



Review of the biogeography of *Artemia* Leach, 1819 (Crustacea: Anostraca) in Argentina

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Abstract

A review of the biogeography of *Artemia* in Argentina is here presented. There are two species of *Artemia* in this country: *A. franciscana*, widely distributed throughout the Americas and the Caribbean, and *A. persimilis* with a more restricted distribution in southern South America. In Argentina *A. franciscana* is located between 24°S (Chaco Province) and 35° S (Buenos Aires Province), approximately; *A. persimilis*, from 36° (La Pampa Province) to 51° S (Santa Cruz Province), approximately, although the southernmost record of the species corresponds to Laguna de los Cisnes (53° 15'S), in the Chilean Tierra del Fuego. Several evidences in the population of Las Tunas (Córdoba Province) suggest the presence of some degree of hybridization and/or introgression in the border strip between the distribution areas of the two species. Temperature is considered as a main factor in the determination of the present geographic distribution of both species in this country. *A. franciscana* and *A. persimilis* are widely regarded as endemic species to the Americas. However, in recent decades, *A. franciscana* was intentionally

introduced or has unintentionally invaded several countries of the New and the Old World, mainly associated with aquaculture practices. Two African populations recently assigned to *A. franciscana* suggest other events of anthropogenic introduction, or raise the hypothesis that the original geographic distribution of this species was not only restricted to the Americas. On the other hand, *A. persimilis* was described based on specimens from the Argentinean population of Salinas Grandes de Hidalgo (La Pampa Province) and from the Italian population of Saline di San Bartolomeo (Cagliari, Sardinia). *A. persimilis* co-occurred with *A. salina* in the later location, but the presence of the first species would have been rare, and at present, the Italian biotope no longer exists. The preliminary assignation of a population from the Peruvian Altiplano to *A. persimilis* within the latitudinal distribution range of *A. franciscana* and the presence of several *Artemia* high-altitude populations (above 4,500 m) in the Altiplano of Peru, Bolivia, Chile and in the Puna of Argentina, could lead to an interesting question. Perhaps in the past, *A. persimilis* would have

retreated to cooler areas at higher altitudes and latitudes, leaving isolated populations in several Andean enclaves. Meanwhile, *A. franciscana* would

have extended its range southward, reaching and occupying more temperate environments.

Key Words: *Artemia persimilis*, *Artemia franciscana*, Argentina, biogeography

Introduction

The genus *Artemia* Leach, 1819 is distributed worldwide, except in Antarctica, in patchy saline or hypersaline, inland and coastal, aquatic ecosystems (salt lakes, coastal lagoons, salines or salt pans). In spite of its wide biogeographic range, the genus should not be considered strictly cosmopolitan since it is not present in all suitable salty environments (Vanhaecke *et al.*, 1987) but in those in which natural dispersion forces, anemochory or zoochory (mainly by waterfowl, especially flamingos) or human activities, allow it to establish (Royan *et al.*, 1969; Amat *et al.*, 2005; Green *et al.*, 2005). Currently it is considered (see below: Biogeography of the genus in the Americas) that the genus includes several bisexual species, *A. franciscana* Kellogg, 1906; *A. persimilis* Piccinelli and Prosdocimi, 1968; *A. salina* (Linnaeus, 1758); *A. sinica* Cai, 1989; *A. tibetiana* Abatzopoulos, Zhang and Sorgeloos, 1998; *A. urmiana* Günther, 1899; *A. sp.* from Kazakhstan, and an assemblage of obligate parthenogenetic lineages, anteriorly grouped under the controversial binomen *A. parthenogenetica* Bowen and Sterling, 1978, but recently reconsidered as a group of *Artemia* parthenogenetic populations (Abatzopoulos *et al.*, 2002). Bisexuals are diploid with $2n = 42$, except *A. persimilis* where $2n = 44$; parthenogens show ploidy levels from $2n$ to $5n$, being the diploid lineages automictic while the polyploid lineages apomictic.

The progressively increasing number of locations with *Artemia* populations compiled in the main global biogeographic studies (Vanhaecke *et al.*, 1987; Triantaphyllidis *et al.*, 1998; Van Stappen, 2002; Muñoz and Pacios, 2010) is a clear evidence of the growing interest of researchers for this anostracan who has been shown not only as a

valuable marketable resource, mainly applied in aquaculture, but also as a very interesting model organism in several fields of basic research.

It was assumed that a key event in the evolutionary history of *Artemia* would have been the separation of the species of the genus into two bisexual lineages, in the Old and the New World; this event would have been followed by the divergence of *A. franciscana* and *A. persimilis* in the Americas, and the divergence of *A. salina* and *A. urmiana* in the Old World (Beardmore and Abreu-Grobois, 1983; Abreu-Grobois, 1987). However, latest views pose a different scenario (Baxevanis *et al.*, 2006, Muñoz *et al.*, 2010), suggesting that *A. persimilis* would have separated from the Gondwana ancestral stock at the Middle Cretaceous, about 80-90 mya, and have come to America with the Gondwanian tectonic fragmentation, while South America was moving westward away from Africa. On the other hand, *A. salina* would have diverged about 40 mya during the formation of the Mediterranean Sea. Eight million years later, at the early Tertiary, *A. franciscana* would have diverged from its sister group comprised of bisexual species of Central Asia and their closely related parthenogens, with which it last shared a common ancestor (Baxevanis, *et al.*, 2006; Maniatsi *et al.*, 2009; Muñoz *et al.*, 2010). During Pleistocene Ice ages, escaping from the cooling of the climate, *A. franciscana* could have entered the New World through the Behring Bridge, intermittently connecting northwestern America with eastern Asia as sea levels rose and fell under the effect of Ice ages. In America the species would have moved into refuges that would have remained warm and moist (Milne, 2006). Then the species would have radiated throughout the entire American continent forming a diverse group of populations strongly differing in

