of *C. raciborskii* dispersal after an initial introduction in the 1950s remains hopeless, however the parallel occurrence in many shallow lakes in Minnesota indicates that the invasive strain occurred there.

Multiple reasons that result in *C. raciborskii* dominance in many different kinds of environments raise the question that either we do have a species that is invading recently and has extremely good multiple competitive abilities or we have to suppose that the species exists in different physiological strains or ecotypes. The data suggest that the genus *Cylindrospermopsis* has been a relatively young product of evolution, *C. raciborskii* has been a recently dispersing “good species” in the sense that the number of ecotypes, if exist at all, must not be large.

Investigations on genetic, biochemical and ecophysiological level in cultured materials deriving from different areas of the world are necessary.

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