

Alien cyanobacteria: an unsolved part of the “expansion and evolution” jigsaw puzzle?

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Abstract Some algal species have extended their native range. Problems in settling on a proper definition of ‘alien’ for microorganisms have made it difficult to unequivocally assess whether their spread was natural or resulted from human intervention. As direct evidence seems to be virtually non-existent, the only option is to rely on circumstantial evidence. In this paper, we discuss the expansion routes of three cyanobacteria species: *Cylindrospermopsis raciborskii*, *Raphidiopsis mediterranea* and *Cuspidothrix issatschenkoi*. We analyse the information available for these species, which are commonly regarded as alien, in order to establish the context in which the migration and evolution of these microorganisms should be understood, so that a proper assessment of their geographic expansion can be made. A more complete picture of the expansion and evolution of microorganisms must combine many types of information, including the history of local expansions,

ecological ranges, and data from studies in morphology, ecology, genetics and paleolimnology.

Keywords Microorganisms · Migration · Geographical distribution · Climate

Introduction

Human activity has led to the introduction of many alien organisms in all ecosystems, including freshwaters (Kilroy & Unwin, 2011). There is ample evidence of unintentional transport of aquatic organisms in shipping (ballast water), trade of species for aquaria, aquaculture, angling, fisheries, etc. (Incagnone et al., 2015). Other activities such as canal construction also facilitate invasions of aquatic alien species without physically moving them (for more details see Incagnone et al., 2015). All those interventions provide opportunities for species to travel long distances and colonise new areas. After reaching new habitats, these travellers may be recognised as alien. It is well known that their impact on ecosystems can pose a threat to biodiversity in many ways, including predation or herbivory, competition and hybridisation, altering ecosystems as a result (Strefataris & Zenetos, 2006).

Different aspects of the problem of biological invasions have been discussed widely in work ranging from simple lists of alien species on local (Najberek & Solarz, 2011), regional (Kaštovský et al., 2010; Wilk-

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Woźniak & Najberek, 2013) or global scales (Lowe et al., 2000) to complex analyses of their ecological and economic impacts (Vilà et al., 2011). Methods of assessing the impact of alien species are relatively well developed for plants, vertebrates and invertebrates in terrestrial, freshwater and marine environments (Vilà et al., 2009). In contrast, changes in freshwater ecosystems due to new introductions of microorganisms (cyanobacteria, algae), and the consequent socioeconomic impacts, are poorly studied. Part of the reason for this is that finding and evaluating alien microorganisms in new habitats is difficult due to their small size, sometimes insufficient taxonomic expertise, disagreements about a given species concept and the confusing terminology of biological invasions.

Due to problems defining what an alien microorganism is, their records are very often reported as exotic species (Cellamare et al., 2010), interesting species (Zapomělová et al., 2012), or first reports of a species in an area (e.g. Manti et al., 2005). Assembling the alien microorganisms jigsaw puzzle requires various kinds of information, among which are proper taxonomic identification and a good description of the native range of the species, so that expansion beyond the native range can be ascertained.

Cyanobacteria form one of the oldest groups of microorganisms, with fossil remains dating back 3.5 billion years (Schopf, 2000). Due to their ability to create toxic blooms (harmful algal blooms—HAB) they are considered dangerous organisms which may harm water habitats and local biodiversity and reduce the value of ecosystem services such as recreational uses or provision of potable water.

Some cyanobacteria are reported to be ubiquitous organisms with a nearly global distribution (Jungblut et al., 2009). Others are said to have extended their native range (Padisák, 1997; Wood et al., 2014). It is very difficult to assess the native/alien status of a taxon, but analyses aimed at determining the true status of these ‘alien’, ‘exotic’ and ‘interesting’ microorganisms can help elucidate their biogeography and ecology. We tracked the long-distance ‘walk’ of three species of cyanobacteria through different climate zones, to see whether we could reliably determine if they have indeed expanded their ranges. The larger aim was to establish the context in which the migration and evolution of these microorganisms should be understood, so that a proper assessment of their geographic expansion can be made.

Materials and methods

We selected 3 species of cyanobacteria, *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya & Subba Raju in Desikachary 1972, *Raphidiopsis mediterranea* Skuja 1937 and *Cuspidothrix issatschenkoi* (Usachev) P. Rajaniemi, Komárek, R. Willame, P. Hrouzek, K. Kastovská, L. Hoffmann & K. Sivonen 2005. Those three species are widely accepted as alien for temperate zone in Europe (Kaštovský et al., 2010), and according to the current knowledge, their taxonomy is accepted (Komárek, 2015).

To gather information on the records of these species from different countries/continents, we made a thorough literature search using the ISI Web of Knowledge, Scopus, Google Scholar, local journals and local libraries. The identification keys of the Algae-Base (Guiry & Guiry, 2014) and Komárek (2013) were used to determine the taxonomic position of each species. Maps were created in ArcGIS 10.1 using the World Climate Zones—Simplified ArcGIS Online basemap. To track the route of each species’ ‘walk’ we determined the site of its first description (*locus typicus*) and subsequent findings. We used the *locus typicus* as the starting point because it is not possible to make a definite determination of the native range of any of the discussed species. On the maps we marked the site of the first record of the species on the local or regional scale (e.g. country, continent). The resolution of the maps ranges from country to global, depending on the availability of data. In the tables, we also present some basic environmental features such as water temperature, depth, trophic status and type of climate.

Results

All three cyanobacteria assessed in this study are recognised as tropical to subtropical species, and were first described from warm zones.

Cylindrospermopsis raciborskii (Woloszynska) Seenayya & Subba Raju in Desikachary 1972 is also known as *Anabaena* (*Anabaenopsis*) *raciborskii* (Woloszynska), *Anabaenopsis raciborskii* (Woloszynska) Elenkin, *A. seriata* Prescott, *A. maksimilianii* Obuchova, *A. koganii* Obuchova, *A. wustericum* Obuchova, *Cylindrospermum kaufmanii* (Schmidle) Huber-Pestalozzi and *C. doryphorum* (Schmidle) Bruhl and Biswas.