several attributes such as genetic polymorphism, thermo-tolerance and halo-tolerance, reproductive and life history characteristics, etc. (Maniatsi *et al.*, 2009). Diploid parthenogenetic lineages may have originated very recently, in the Holocene, in Central Asia, with the closest bisexual relatives being from around Kazakhstan and Iran (Muñoz *et al.*, 2010). From there, they may have experienced a rapid expansion throughout their present broad distribution in vast areas of Europe, Africa, Asia, and even Australia (Baxevanis *et al.*, 2006; Muñoz and Pacios, 2010; Muñoz *et al.*, 2010), where they comprise the majority of the populations of *Artemia* (Muñoz *et al.*, 2010).

Brine shrimps can persist in the environment as cysts banks, a gene pool reserve of populations that allow them to recover if the environmental conditions are restored or become suitable. This is probably the 'secret weapon' of the great geological age of the Anostracans.

A great gene flow amongst *Artemia* populations can be expected through the passive dispersion of cysts by winds and waterfowl. However, it has recently been shown that sexual *Artemia* populations display a marked endemism, with a large proportion of intraspecific local genetic diversity (Maniatsi *et al.*, 2009). De Meester *et al.* (2002) have proposed for many continental zooplankters, a monopolization hypothesis to explain the paradox of the 'high potential dispersal by cysts versus the reduced gene flow among populations'. They proposed that, in a colonization event, the high adaptability of first colonists to the local environment, a rapid growth rate, and the building-up of a cyst bank as gene pool reservoir, may be the key forces that reduce the gene flow among populations (mediated by dispersal forces), by reducing successful invasion by immigrants (De Meester *et al.*, 2002; Ketmaier *et al.*, 2005; 2008; Ishida and Taylor, 2007). Colonization events rather than gene flow could shape the genetic diversity of the species at a large scale.

The process of species diversification has proven to be strongly linked to tectonism and climate. As demonstrated by the fossil record, during the global Ice Ages of the Quaternary, temperatures dropped and water availability was reduced, causing

great changes in the distribution of surviving species. With the advance and retreat of ice sheets, the organisms could have moved latitudinally, altitudinally (in major mountain ranges), and/or even longitudinally, when new dispersal routes became available by the lowering of the sea level (e.g. Behring bridge) (Hewitt, 2004). In South America, the uplift of the Andes Range may have had a major effect on lineages splitting, acting as generator and reservoir of lineages and species (Hewitt, 2004). It has been suggested that the present populations from both *A. franciscana* and *A. persimilis* could be descendants of populations that may have been isolated in refuges on both slopes of the Andes, to withstand the repeated glaciations (Maniatsi *et al.*, 2009).

Biogeography of *Artemia* in the Americas

At the present, the genus is represented in the Americas by the bisexuals *A. franciscana* and *A. persimilis*, geographically separated from their Old World relatives, *A. salina*, *A. urmiana*, *A. sinica*, *A. tibetiana*, and *A. sp* Kazakhstan. On the other hand, parthenogenetic populations have not been confirmed in America. Baxevanis *et al.* (2006) hypothesized that their absence could be due to some genetic or ecological reasons. Recent reports of some undescribed highly differentiated lineages, *Artemia* sp 'Cape Verde', *Artemia* sp. 'Mexico', *Artemia* sp. 'Tibet', *Artemia* sp. 'Veldrif' (Muñoz and Pacios, 2010) could change this pattern of geographic speciation and the phylogenetic relationships among lineages previously reported for *Artemia* (Beardmore and Abreu-Grobois, 1987; Abreu-Grobois and Beardmore, 1989; Baxevanis *et al.*, 2006). Particularly striking is the allocation to *A. franciscana* of two African bisexual populations from Sal Island (Cape Verde), Santa Maria and Pedra de Lume (Muñoz and Pacios, 2010), that are completely out of the present range of the species currently considered endemic to the Americas and the Caribbean. This finding leads those authors to an intriguing discussion about the possibility of a recent anthropogenic introduction of a single *A. franciscana* strain in these locations in the same way as strains of this species have invaded the Old World, and/or to

hypothesize that the original geographic distribution range of the species was not exclusively American. The close phylogenetic relationship among *A. franciscana* and the Asian *Artemia* bisexuals and some parthenogens (Baxevanis *et al.*, 2006; Muñoz *et al.*, 2010; Muñoz and Pacios, 2010) could support this last view.

