Research Article

Zoogeography of Chilean inland water crustaceans

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ABSTRACT. The Chilean inland water crustaceans are characterized by a combination of endemic and cosmopolitan species: some occur throughout the territory of continental Chile, while others are restricted to specific latitudinal regions. This study examined the zoogeographical patterns exhibited by Chilean inland water crustaceans. We considered six regions: Northern Chile (18º-27°S), North-Central Chile (27º-30°S), Central Chile (30º-38°S), Northern Patagonia (38°-41°S), Central Patagonia (41º-51°S), and Southern Patagonia (51º-55°S), and these were identified based on literature records of inland water crustaceans. The classification analysis generated dendrograms for the following groups considered in this categories: all inland water crustaceans (Branchiopoda, Copepoda and Malacostraca), the zooplanktonic crustaceans (Branchiopoda and Copepoda), the Malacostraca alone, and each group separately. Analysis of total data and of the zooplankton group taxa alone revealed the existence of a main grouping consisting of the three Patagonian zones plus Central Chile, that is distinct from that of Northern Chile and North-Central Chile. Similarly, analysis of the malacostracan data revealed the existence of two main groups, one comprising the three Patagonian zones plus Central Chile, contrasted with a second group of Northern and North-Central Chile combined. Our results are in agreement with other panbiogeographical studies of South American crustaceans and insects. Possible factors responsible for generating this pattern are the dispersal and colonization potential of zooplanktonic crustaceans and the marked endemism of the malacostracans.

Keywords: Branchiopoda, Copepoda, Amphipoda, Decapoda, endemism, dispersal, Chilean inland waters.

Zoogeografía de crustáceos de aguas continentales chilenas

RESUMEN. Los crustáceos de aguas continentales chilenas se caracterizan por una combinación de especies endémicas y cosmopolitas, algunas se encuentran a lo largo del territorio de Chile continental, mientras que otras están restringidas a regiones latitudinales específicas. El presente estudio examinó los patrones zoogeográficos exhibidos por crustáceos de aguas continentales chilenas. Se consideraron seis regiones: Norte de Chile (18º-27ºS), Norte-Central de Chile (27º-30ºS), Chile Central (30º-38ºS), Norte de la Patagonia (38º-41ºS), Patagonia Central (41º-51ºS), y Sur de la Patagonia (51º-55ºS), identificadas sobre la base de registros de la literatura de crustáceos de aguas continentales. Los análisis de clasificación generaron dendrogramas para las siguientes agrupaciones consideradas en estas categorías: todas las especies de crustáceos de aguas continentales (Branchiopoda, Copepoda y Malacostraca), crustáceos zooplanctónicos (Branchiopoda y Copepoda), sólo Malacostraca, y cada grupo por separado. El análisis de todos los grupos y de los grupos zooplanctónicos reveló la existencia de un gran grupo con las tres regiones de la Patagonia más Chile central, diferente al de la zona norte y norte-central de Chile. De manera similar el análisis de datos de malacostracos reveló la existencia de dos grandes grupos, uno con las tres zonas de la Patagonia y Chile central, contrastado con un segundo grupo conformado por la zona norte y norte-central. Estos resultados concuerdan con estudios panbiogeográficos de crustáceos e insectos sudamericanos. Como posibles factores responsables podrían ser la dispersión y potencial colonización de crustáceos zooplanctónicos y el marcado endemismo de los malacostracos.

Palabras clave: Branchiopoda, Copepoda, Amphipoda, Decapoda, endemismo, dispersión, aguas continentales chilenas.

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INTRODUCTION

Chilean inland water crustaceans are characterized by their marked endemism at different spatial scales: there are widespread species, distributed along Chilean continental territory, and there are other species restricted to narrow geographical ranges (Jara *et al.,* 2006; Villalobos, 2006; De los Ríos-Escalante, 2010). Species exhibiting such marked endemism are at risk of extinction, due to habitat fragmentation or habitat alteration, as has been reported for decapods by Jara *et al.* (2006).

The geographical patterns of Chilean inland water crustaceans might reflect habitat heterogeneity. Thus De los Ríos-Escalante (2010), based on Niemeyer & Cereceda (1984) who used climatic, topographic and hydrological characteristics, proposed the following four regions in according to a zoogeographical review of inland water Branchiopods and Copepods: Northern Chile (18º-27ºS); Central Chile (27º-37ºS), Northern and Central Patagonia (37º-51ºS) and Southern Patagonia (51º-55ºS). For both branchiopods and copepods species were found that were restricted to a specific geographical range, as well as more widespread species (De los Ríos-Escalante, 2010).

The aim of the present study is to undertake a zoogeographical analysis of Chilean inland water crustaceans (Branchiopoda, Copepoda and Malacostraca) in continental Chilean territory in order to characterise their distribution patterns.