Locus typicus: Rava Demangan pond in Java (Wołoszyńska, 1912). The species was described from material collected in 1899–1900. However, it was found earlier in 1887 in the Nile, reported as *C. kaufmannii* (Schmidle) Huber-Pestalozzi, (Wołoszyńska, 1912).

Cylindrospermopsis raciborskii expanded rapidly to Europe in the last century and is considered an invasive alien species of the temperate zone (Padisák, 1997). The temporal sequence of the earliest local or regional records (Fig. 1) does not yield any solid conclusions about its potential routes of expansion, but the distribution of those records, ignoring their dates, suggests the following possible migration scenarios: (1) from the centre of Africa towards the north of the continent; (2) from North Africa to Europe; (3) from Java to eastern Australia; (4) from Java through South Asia to Europe and (5) from Australia to Southern Africa and on to the eastern parts of North, Central and South America.

Currently, the species is already found on almost all continents and in various climate zones: humid continental, humid subtropical, tropical wet, tropical dry, semi-arid, Mediterranean, marine and humid continental/subarctic (Fig. 1; Table 1). We have found no reports of it having colonised these other zones: subarctic, tundra and ice cap (Fig. 1). The majority of waters where *C. raciborskii* was first recorded at local and regional levels were shallow, warm (>20°C), of low transparency and high-nutrient concentrations (e.g. Padisák, 1997). However, there are some records from the Old Danube (Austria), Albano Lake (Italy) and other sites where local conditions were different (Table 1).

Raphidiopsis mediterranea Skuja 1937; heterotypic synonym: *R. subrecta* Frémy ex Skuja 1949.

Locus typicus: Kastoria Lake, Greece (Fig. 2; Table 2). It is considered an invasive alien species of the temperate zone (Kaštovský et al., 2010).

As in the case of *C. raciborskii*, the temporal sequence of the earliest local or regional records (Fig. 2) does not easily lead to hypotheses on possible expansion routes but the spatial clustering of records suggests the following routes: (1) from Southern Europe to northern and western parts of the continent; (2) from Southern Europe to North Africa and (3) from Europe to the east coast of North America. The Australian and South Asian records also seem to form a cluster separated from the European ones, a potential base for expansion to the east coast of South America.

The species has been recorded on all continents except Antarctica. Currently, it occurs in different climate zones: Mediterranean, humid continental, humid subtropical and arid. There is no information indicating a shift towards these cold zones: subarctic, tundra, ice cap or montane (Fig. 2). The locations of the first local or regional records of *R. mediterranea* included a wide variety of waterbodies, from shallow to very deep (Lake Biwa), and from eutrophic to hypertrophic (Table 2).

Cuspidothrix issatschenkoi (Usachev) P. Rajaniemi, Komárek, R. Willame, P. Hrouzek, K. Kas-tovská, L. Hoffmann & K. Sivonen 2005; homotypic synonyms: *Anabaena issatschenkoi* Usachev 1938, *Aphanizomenon issatschenkoi* (Usacev) Proshkina-Lavrenko 1968.

Locus typicus: Caspian Sea and Sea of Azov; shallow (max. depth 14 m) and of low salinity. It is known as a halophytic species. This cyanobacterium is considered to be an alien (but not invasive) species of the temperate zone (Zapomělová et al., 2012). The distribution of its records (Fig. 3) may suggest the following expansion routes: (1) from Western Asia to Europe; (2) from Europe to the east coast of North America; (3) from New Zealand and Australia to Far East Asia and (4) from New Zealand and Australia to Southern Africa and further to the east coast of South America. It has been found on almost all continents and is known from different climate zones: humid continental, tropical wet and arid. There are no reports of its progress towards these colder zones: subarctic, tundra or ice cap (Fig. 3). Many waters where *C. issatschenkoi* was first noted at local or regional levels were shallow and slightly saline (e.g. Baltic Sea). Salinity may be the key factor driving its expansion because it corresponds to its habitat preference. However, there are also some records from non-typical environmental conditions, including Lake Volvi (deep freshwater) in Greece, Lake Okaro in New Zealand (Table 3) and waters of low conductivity (Ferrari et al., 2011).

Discussion

Cyanobacteria are very abundant in all types of waters but our knowledge of their biogeography, migration and evolution is still insufficient. The ubiquity hypothesis (Finlay, 2002), which attributes almost