Whether the origin of *A. franciscana* has been in America or in the Old World, at present the species is extensively distributed in the Americas, with the possible exception of the above mentioned African populations (Muñoz and Pacios, 2010). Several records outside America, in Australia, People's Republic of China, France, Iran, India, Italy, Japan, Kenya, Madagascar, Morocco, New Zealand, Spain, Portugal, Tunisia, and Vietnam, are probably the result of the intentional or unintentional inoculation of the species, mainly associated with aquaculture practices (Clark and Bowen, 1976; Geddes 1980; Vanhaecke *et al.*, 1987; Triantaphyllidis *et al.*, 1994, Triantaphyllidis *et al.*, 1996; Triantaphyllidis *et al.*, 1998; Van Stappen, 2002; Amat *et al.*, 2005; Green *et al.*, 2005; Abatzopoulos *et al.*, 2006; Mura *et al.*, 2006; Ruebhart *et al.*, 2008; Timms, 2006; Ben Naceur, *et al.*, 2010; Muñoz, 2010; Vikas *et al.*, 2012). Due to the recent introductions (or reintroductions) of this species in the Old World, these records highlight that the species is extending its current geographic range and that the biogeographical map of the genus will inevitably change.

A. franciscana shows a great phenotypic plasticity and a very high biotic potential (Browne and Wanigasekera 2000; Kappas *et al.*, 2004; Mura *et al.*, 2006; Medina *et al.*, 2007) associated with a rich genetic and quickly changing gene pool, which makes it highly adaptable to diverse environmental conditions. Triantaphyllidis *et al.* (1998) pointed out that most of material used worldwide for inoculation, to improve the production of salt from a saltwork and /or to establish a population that can be exploited to harvest cysts and biomass to be applied in aquaculture (Sorgeloos and Tackaert, 1991), belong to this species, whose performance far exceeds that of other bisexual or parthenogenetic species (Browne and Halanych, 1989; Kappas *et al.*, 2004;

Ruebhart *et al.*, 2008). Several authors have firmly warned about the serious potential threat to the global biodiversity of the genus that implies the deliberate indiscriminate introduction of exotic, more productive but also more competitive *Artemia* species, such as *A. franciscana* strains, on saline ecosystems of the world (Abreu-Grobois, 1987; Triantaphyllidis *et al.*, 1998; Van Stappen, 2002; Ruebhart, 2008; Muñoz and Pacios, 2010; Geddes and Williams, 1987; Kappas *et al.*, 2004; Vanhaecke *et al.*, 1987). We should be careful in preserving the native populations and their environments, and extremely vigilant to detect and monitor the presence of exotic species. Also, in order to preserve the genetic diversity, cysts of native strains should be collected and stored in banks (Sorgeloos and Tackaert, 1991; Ruebhart *et al.*, 2008). Other significant threats to the diversity of *Artemia* are linked to human activities such as agriculture, mining, engineering and urbanization projects, which could lead to a significant damage to their biotopes such as physical and chemical alterations, pollution, decreasing the level of water, or their disappearance by backfilling of saline ecosystems. Finally, global climate change effects are shaping a new biogeographic map of *Artemia* species (Van Stappen, 2002).

Currently, in the entire American continent, *A. franciscana*, is widely distributed latitudinally from, approximately, 52° N latitude in Canadian lakes, to approximately 35° S latitude in hypersaline ecosystems of Argentina and Chile (Triantaphyllidis *et al.*, 1998; Amat *et al.*, 2004; Gajardo *et al.*, 2004). The other American species, *A. persimilis*, is geographically restricted to southern South America, from approximately 36-37° S latitude to higher latitudes, in Argentina and Chile (Amat *et al.*, 2004), including the southernmost record of the genus, in Laguna de Los Cisnes (53° 15'S; 70° 22'W, Tierra del Fuego, Chile) (Amat *et al.*, 2004; Gajardo *et al.*, 2004; Papeschi *et al.*, 2008; Ruiz *et al.*, 2008).

Biogeography of *Artemia* in Argentina

Table 1 shows the biogeography and distribution of *Artemia franciscana* and *A. persimilis* populations from Argentina. Argentina is an extensive triangular-

Table 1: Geographical coordinates of *Artemia franciscana* and *A. persimilis* populations from Argentina

<i>Artemia franciscana</i> populations			
Lagoon Comandancia Frías	Chaco Province.	24° 30' S, 62° 15' W	preserved sample
Salinas Grandes	NW NO Córdoba province	26° 30'-31° 40'S, 64° 15'-66° 25' W	
El Saladillo Lagoon	Santiago del Estero province	28° 02' S, 62° 07' W	
Los Cachilos Lagoon	Santiago del Estero province	28° 05' S, 61° 59' W	
Salina La Antigua	La Rioja province	29° 54' S, 66° 07' W	
Mar Chiquita Lake	Córdoba province	29° 54' S, 66° 07' W	
Pampa de las Salinas	San Luis-La Rioja provinces	32° S, 66° 41' W	
Las Tunas Lagoon	Córdoba province	33° 44' S, 62° 32' W	
Lagoon in Trenque Lauquen	Buenos Aires prov.	35° 48' S, 62° 55' W	preserved sample
<i>Artemia persimilis</i> populations			
Lagoon in Area de Naicó	La Pampa province	c. 36°52'S, 64°24' W	preserved sample
Salinas Grandes de Hidalgo	La Pampa Province	37° 13' S, 63° 26' W	
salina Colorada Grande	La Pampa province	38° 18' S, 63° 42' W	
Salina Colorada Chica	La Pampa province	38° 23' S, 63° 36' W	
Salina Callaqueo	La Pampa province	38° 34' S, 63° 32' W	
Salina El Chanco	La Pampa province	38°37' S, 65°45'W	
Salinas Grandes Anzoátegui	La Pampa province	39° S, 63°47' W	
Salinas Chicas	Buenos Aires prov.	38°44' S, 62°57' W	
Salitral Negro	Buenos Aires prov.	38°44' S, 63°13' W	
Salitral de la Vidriera	Buenos Aires prov.	38°42' S, 62°40' W	
Epecuén Lake	Buenos Aires prov.	37°13' S, 62°81'W	preserved sample
Winchel Lagoon	Buenos Aires prov.	c. 39° S, 62° 30' W	
Villalonga Lagoon	Buenos Aires prov.	39° 51' S, 62° 32' W	
Salina de Luzzetti	Buenos Aires prov.	c. 40° 35' S, 62° 40' W	
Pond at Route 3, km 1128	Río Negro province	c. 40° 43'S, 65° W	
Salitral Bajo del Gualicho	Río Negro province	40° 24' S, 65° 13' W	
Lagoon near Rada Tilly	Chubut province	45° 55' S, 67° 34' W	
Primera Lagoon (Caleta Olivia)	Santa Cruz province	46° 27' S, 67° 31' W	
Segunda Lagoon (Caleta Olivia)	Santa Cruz province	46 °27' S, 67° 32' W	
Salina in Estancia La Pava	Santa Cruz province	47° 32' S, 66° 38' W	
Lagoon in Estancia El Caburé	Santa Cruz province	47° 34' S, 66° 31' W	
Salitral Bajo Pichinini in Estancia Cerro Pancho	Santa Cruz province	47° 45' S, 66° 14'5 W	
Salitral Route 3, km 2035	Santa Cruz province	47° 28' S, 67° 16' W	
Coastal salares Bahía Laura	Santa Cruz province	48° 4' S, 66° 48' W	From Birabén (1954)
Salitral from San Julián	Santa Cruz province	49° 18' S, 67°44' W	
Laguna Seca, near San Julián	Santa Cruz province	49° 17' S, 67°46' W	
Coastal salares in Gallegos N	Santa Cruz province	51° 45' S, 69° 13' W	From Birabén (1954)

shaped country, 3,694 km long from North to South and 1,423 km long from East to West in its widest part, at the North. It is situated at the meridional extreme of South America, between 21° 46' S to 55° 03' S latitudes and between 53° 35' W to 73° 38' W longitudes. To the west, the Andes Mountain Range constitutes the border with Chile from north to south, all along the territory. To the East, from the estuary

of the Rio de la Plata (at 34° S approximately) to the South, it is delimited by the Atlantic Ocean, through a coastline extending along 4,665 km. In addition to the large extension of its territory, it also shows a great altitudinal variation, ranging from the highest peak of the entire Western Hemisphere, the Cerro Aconcagua (6,962 m asl, Mendoza Province) to the lowest South American depression, in Laguna del

Carbón (105 m below sea level, Santa Cruz Province). The broad latitudinal and altitudinal variation, the modeling action of the Andes and the moderating effect on thermal amplitudes by the Atlantic Ocean, determine a great diversity of climates, and have originated a wide diversity of aquatic environments. The Andes Range shapes the west-east dominant climatic gradient, North of 38°S, aridity increases westward whereas south of 38°S, aridity decreases westward (Drago and Quirós, 1996; Quirós and Drago, 1999). The predominant climate of the country is temperate, except for a small warm humid portion, north of the Capricorn Tropic, and a cold humid climate at the southern extreme. Quirós and Drago (1999) established six geographic limnological regions for Argentina. Saline and hypersaline lakes are found in four of these regions: Puna, Chaco-Pampa plains (Pampa lakes, endorheic basins), Peripampean Sierras ('Bolsones', endorheic) and Patagonian Plateau (endorheic basins). Mean values of salinity (total dissolved solids) in inland saline ecosystems of Argentina vary from low (0,6-3,0 g.L⁻¹), medium (3-50 g.L⁻¹), high (50-100 g.L⁻¹) and hypersaline (>100 g.L⁻¹) (Drago and Quirós, 1996). The major mechanism controlling the chemical composition in these saline biotopes would be dominated by the relation between evaporation and precipitations (Drago and Quirós, 1996; Ruiz *et al.*, 2007).