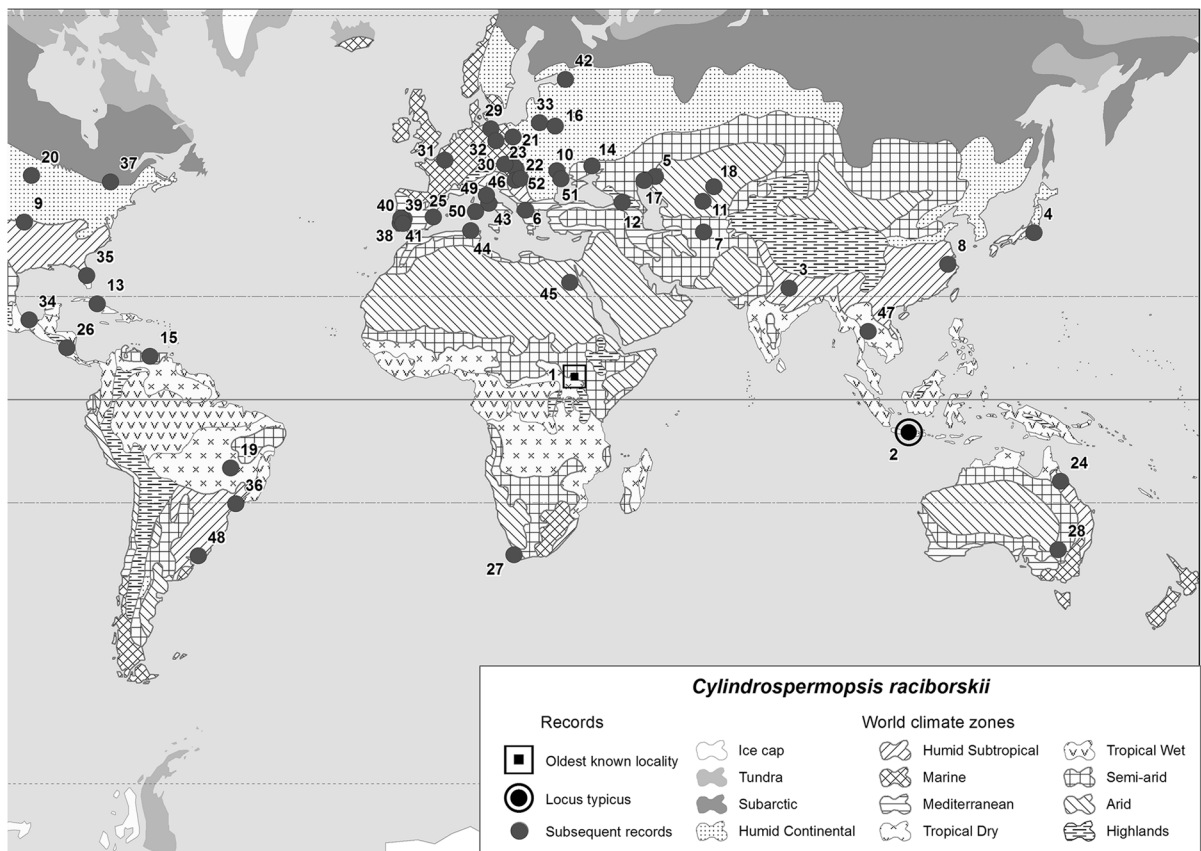


Fig. 1 *Locus typicus* and selected locations of the first records of *C. raciborskii*. Numbers mean subsequent years of observations: 1 Nile, tropical zone; 2 East, central, Java and Bali; 3 India, Varanasi; 4 Japan, Ganoike pond; 5 Northern Caspian Sea; 6 Greece, Lake Kastoria; 7 Turkmenia, Hindukush Res.; 8 China, Xi-hu Lake; 9 USA, Wooseter Lake; 10 Moldavia; 11 Uzbekistan; 12 Georgia; 13 Cuba; 14 Russia Zuevskoe cooling reservoir; 15 Venezuela, Lagartijo reservoir; 16 Belarus; 17 Caspian Sea near the mouth of Volga; 18 Kazakhstan, Farkhadskoe Res.; 19 Brasil, Paranoa Res.; 20 USA, Minnesota; 21 Poland, Lake Pątnowskie; 22 Hungary; 23 Slovakia, Borycki Res.; 24 Australia, Queensland, Solomon Dam Palm Island; 25 Spain, Albufera la Valencia; 26 Nicaragua, Lake Masaya i Lake

Xolotlan; 27 RPA, Zeekoevlei; 28 Australia, Murray Darling River Basin; 29 Germany, See Lieps; 30 Austria, the Old Danube; 31 France, small private fishpond; 32 Germany, lakes near Cottbus; 33 Lithuania, Glūko Lake; 34 Mexico, Lake Asmolapan Vera Cruz; 35 USA, Florida; 36 Brazil, Garças Pond; 37 Canada, Constance Lake; 38 Portugal, Odivelas Res.; 39 Portugal, Caia Res.; 40 Portugal, Maranhão Res.; 41 Portugal, Ardila River; 42 Russia, St. Petersburg; 43 Italy, Albano Lake; 44 Algeria, Lake Oubeira; 45 Egypt, El-Dowyrat fish farm; 46 Croatia, Kopački Rit and Lake Sakadaš; 47 Thailand; 48 Coastal region of Uruguay; 49 Italy, Trasimeno Lake; 50 Sardinia Island, Cedrino Lake; 51 Ukraine, Dnieper River and Danube Delta; 52 Serbia, Aleksandrovac Lake

unlimited dispersal abilities to microorganisms, leads to the common belief that geographic isolation does not operate in the micro-world. The resulting conclusion is that allopatric speciation is rare or absent and that therefore, the global morphospecies diversity of microbial organisms is low (Finlay, 2002). The moderate endemism model (Foissner, 2006), on the other hand, suggests that even microorganisms can have restricted geographic ranges (Papke & Ward, 2004; Boenigk et al., 2006). In the changing world,

with increasing pollution, global warming, carbon dioxide effects and rising salinity, species expansions are often recorded (Paerl & Huisman, 2009). However, in the micro-world, the uncertain provenance of species obscures their expansions even more. The scattered bits of information we have on the geographic range, *locus typicus* or ecological requirements of a species are puzzle pieces that can help complete the picture and answer the question of its status.

Table 1 Selected locations of the first records of *C. raciborskii* at local and regional levels (for more information about the spread of *Cylindrospermopsis raciborskii* before 1997 see Padisák, 1997)