Except for some isolated records, temporary shallow and muddy freshwater ponds and saline ecosystems, inhabited by fairy shrimps and brine shrimps, were overlooked for a long time in this country. In particular, much of the great extensions of large salinas and salares were only studied from the point of view of their geomorphology, mineralogy, water chemistry and productive potential for salt production (Angelelli *et al.*, 1976, 1980; Schalamuk *et al.*, 1983; Drago and Quirós, 1996; Quirós and Drago, 1999). Recently, Echaniz and Vignatti (2011) mentioned the few reports made on some scattered saline lakes in Argentina (in Buenos Aires, La Pampa, Santa Fe and Córdoba Provinces, and in the northwest of the country), emphasizing the scarcity of available limnological information on these ecosystems. Historically, salt producers exploiting

large salinas have strongly prevented the access to their salt extraction concessions, fearing that any alteration in the environment could interfere with the crystallization process or could contaminate the bed of the salina. In other cases, the access to these biotopes is very difficult due to the lack of roads, the roughness of the environment and/or because of the sinking soft ground in the surroundings of the water body.

By the 1950s, a few isolated populations of brine shrimps referred as *A. salina* (at that time considered as the unique valid species distributed worldwide) (Linder, 1941; Picinelli and Prosdocimi, 1968), were reported in small coastal salares from Bahía Laura (48° 3' S) and Gallegos Norte (51° 4' S) (Santa Cruz Province), Epecuén Lake (37°8'4"S 62°51'57"W, Carhué, Adolfo Alsina, Buenos Aires Province) and Mar Chiquita Lake (30° 20'-31° S, 62° 10'-63° 10' W, Córdoba Province) (Birabén, 1954; Guiñazú, 1960). In 1968 Picinelli and Prosdocimi described *A. persimilis*, on the basis of specimens from the Argentinean Salinas Grandes de Hidalgo (La Pampa Province), considered by the authors as the type locality (type material deposited in Museo Civico di Storia Naturale di Verona), and from a disjunct Italian environment, the saline di San Bartolomeo (Cagliari, Sardinia). These authors differentiated *A. persimilis* on the basis of a reduced number of setae in the furcae; a basal verrucous subspheric and bigger frontal knob in the basal article of the male antenna 2; a brood pouch with lateral projections, each with a spine at the tip; and a somatic number of 2n= 44 chromosomes, all of them shorter than the 42 chromosomes of *A. salina*. According to them, *A. salina* and *A. persimilis* coexisted simultaneously in both locations, but in the Argentinean biotope, the majority of specimens belonged to *A. persimilis*, whereas in the Italian biotope, its presence was considered as rare. Halfer-Cervini *et al.* (1968) tried unsuccessfully to conduct cross-breeding tests between the Italian and the Argentinean populations, and they concluded that both populations were not con-specific. Currently, the saline di San Bartolomeo no longer exists (Mura *et al.*, 1989) and the occurrence of *A. persimilis* in Sardinia could not be confirmed (Barigozzi, 1989).

Up to now, the co-occurrence of bisexuals and parthenogenetic strains has been recorded in Spain, Italy, China, India and Iran (Amat *et al.*, 1983; Van Stappen *et al.*, 2003; Zheng *et al.*, 2004; Mura *et al.*, 2006; Agh *et al.*, 2007; Vikas *et al.*, 2012), but the natural sympatry of bisexual *Artemia* species was not confirmed in any place.

From its description, it has been considered that the distribution of *A. persimilis* was restricted to Argentina (Vanhaecke *et al.*, 1987; Triantaphyllidis *et al.*, 1998). This viewpoint was mainly supported by its presence in Salinas Grandes de Hidalgo (Piccinelli and Prosdocimi, 1968; Halfer-Cervini *et al.*, 1968), and by the lack of records in other American countries (Vanhaecke *et al.* 1987; Triantaphyllidis *et al.*, 1998). Also, it was assumed to be the only species of the genus in this country, therefore assigning to *A. persimilis* all the previous records of brine shrimps populations earlier referred to *A. salina*, including that of Mar Chiquita Lake, later allocated to *A. franciscana* (Papeschi *et al.*, 2000; Amat *et al.*, 2004). Only in the 1990s, with national and international support through diverse collaborative actions (ICI, CYTED, INCO) started an extensive prospection of the abundant saline ecosystems present throughout this country (Angelelli *et al.*, 1976, 1980; Schalamuk *et al.*, 1983; Drago and Quirós, 1996; Canevari *et al.*, 1998) for the localization and identification of *Artemia* populations. Given the great genetic and ecological variation among populations it was strongly recommended to perform the characterization of each population through a multidisciplinary approach, and to standardize the protocols of the methodologies used worldwide. This approach has included so far the application of diverse techniques such as: morphological differentiation of adults by optic and SEM microscopy, discriminant multivariate analysis of morphologic and morphometric adult traits, biometry of cysts and nauplii, cytogenetic studies, allozyme divergence by electrophoresis, cross-breeding tests, and mitochondrial and nuclear DNA sequencing.

During the 1990s and mid-2000s numerous new *A. persimilis* populations were recorded and characterized (Table 1) (Amat *et al.*, 1994;

Cohen, 1995; Cohen, 1998; Rodríguez Gil *et al.*, 1998; Cohen *et al.*, 1999a, b; Pastorino *et al.*, 2002; Pastorino and Cohen, 2006).

In 2000, cytogenetic studies carried out on two populations from Córdoba Province, Mar Chiquita Lake (29° 54' S, 66° 07' W) and Las Tunas Lagoon (33° 44' S, 62° 32' W), produced a surprising an unexpected result. In the Mar Chiquita population, the morphology of adults and the cytogenetic data, haploid and diploid number of chromosomes, and number of chromocentres were wholly congruent and allowed the assignation of this population to *A. franciscana* (Papeschi *et al.*, 2000). Later, adult morphological and morphometric evidences, biometry of cysts and nauplii (Amat *et al.*, 1994, 2004; Lipko *et al.*, 2004), and molecular techniques (Ruiz *et al.*, 2008; Maniatsi *et al.*, 2009) provided additional support to the first record of this species from Argentina, also representing the fall of the distribution paradigm of the genus in America. On the other hand, Las Tunas population posed a puzzling situation. Meanwhile morphometric analysis of adults clustered Las Tunas with *A. franciscana* populations (Amat *et al.*, 2004), and all the sampled specimens showed the morphotype of *A. franciscana*, cytogenetic evidences (Papeschi *et al.*, 2000), biometrics of cysts and nauplii, the buoyancy behavior of cysts and cross-breeding tests, located this population close to *A. persimilis* (Amat *et al.*, 2004). This controversial situation leads to support the hypothesis of a hybrid population between *A. persimilis* and *A. franciscana* (Papeschi *et al.*, 2000; Amat *et al.*, 2004), and of the possible existence of a hybrid zone between the distribution ranges of *A. persimilis* and *A. franciscana* in Argentina, in a land belt between parallels 35° to 36°S (originally defined between 36° to 37°), with *A. franciscana* distributing northwards and *A. persimilis*, southwards (Amat *et al.*, 2004). Since specimens with the *A. persimilis* morphotype were not found in Las Tunas, it was assumed that the population was made up of hybrid and introgressants, in addition to the parental form *A. franciscana* (Papeschi *et al.*, 2000). However, recent molecular evidences have confronted this hypothesis. The restriction fragment length polymorphism analysis (RFLPs) of a fragment of the 16S

rRNA mitochondrial gene (Ruiz *et al.*, 2008) of specimens from Las Tunas and Mar Chiquita (with San Francisco Bay, USA, as reference strain) have shown no diversity of DNAmT haplotypes within these populations, all of them corresponding to *A. franciscana*. Maniatsi *et al.* (2009) employed mitochondrial (16S, COI) and nuclear (ITS1, p26) markers to carry out a phylogeographic study of *A. franciscana* throughout the Americas. Their inferred genealogy is consistent with the Pleistocene splitting of this species from its ancestral Central Asiatic lineages (Baxevanis *et al.*, 2006; Muñoz *et al.*, 2010), and his arrival in America escaping from the cold. In America, *A. franciscana* could have radiated forming at least three reciprocally monophyletic mitochondrial phylogroups, with a high degree of regional endemism. One of these phylogroup clusters Las Tunas, Mar Chiquita and Santiago del Estero Argentinean populations, together with some Chilean populations (Maniatsi *et al.*, 2009). Taking into account the different results in the multidisciplinary approach, the specific status of Las Tunas could be considered controversial. Currently, phylogeographic evidences could suggest that *A. franciscana* could be experiencing an incipient speciation process.

The current distribution range of *Artemia* in Argentina is outlined mainly based on recently sampled populations (Amat *et al.*, 1994; Cohen *et al.*, 1999b; Papeschi *et al.*, 2000; Amat *et al.*, 2004; Lipko *et al.*, 2004; Papeschi *et al.*, 2008), and also on previously collected and preserved samples, which could be preliminary identified by their morphology (Amat *et al.*, 2004) and should be later confirmed. The latitudinal boundary at 35-36° S latitude between the distribution ranges of *A. persimilis* and *A. franciscana* seems to reflect the particular performance of both species in relation to the temperature regimes of their respective habitats (Ruiz *et al.*, 2008), and agrees well with the average annual isotherms map of this country.

In the northern boundary of the hypothetic hybrid area, we placed the population of a shallow lake in Trenque Lauquen (35° 48' S, 62° 55' W, Buenos Aires Province), which corresponds to a preserved sample, and could be allocated to *A.*

franciscana only by morphological traits. The southern boundary would correspond to the populations of Epecuén Lake (37.13° S, 62.81° W, Buenos Aires Province), a shallow lake in Naicó (approximately 36° 52' S, 64° 24' W, La Pampa Province), and to the reference population of the species: Salinas Grandes de Hidalgo (37° 13' S, 63° 26' W, La Pampa Province); the two former populations correspond also to preserved samples, assigned by morphological traits to *A. persimilis*. *A. persimilis* is distributed southwards of this boundary (Amat *et al.*, 2004; Papeschi *et al.*, 2008). The southernmost record in Argentina corresponds to small salares near the Mar Argentino coastline, in Gallegos Norte, (51° 4' S), near Cabo Buen Tiempo (Santa Cruz Province) (Birabén, 1954), even though the species reaches higher latitudes, in Laguna de los Cisnes (53° 15' S, 70° 10' W, Tierra del Fuego, Chile) (Amat *et al.*, 2004; Gajardo *et al.*, 2004; Papeschi *et al.*, 2008; Ruiz *et al.*, 2008).