Continent, climate zone	Country, place, year of record, if available	Basic features of water habitat, if available (depth, temperature, trophy status)	References
Asia, tropical wet	Java, 1899	Not available	Woloszyńska (1912) (Fig. 1, nb. 2)
Asia, humid continental	Japan, Ganoike pond, Ibaraki Prefecture 1935	Not available	Negoro (1935) (Fig. 1, nb. 4)
Europe, marine/continental	Austria, Urban lake (oxbow lake Old Danube), 1995	Shallow; max depth 6.8 m; water temperature 15–18°C	Dokulil & Mayer (1996) (Fig. 1, nb. 30)
Europe, humid continental	Belarus, eutrophic lakes	Not available	Mikheeva (1967) (Fig. 1, nb. 16)
Europe, mediterranean/continental	Croatia, Lake Sakadaš, 2003	Mean depth 7 m; hypertrophic lake	Mihaljevič & Stevič (2011) (Fig. 1, nb. 46)
Europe, marine/continental	Czech Republic, gravel-pit lake in Chomutov	Shallow ponds; from meso- to eutrophy	Horecká & Komárek (1979)
Europe, mediterranean	Italy, Albano Lake , Trasimeno (Central Italy) and Cedrino Lake in Sardinia Island, 2002	Albano Lake; deep; a volcanic crater lake; max depth 170 m ; Trasimeno Lake; shallow lake; max depth 6 m; endorheic water body; Cedrino lake; an artificial deep lake; mean depth 26.5 m	Manti et al. (2005) (Fig. 1, nb. 43)
Europe, humid continental	Lithuania, Glūko Lake	Not available	Vitenaite (2001) (Fig. 1, nb. 33)
Europe, humid continental	Poland, Pątnowskie Lake, 1972	Shallow lake; max depth 5.5 m; water temperature (April–November) >20°C; high eutrophic lake	Burchardt (1977) (Fig. 1, nb. 21)
Europe, mediterranean	Portugal, dam reservoirs: Odivelas Res., Caia Res. and Maranhão Res., 1999	Warm reservoirs; water temperatures 18.2–28.2°C	Saker et al. (2003) (Fig. 1, nb. 38–40)
Europe, humid continental	Russia Leningrad (St Petersburg) and surroundings	Not available	Balashova et al. (1999) (Fig. 1, nb. 42)
Europe, marine	Serbia, Slatina pond, Voivodina, 2006	Shallow lake; depth 0.9 m; water temperature 28°C; high concentration of ions	Cvijan & Fužinato (2012)
Europe, continental	Ukraine, the Dniepr River	Not available	Tsarenko et al. (2006) (Fig. 1, nb. 51)
Africa, mediterranean	Algeria, Lake Oubeira, 2000	Shallow lake; max depth 3 m	Bouaicha & Nasri (2004) (Fig. 1, nb. 44)
Africa, arid	Egypt, The El-Dowyrat fish farm	Shallow freshwater pond; max depth 4 m	McGregor et al. (2011) (Fig. 1, nb. 45)
Africa, mediterranean	South Africa, RPA, Zeekoevlei, 1990s	Shallow reservoir; max depth 5.2 m; water temperature varies between 10.3 and 28.5°C through the year; eutrophic reservoir	In: Padisák (1997) (Fig. 1, nb. 27)
South America, tropical dry	Brazil, Paranoá Reservoir 1960s	Deep reservoir; max depth of 38 m ; eutrophic reservoir	In: Padisák 1997

Table 1 continued

Continent, climate zone	Country, place, year of record, if available	Basic features of water habitat, if available (depth, temperature, trophy status)	References
South America, tropical dry	Nicaragua, Lake Xolotlan, 1990s	Deep reservoir, max depth of 26 m ; water temperature >20°C; endorheic lake	In: Padišák 1997 (Fig. 1, nb. 26)
South America, humid subtropical	Uruguay, Laguna Blanca 2004; Lago Javier 2005; Laguna Chica 2005; Laguna del Sauce 2004	Polymictic; natural and artificial water systems; shallow to medium depth: max depth 2.6–9.8 m; water temperature ca. 24°C; eutrophic	Vidal & Kruk (2008) (Fig. 1, nb. 48)
South America, semi-arid	Venezuela, Lagartijo reservoir 1966–1968	Small reservoir	In: Padišák 1997 (Fig. 1, nb. 15)
North America, humid continental	Canada, Constance Lake	Shallow lake; max depth 3.3 m; water temp. 23.5–24.4°C; meso- to eutrophic waters	Hamilton et al. (2005) (Fig. 1, nb. 37)
North America, humid continental	USA, Wooseter lake in Kansas recorded as <i>Anabaenopsis seriata</i>	Not available	Prescott & Andrews (1955) in Kling (2009) (Fig. 1, nb. 9)
Australia, humid subtropical	Australia, Solomon Dam Palm Island, Queensland, man-made reservoir, 1979	Not available	In: Padišák (1997) (Fig. 1, nb. 24)

Bold—parameters of habitats not typical for the species

Cylindrospermopsis raciborskii, *Raphidiopsis mediterranea* and *Cuspidothrix issatschenkoi*—products of migration and speciation?

It is believed that these three species originated from a region of warm climate (Kaštovský et al., 2010). According to the classification proposed by Schabetsberger et al. (2009), *C. raciborskii*, originally reported from habitats between the Tropic of Cancer (23°27'N) and Tropic of Capricorn (23°27'S), is a circumtropical species. *R. mediterranea* and *C. issatschenkoi* were classified as tropicopolitan species, meaning that they are found frequently throughout the tropical and subtropical zones (Schabetsberger et al., 2009).

According to Padišák (1997), the primary evolutionary centre of *C. raciborskii* is in tropical Africa, from where it expanded to Europe, and the second evolutionary centre, from where the species expanded to South America and Asia, is Australia. Although it is difficult to support this by tracking the temporal sequence of the first local or regional records, we drew similar conclusions from our assessment of the spatial distribution of records irrespective of their dates. The mechanisms of those expansions are not clear,

however. So far the presence of *C. raciborskii* has been confirmed in all climate zones except for the subarctic or any other cold zones. Its northernmost locality lies within humid continental climate.

Several hypotheses might explain the success of *C. raciborskii* outside its evolutionary centres. One of them considers its wide physiological tolerance of various environmental conditions (Kokociński et al., 2010; Piccini et al., 2011). Others invoke the trend towards warming of waters as an effect of, for example, the North Atlantic Oscillation (Briand et al., 2004), or global warming (Paerl & Huisman, 2009).