In Chile, the population of Saltworks de Cahuil in the locality of Pichilemu (VI Region, 34° 48' S, 72° 10' W) showed some controversial results in its identification, according to the methodology applied in the multidisciplinary approach (Amat *et al.*, 2004). While electrophoretic results (Gajardo *et al.*, 1995) and discriminant multivariate morphological analysis of adults (Gajardo *et al.*, 1998) indicate that the population could be assigned to *A. franciscana*, the cytogenetic results (Colihueque and Gajardo, 1996; Gajardo *et al.*, 2001), the morphology and morphometrics of adults (Gajardo *et al.*, 1998; Zúñiga *et al.*, 1999), RFLPs studies (Gajardo *et al.*, 2004), and recent morphological SEM studies (Mura and Gajardo, 2011) lead to allocate the population closer to *A. persimilis*. Accordingly, Gajardo *et al.* (2004) considered the specific status of this population as controversial, and suggested a probable hybridization and presence of a hybrid zone, almost at the same latitude of the hypothesized hybrid area in Argentina. In Chile, the population of Pichilemu represents the southern limit reported to date in the distribution of *A. franciscana*, ranging between 20 and 34° S (Gajardo *et al.*, 2004). The nearby population of El Convento (33° 52' S, 71° 44' W), allocated to *A. franciscana*, may have contributed

natural dispersed cysts of this species to Pichilemu population (Gajardo *et al.*, 2004). At this latitude the highest altitude of the Andes mountain range, would act as an effective barrier preventing any genetic exchange among populations of Chile and Argentina. Other consideration to take into account is the fact that Salinas de Cahuil is a coastal artisanal saltwork, in which *Artemia* was probably introduced by workers (Gajardo *et al.*, 1998). Tracing the origin of the cysts inoculated would be very informative, especially taking into account the frequent movement of people between both neighboring countries at these latitudes for trade or tourism. Apart from the *A. persimilis* population from Laguna de los Cisnes, another southern Chilean population, laguna La Amarga (50° 29'S, 73°45' W) in Torres del Paine National Park (Gajardo *et al.*, 1999) was found in a peculiar area containing semiarid and humid biotopes (Campos *et al.*, 1996). No additional records of *Artemia* populations between the Pichilemu and La Amarga populations have been reported so far (Gajardo *et al.* 1999; Gajardo *et al.*, 2004). La Amarga population was assigned to *A. persimilis* by means of allozyme studies, cross-breeding tests, morphological observations (Gajardo *et al.*, 1999), and RFLPs studies (Gajardo *et al.*, 2004). However, cytogenetic studies (number of chromosomes $2n=44$ and a high average number of chromocentres: 17.7) suggested that the population should be assigned to *A. franciscana* (Gajardo *et al.*, 2001; Gajardo *et al.*, 2002). It was a general assumption that the number of chromocentres was a reliable taxonomic trait and a good marker for speciation in *Artemia*: *A. persimilis* showed the typical low average number of chromocentres (< 3), whilst *A. franciscana* showed higher average numbers (> 5) (Gajardo *et al.*, 2001). In accordance to this, some authors (Gajardo *et al.*, 2001; Gajardo *et al.*, 2002) showed a latitudinal variation in several *A. franciscana* populations throughout the whole American continent. In the Northern Hemisphere there is a north-south steady latitudinal decline in the number of chromocentres towards the equator. On the other hand, in the southern Hemisphere, this trait increased from the equator southwards (Parraguez *et al.*, 2009). The

most meridional population exhibiting the highest chromocentre frequency was precisely the Chilean Laguna La Amarga. This puzzling situation led the author to support the validity of the hypothesis that *A. persimilis* was geographically restricted to Argentina (Gajardo *et al.*, 2001). However, a later RFLPs analysis (Gajardo *et al.*, 2004) conclusively showed that Torres del Paine presents haplotypes closely related with the *A. persimilis* reference sample (Buenos Aires, 34°30' S, 58° 20'W), in spite of its cytogenetic results. On the other hand, Papeschi *et al.* (2008) made a comparison on the heterochromatin content among several Argentinean *A. persimilis* and *A. franciscana* populations and the Chilean population of Laguna de los Cisnes; they included as reference populations, strains from Salinas Grandes de Hidalgo and Great Salt Lake (USA), respectively. Using two heterochromatin estimators: number of chromocentres and relative C-positive area, these authors found that the *A. franciscana* populations showed relatively low C-positive heterochromatin content. The populations of *A. persimilis* showed scarce C-positive heterochromatin between 36° and 39°S, but those populations located southwards 40°S, increased noticeably the amount of heterochromatin, the highest being observed in Laguna de los Cisnes (relative C-positive area: 10,32; number of chromocentres: 7). These results do not support the hypothesis of the latitudinal cline of heterochromatin content in *A. franciscana* (Gajardo *et al.*, 2001) and show that populations from both species could display variability in this cytogenetic trait. The general assumption of higher heterochromatin content in *A. franciscana* than in *A. persimilis* should be reconsidered. Furthermore, these results give additional support to the assignation of the Chilean population of La Amarga, which showed a reported high average number of chromocentres (17.7) (Gajardo *et al.*, 2001), to *A. persimilis*. The variability in the heterochromatin content observed in populations of the two American species suggests an adaptive relationship between this content and some environmental parameters (unfavorable conditions) which could vary with latitude or altitude. A very high C-positive heterochromatin content (and

>5 chromocentres) observed in a high altitude population from Arequipa (Perú) (Cohen, unpubl. data), preliminary assigned to *A. persimilis* on the base of morphological traits (V. H. Vera, pers. comm.), could support this view. This record poses a very interesting biogeographic problem. If this identification is confirmed, this disjunct high altitude location, together with several west Bolivian, south Peruvian, north Chilean, and northwestern Argentinean populations, which share the high altitude plain of the Altiplano (approximately above 4,500 m asl.), could represent altitudinal relicts of an ancient wider distribution of *A. persimilis*. Some high altitude populations of *Artemia* (referred as *Artemia salina*) has been reported in several shallow lakes in the Bolivian province del Sur Lipez, Potosí (Hurlbert *et al.*, 1984, 1986; Dejoux, 1993), in Perú, Arequipa, assigned to *A. persimilis* (V.H. Vera pers. pers. comm.), in the Chilean I Region, Salar de Surire, assigned to *A. franciscana* (Zúñiga *et al.*, 1999; Crespo and Baessolo, 2002), and also recently some *Artemia* populations not yet identified have been found in the Argentinean Puna (Cohen, unpublished data).

It is possible to hypothesize that global warming could have pushed Argentinean *A. persimilis* populations to cooler areas at higher altitudes and latitudes, reaching its current known distribution south of 36 °-37 ° S latitude, while some populations were isolated to high-altitude sites. Medina *et al.* (2007) have shown experimentally that *A. persimilis* is much more tolerant than *A. franciscana* to low temperatures, but at salinities lower than 30‰ it cannot survive whatever the temperature. *A. franciscana* shows a better performance in several fitness-related traits at all temperature-salinity combinations, except at lower temperatures (<10-12°C). However, mainly in the extensive and shallow salinas of the Chaco-Pampean plain, where *A. persimilis* thrives, the salinity is usually very high and the temperature of the water may increase significantly during the day due to the high insulation and absorption of heat by the pink saline waters. Instead, at higher latitudes, in the saline ecosystems of the Patagonian plateau, the temperature of the water is lower even in very sunny days, and the level

of UV radiation is higher than at lower latitudes. During long time, each population has adapted to the local environmental conditions of its biotope, which is in balance with the general climate of the region. Cytogenetic results may support latitudinal differences among *A. persimilis* populations (Papeschi *et al.*, 2008), with southern populations having evolved the ability to adapt to more rigorous environmental conditions (colder climates, higher UV radiation). Through RFLPs, *A. persimilis* showed higher nucleotidic and haplotype diversity than *A. franciscana* (Gajardo *et al.*, 2004; Ruiz *et al.*, 2008). Taking into account recent findings of the ancient divergence of *A. persimilis* from the ancestor lineage (Baxevanis *et al.*, 2006), it could be expected a greater accumulation of mutations in mtDNA than in *A. franciscana* (Gajardo *et al.*, 2004). However, the eight South American populations of *A. persimilis* analyzed by RFLPs (including the reference strain), clustered in two main distinct haplotype clades. One of them appears to be the basal haplotype of the species, and the other (Ruiz *et al.*, 2008) branched off into two sub clades, each one grouping populations that are separated by a wide latitudinal range. Additional studies, using nuclear markers, involving *A. persimilis* populations would be helpful to clarify these discrepancies.

In agreement with the results of Medina *et al.* (2007) on Argentinean populations, Van Stappen (2002) noted that *A. franciscana* can not tolerate temperatures below 5°C for long periods of time. However, in the Northern Hemisphere the species overcomes the very cold temperatures of the winter, in the form of cysts stored in the biotope; when summer comes, the increased temperatures allow the hatching of cysts and the recolonization of the biotopes. An environment very similar to the South American Altiplano is the Tibet high plateau. The Qinghai-Tibet Plateau, located in southwest China is characterized by its high altitude (above 4500 m asl.), very extreme temperatures and high UV radiation. Van Stappen (2003), who studied the *Artemia* populations from several saline lakes of the region (Xin *et al.*, 1994; Zheng, 1997), found that they showed similarities with *A. tibetiana*, although their specific status should be confirmed. These

populations were characterized by a high tolerance to low temperatures, large cysts, and high levels of polyunsaturated fatty acids content (HUFA, mainly eicosapentaenoic acid, EPA), which could be related with some protection against the high UV radiation (Van Stappen, 2003). Since the current accepted view supports the early divergence of *A. persimilis* from the ancestral stock of *Artemia* 80-90 mya (Baxevanis *et al.*, 2006; Muñoz *et al.*, 2010), the finding of Asian *Artemia* populations tolerant to extremely cold conditions, poses an interesting phylogeographic case. This species may have retained the ancestral ability to bear low temperatures when dispersed in America, which may provide some interesting clues to interpret the present distribution pattern of its populations.

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