Usually, the first local records of *C. raciborskii* outside its *locus typicus* were from shallow, warm, turbid waters with different concentrations of nutrients. Exceptions include deep and cold waters in different parts of the world such as Austria (Dokulil & Mayer, 1996), Canada (Kling, 2009) or Uruguay (Bonilla et al., 2012). Such diversity of conditions under which this cyanobacterium occurs may be explained by the existence of different ecotypes and genotypes (Piccini et al., 2011; Sinha et al., 2012, 2014). Physiological and ecological studies showed

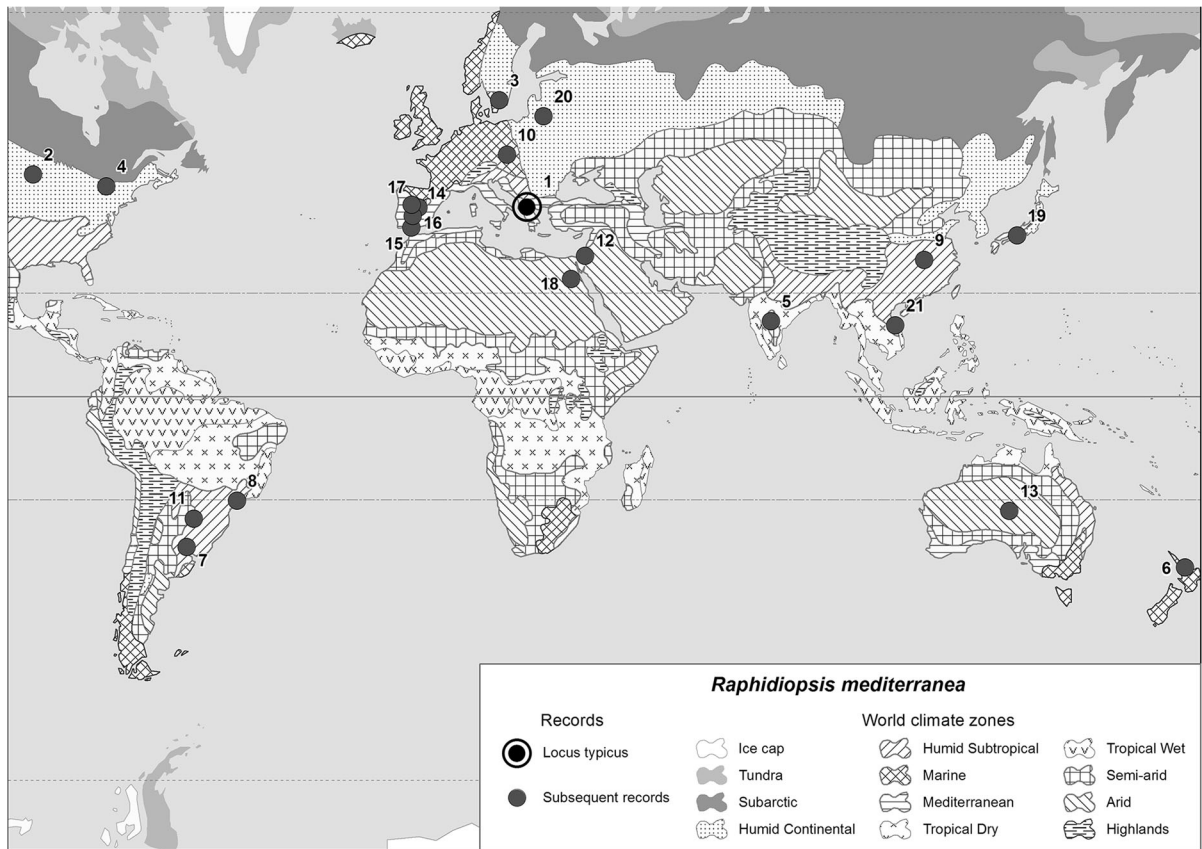


Fig. 2 *Locus typicus* and selected locations of the first records of *R. mediterranea*. Numbers mean subsequent years of observations: 1 Greece, Lake Kastoria; 2 USA, Minnesota Lakes; 3 Sweden, Lake Trummen; 4 Canada, Bay of Quinte; 5 India, Osman Sagar, Husain Sagar, South Indian Lakes; 6 New Zealand, Lake Hakanoa; 7 Argentina, Salado River; 8 Brazil, Garças Pond; 9 China, Fishpond in Wuhan; 10 Czech Republic, South Moravia; 11 Argentina, The Yacyretá Res.; 12 Israel; 13

Australia, tropical reservoirs; 14 Spain, reservoirs: El Atazar, El Vello, Cazalegas, Lozoya, Picadas, Rio Sequillo, Rosarito, San Juan, Santillana, Valmayor; 15 Spain, Arcos Reservoir; 16 Spain, Zujar Reservoir; 17 Spain, Puentes Viejas Reservoir; 18 Egypt, El-Dowyrat fish farm; 19 Japan, Lake Biwa; 20 Lithuania, Lake Gineitiškes; 21 Vietnam, Huong River, Hoamy Reservoir

that genetically and ecophysiologically differing ecotypes of *C. raciborskii* occur in temperate lakes (Kokociński & Soininen, 2012). They are able to persist at temperatures lower than the laboratory optimum (Briand et al., 2004). The occurrence of this cyanobacterium in such habitats suggests its wider ecological tolerance (Kling, 2009) and high phenotypic plasticity (Bonilla et al., 2012), and a capacity for fast adaptation to various conditions, which may lead to changes in genetic structure and consequently to speciation. This falls in line with the conclusion that the success of *C. raciborskii* is “due to a combination of several factors” and that it is “based on the existence of different ecotypes” (Piccini et al., 2011). It also points to the need for genetic studies as a key

component of any framework developed for distinguishing between native and alien species.

As different ecotypes reflect different genotypes, genetic analyses should lead to a better understanding of the expansion of small planktonic organisms. A phylogenetic tree constructed using the 16S rRNA gene sequences of strains of *C. raciborskii* isolated from freshwaters in Australia, Brazil, Germany, Hungary, Portugal and the USA showed phylotypes grouped into Australian, European and North/South American ones (Neilan et al., 2003). Other work showed that the taxon found in Constance Lake (Canada) corresponded to one of the two basic morphologies first described in Australian reservoirs, and to some strains from Florida lakes (Hamilton et al.,

Table 2 Selected locations of the first records of *Raphidiopsis mediterranea* at local and regional levels

Continent, climate zone	Country, place, year of record, if available	Basic features of water habitat, if available (depth, temperature, trophic status)	References
Europe, marine/continental	Czech Republic fishpond	Shallow ponds; eutrophic	Keršner (1997) (Fig. 2, nb. 10)
Europe, mediterranean	Greece, Lake Kastoria formed ca. 10 mya ago	Shallow lake; max depth 8.5 m; hypertrophic	Skuja (1937), Skoulikidis et al. (1998) (Fig. 2, nb. 1)
Europe, humid continental	Lithuania Lake Gineitiskes	Shallow lake; max depth 3 m; hypertrophic	Kasperovičienė et al. (2005) (Fig. 2, nb. 20)
Europe, humid continental	Poland, Dymaczewo Lake, 2004–2006	Shallow lake; max depth 12.0 m; highly eutrophic	Zagajewski et al. (2009)
Europe, mediterranean	Spain, reservoirs: Arcos Zujar Puentes Viejas	Shallow and deep reservoirs: max depth 12 m max depth 47 m max depth 56 m	Carrasco et al. (2007) (Fig. 2, nb. 15–17)
Europe, marine	Sweden, Lake Trummen (South Swedish Highlands)	Shallow lake; max depth 2.5 m; water temperature 0.5–17.9°C , progressive eutrophication	Cronberg (1973) (Fig. 2, nb. 3)
Australia, humid subtropical	Australia reservoirs in Queensland	Area within the tropics, a tropical to subtropical climate	McGregor et al. (2011)
Australia and Oceania, humid subtropical	New Zealand, Lake Hakanoa in the lower Waikato River basin	Shallow lake; max depth 2.5 m	Wood et al. (2007) (Fig. 2, nb. 6)
Asia, humid subtropical	China, fishpond in Wuhan	Hypertrophic pond	Li et al. (2008) (Fig. 2, nb. 9)
Asia, humid subtropical	Japan, Lake Biwa tectonic origin and is one of the world's twenty oldest lakes, dating to almost 4 million years ago	Deep lake; max depth 103.58 m	Watanabe et al. (2003) (Fig. 2, nb. 19)
Africa, arid	Egypt, The El-Dowyrat fish farm	Shallow freshwater pond; max depth 4 m	McGregor et al. (2011) (Fig. 2, nb. 18)
South America, humid subtropical	Argentina, Salado River, 1990s; The Yacyretá reservoir (High Paraná river near Ituzaingó (Argentina) and Ayolas (Paraguay), 1996	Deep reservoir; max depth 35 m	Izaguirre & Vinocur (1994) (Fig. 2, nb. 7); Zalocar de Domitrovic et al. (2007) (Fig. 2, nb. 11)
South America humid subtropical	Brazil, Garças Pond, 1991–1992	Polymictic; shallow pond; max depth 4.7 m; eutrophic pond	Sant'Anna & Azevedo (2000) (Fig. 2, nb. 8)
North America, humid continental	USA, Minnesota Lakes	Not available	Hill (1970) (Fig. 2, nb. 2)

Bold—features of habitat not typical for the species

2005). Those findings support the suggestion that it dispersed from Africa. Using different techniques, Haande et al. (2008) separated strains of *C. raciborskii* into American, European and Australian-African groups (ITS1, *nifH*), or American and European-Australian-African groups (PC-IGS, *rpoC1*). Wood et al. (2014) showed a close relation between strains from New Zealand and South America. But the high genetic similarity between the Brazilian and

Uruguayan strains suggests recent population exchange (Piccini et al., 2011). Using sequences from the phycocyanin intergenic spacer region, Haande et al. (2008) and Dyble et al. (2002) found that the American *C. raciborskii* populations split very early and posited early evolution on the American continent. The possible expansion pathways inferred from the map of the sequence of first records of *C. raciborskii* are in partial accord with genetic findings. The claim

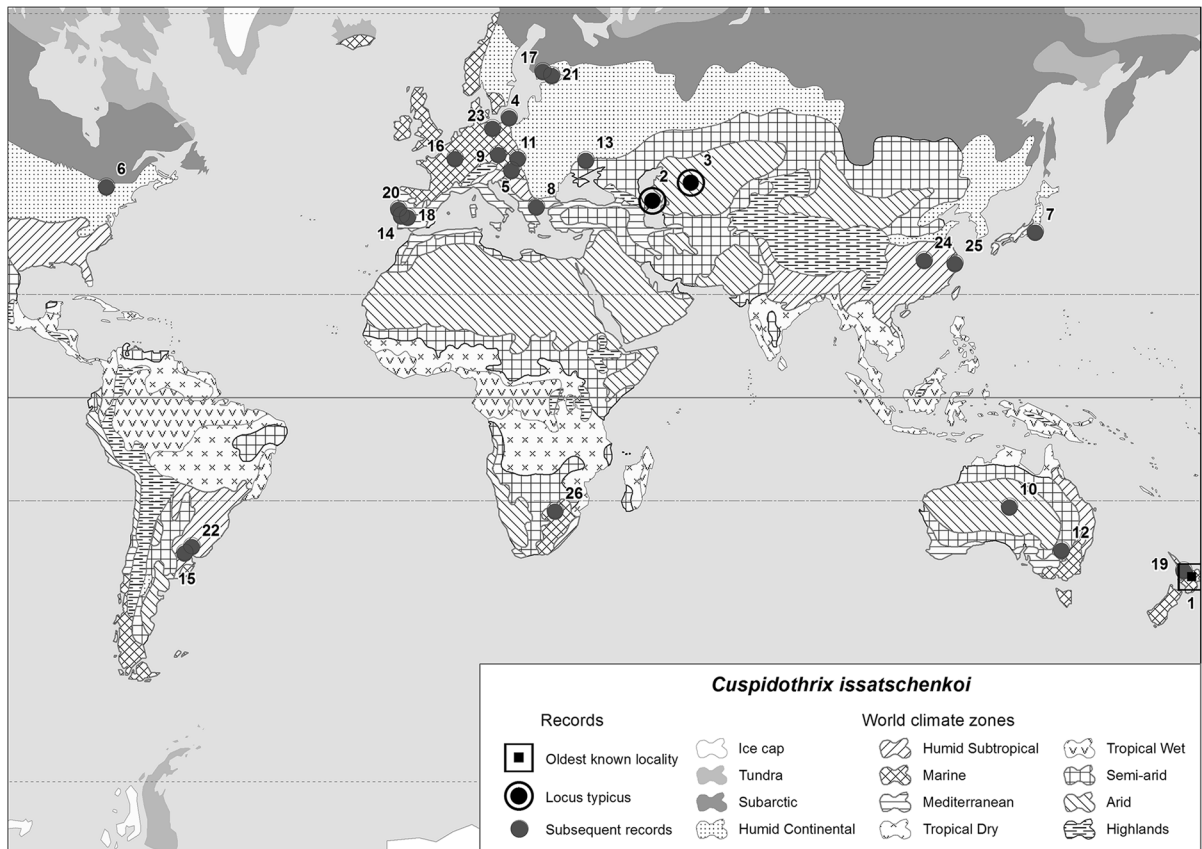


Fig. 3 *Locus typicus* and selected locations of the first records of *C. issatschenkoi*. Numbers mean subsequent years of observations: 1 North Island of New Zealand, Lake Okaro; 2 Caspian Sea; 3 Sea of Azov; 4 Poland, Lake Gardno; 5 Hungary, Lake Balaton; 6 Canada, Bay of Quinte; 7 Japan, Lake Kasumigaura; 8 Greece, Lake Volvi; 9 Czech Republic, fishponds in South Bohemia; 10 Australia; 11 Slovakia; 12 Australia, New South Wales; 13 Ukraine, Zaporozh'ye Nuclear Power Station; 14 Portugal, Montargil Res.; 15 Argentina,

Otamendi Natural Reserve, Laguna Grande; 16 North-Eastern France, Saint-Rémy; 17 Finland, Lake Tuusulanjärvi; 18 Spain, Guadiana River between Merida and Badajoz; 19 New Zealand, Lake Hakanoa; 20 Portugal, Lake Vela; 21 Baltic Sea, Gulf of Finland; 22 Lower Uruguay River; 23 Germany, Lake Stolpsee; 24 China, Nanhu Lake, Chidonghu Lake, Honghhu Lake, Donghu Lake, Xihu Lake, Dongping Lake; 25 China, Yuehu Lake; 26 RPA, Hartbeespoort Dam

of Australia–New Zealand as a potential starting point of its expansion is supported by its long presence in New Zealand (Wood et al., 2014).

When the ecological (Padišák, 1997; McGregor & Fabbro, 2000), physiological (Burford & Davis, 2011; Sinha et al., 2012) and genetic data (e.g. Gugger et al., 2005) are put together, the hypothesis that *C. raciborskii* expanded from Africa and from Australia to Eurasia and the Americas seems highly probable. The contrasting hypothesis that the recent ‘invasion’ into Europe was due to its spread from warm refuges within the continent (Gugger et al., 2005; Haande et al., 2008) would support the claim that *C. raciborskii* is native to Europe. According to Gugger

& Hoffmann (2004), Kling (2009) and Sinha et al. (2012), *C. raciborskii* survived multiple glaciations and climatic changes in the Pleistocene by forming akinetes, and recent climate change and increasing eutrophication have promoted its spread through Europe and the Americas.

Vectors of introduction are another significant piece of the alien/endemic puzzle. For example, if the African route involved the Suez Canal, then the expansion was human caused, and hence, *C. raciborskii* should be classified as alien in Europe. It is also possible that it was brought from Africa with migrating birds, a natural phenomenon which would confer native European status to this cyanobacterium.

Table 3 Selected locations of the first records of *Cuspidothrix issatschenkoii* at local and regional levels

Continent, climate zone	Country, place, year of record, if available	Basic features of water habitat, if available (depth, temperature, trophy status)	References
Asia, continental	Caspian sea, Azov sea	Low salinity	Usachev (1938) in: Kástovský et al. (2010) (Fig. 3, nb. 2 and 3)
Asia, humid subtropical China	China, Dongping Lake	Shallow lake; mean depth 1.59 m; hypertrophic	Lu et al. (2013) (Fig. 3, nb. 24)
Europe, marine/continental	Czech Republic, eutrophic waters	Meso-to eutrophic ponds and reservoirs	Albay & Pokorný (1999) (Fig. 3, nb. 9)
Europe, humid continental	Lake Tuusulanjärvi, Finland, 2000	Shallow lake; max depth 3.2 m	Rajaniemi et al. (2005) (Fig. 3, nb. 17)
Europe, humid continental	Baltic sea, Gulf of Finland	Low salinity	Hällfors (2004) (Fig. 3, nb. 21)
Europe, marine	Germany Stolpsee, 2008	Shallow lake	Ballot et al. (2010) (Fig. 3, nb. 23)
Europe, mediterranean	Greece, Lake Volvi	Deep lake; max depth 22 m	Hindák & Moustaka (1988) (Fig. 3, nb. 8)
Europe, marine/continental	Hungary, Lake Balaton (the largest lake in Central Europe with the Mediterranean-like climate)	Shallow lake; max depth 12 m	H.-Bartha (1974) (Fig. 3, nb. 5)
Europe, humid continental	Poland, Lake Gardno, 1971	Shallow lake; max depth 2.6 m; saline lake	Strzelecki & Pótorak (1971) (Fig. 3, nb. 4)
Europe, Central Portugal, mediterranean (reported as <i>Aphanizomenon flos-aquae</i>)	Portugal, Montargil reservoir, artificial reservoir, 1996	Not available	Pereira et al. (2000) (Fig. 3, nb. 14)
Europe, mediterranean	Spain, two ponds located in Los Barruecos and Barruecos de Abajo in Malpartida de Cáceres	Shallow ponds with max depth ca. 9.0 m; high water temperatures 27–28°C	Moreno et al. (2011)
Europe, humid continental	Ukraine, Zaporozh'ye Nuclear Power Station 1990s	Cooling pond of Nuclear Power Station, water of pond thermally polluted	Kalinichenko et al. (1999) (Fig. 3, nb. 13)
Africa, arid	South Africa, RPA, Hartbeespoort Dam 2011	Shallow artificial reservoir completed in 1923; a mean depth of 9.6 m; eutrophic reservoir	Ballot et al. (2014) (Fig. 3, nb. 26)
Australia and Oceania, marine	New Zealand, North Island, Lake Okaro, 2006	Max depth 15 m; eutrophic lake	Wood et al. (2009) (Fig. 3, nb. 1)
North America, humid continental	Canada, Bay Quinte	Not available	Nicholls & Carney (1979) (Fig. 3, nb. 6)
South America, humid subtropical	Uruguay , Lower Uruguay River, which belong to the Department of Río Negro	Surface temperature varied seasonally, between 11.6 and 28.8°C	Ferrari et al. (2011), Bonilla et al. (2012) (Fig. 3, nb. 22)
South America, humid subtropical	Argentina, Laguna Grande (between 1998 and 2013)	Deep lake; max depth 113 m ; average water temperature 20.5°C	O'Farrell et al. (2015) (Fig. 3, nb. 15)

Bold—features of habitat not typical for the species

In natural environments, *C. raciborskii* displays high morphological plasticity which is not fully explained by genetic distance (McGregor & Fabbro,

2000). Due to its wide morphological variability, the species has been misidentified as *Anabaenopsis*, *Raphidiopsis* and *Cylindrospermum* (Hawkins et al.

1997). Thus, some authors speculated that *R. mediterranea* may in fact be a form of *C. raciborskii* (Moustaka-Gouni et al., 2009).

Raphidiopsis mediterranea is believed to have originated from the Mediterranean zone (Greece; Kaštovský et al., 2010). Due to morphological and ecological similarity and the frequent co-occurrence of *Raphidiopsis* and *Cylindrospermopsis*, the idea that the two genera are in fact one genus was proposed in the 1970s (Hill, 1970). The possible relation between the two species has been discussed on the basis of an examination of samples from lakes in New Zealand (Hill, 1970). Komárek & Mareš (2012) suggested that identification of both of species is difficult and that young filaments of *C. raciborskii* without heterocysts are often misidentified as *R. mediterranea*. In studies provided in Lake Kastoria, morphological and phylogenetic evidence suggests that *R. mediterranea* represents a non-heterocytous life-cycle stage of *C. raciborskii* (Moustaka-Gouni et al., 2009, 2010). The two taxa co-occur in tropical and subtropical reservoirs (McGregor & Fabbro, 2000; Chellappa & Costa, 2003; Mohamed, 2007; Fonesca & de Bicudo, 2008). According to Komárková et al. (1999), *R. mediterranea* populations mixed with *C. raciborskii* were most likely filaments of *C. raciborskii* lacking heterocysts. Other researchers considered *R. mediterranea* trichomes to be environmental morphotypes of *C. raciborskii*, which could be induced to form heterocysts under conditions of abundant phosphorus (McGregor & Fabbro, 2000), as found earlier in Lake Paranoá, Brazil (Cronberg, 1978).

Genetic studies suggest that *C. raciborskii* and *R. mediterranea* are different forms of one genus (Gugger et al. 2005; Moustaka-Gouni et al., 2009) or that they descended from a common ancestor that produced heterocysts (McGregor et al., 2011). Morphological changes led to the loss of the ability to produce heterocysts, separating them into two genera (McGregor et al., 2011). If they share a congenetic origin, *Raphidiopsis* is expected to lose its nitrogen fixation ability and deviate from *Cylindrospermopsis* (Wu et al., 2011).

The third species, *Cuspidothrix (Aphanizomenon) issatschenkoi*, is also difficult to separate from the others. The non-heterocytous stage of it can be misidentified as *R. mediterranea* (Wood et al., 2007). Molecular studies showed that there are at least three ecotypes of *C. issatschenkoi*, and that some trichomes

identified as *R. mediterranea* var. *grandis* are one ecotype of *C. issatschenkoi* (Wood et al., 2007). The genotypic diversity of *C. issatschenkoi*, accompanied by ecotypic diversity, is the key to its successful range expansion, allowing it to adapt to a wide range of environments (Hodoki et al., 2013). This is also true for other cyanobacteria such as *M. aeruginosa* (Briand et al., 2009). Again, the possible pathways of migration/expansion are quite similar to the other species. Although its *locus typicus* is in the Ponto-Caspian region, recent studies of sediments from Lake Okaro revealed that *C. issatschenkoi* was already present in New Zealand 120 years ago (Wood et al., 2009).

Our consideration of all these results demonstrates how complex and uncertain is the task of understanding the migration, expansion and evolution of microorganisms. With all these pieces of the puzzle at our disposal, we still cannot unequivocally decide which species are alien. Tracking three species commonly regarded as alien through their long-distance walk through different climate zones, we were not able to reliably determine if they have indeed expanded their geographical range. By adding more parameters, such as ecological requirements, physiological responses and genetic structure, we were, however, in a position to suggest that the three species may be close relatives or may descend from a common ancestor.

Conclusion

We discussed the routes of expansion of three cyanobacteria commonly regarded as alien species of the temperate zone. Global warming has become the subject of much research focusing particularly on species that have expanded from regions of warmer climate. Many pieces of the puzzle are missing from the discussion of the warm origin of species and their expansion, but the picture is gradually being completed. To have a better view of the expansion and evolution of microorganisms we need to combine many types of information, including the history of local expansions, ecological ranges, and data from studies in morphology, ecology, genetics and paleolimnology. In the case of microorganisms, assessing the role of human intervention in range expansions will always be a problem. As direct evidence seems to be virtually non-existent, the only option is to rely on circumstantial evidence.

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