MATERIALS AND METHODS

Data on inland water crustaceans were obtained from literature records (Araya & Zúñiga, 1985; Bayly, 1992; González, 2003; De los Ríos-Escalante, 2010; De los Ríos-Escalante *et al.*, 2012; Jara, *in press*; Morales & Meruane *in press*; Rudolph, *in press*), and these were collated into a presence-absence matrix (Table 1, Fig. 1), with respect to the following six geographical zones: 1) Northern Chile: 18º-27ºS, 2) North-Central Chile: 27º-30ºS, Central Chile: 30º-38ºS, Northern Patagonia: 38º-41ºS; Central Patagonia: 41º-51ºS, and Southern Patagonia: 51º-55ºS. These data were explored by cluster analysis (Bray-Curtis with single link), using the Biodiversity Pro software package (McAlleece *et al.*, 1997). Data were analyzed considering the following categories: 1) All crustacean species, 2) Branchiopoda and Copepoda species, and 3) Malacostracan species.

In a second analytical step, an external area zero was added to the species presence-absence matrix to codify for rooting the cladogram (Rosen & Smith, 1998; Morrone, 2004; Fuentealba *et al.,* 2010). The most parsimonious cladograms were found by heuristic search with 1000 replicates; replicates of 100 initial trees were used with an output of up to 10000 trees were calculated using reiterative bisection and multiple reconnection (multiple TBR + TBR). The strict consensus tree was calculated from heuristic search. Node support was evaluated by bootstrap analysis (Felsenstein, 1985). Bootstrap support values were estimated (with 1000 replicates) for selected branches as endemism areas, using the Nona program (Goloboff, 1998) within Winclada (Nixon, 2002). It was applied to one analysis for understanding endemicity patterns and similarities between studied areas.

RESULTS

Cluster analysis revealed for all crustacean species and for Branchiopoda and Copepoda, the existence of a main grouping comprising the three Patagonian zones plus Central Chile, that is separate from Northern and North-Central Chile (Figs. 2 and 3). Similarly, for malacostracan species, the analysis revealed the existence of two main groupings, one consisting of the three Patagonian zones plus Central Chile, and the other comprising Northern and North-Central Chile (Fig. 4). Analysis of the decapods identifies an isolated main group comprising Northern and North-Central Chile, which are very similar, and a second major grouping of Central Chile with Northern and Central Patagonia (Fig. 5).

The analysis of amphipods revealed one main group, comprising Central Chile with Northern and

Table 1. List of inland water crustacean species reported for continental Chilean territory (0: absence, 1: presence).

	Northern Chile (18º-27°S)	North-Central Chile (27º-30°S)	Central Chile (30º-38°S)	Northern Patagonia (38º-41°S)	Central Patagonia (41º-51°S)	Southern Patagonia (51º-55°S)
Class Branchiopoda						
Order Anostraca						
Family Artemiidae						
Artemia franciscana Kellog (1906)	1	1	1	0	0	0
A. persimilis Piccinelli & Prosdocimi (1968)	0	0	0	0	0	1
Family Branchinectidae						
Branchinecta gaini Daday (1910)	0	0	0	0	0	1
B. granulosa Daday (1902)	0	0	0	0	0	1
B. palustris Biraben (1946)	1	0	0	0	0	0
B. papillata Rogers *et al.* (2008)	1	0	0	0	0	0
B. valchetana Cohen (1981)	1	0	0	0	0	0
B. vuriloche Cohen (1985)	0	0	0	0	1	0
Order Cladocera						
Family Sididae						
Diaphanosoma chivense Daday (1902)	1	0	1	1	1	0
Latonopsis occidentalis Birge (1891)	0	0	1	0	0	0
Family Daphnidae						
Ceriodaphnia dubia Richard (1894)	0	0	1	1	1	1
Daphnia ambigua Scourfield (1947)	0	0	1	1	0	0
D. dadayana Paggi (1999)	0	0	0	0	1	1
D. obtusa Kurz (1874)	0	0	1	0	0	0
D. peruviana Harding (1955)	0	0	0	0	0	0
D. pulex Leydig (1860)	1	0	1	1	1	0
Daphniopsis chilensis Hann (1986)	0	0	0	0	0	0
Moina micrura Kurz, 1874	1	0	1	0	0	0
Scapholeberis spinifera (Nicolet, 1849)	0	0	1	1	0	0
Simosa exspinosa De Geer (1778)	0	0	1	1	0	0
Simosa serrulata Koch (1841)	0	0	1	0	0	0
Simosa vetula Müller (1776)	1	0	0	0	0	0
Family Bosminidae						
Eubosmina hagmanni Stingelin (1904)	1	0	1	1	1	1
Family Macrothricidae						
Ilyocryptus spinifer Herrick (1884)	0	0	1	1	1	0
Macrothrix hirsuticornis Norman & Brady (1867)	0	0	1	0	0	0
Macrothrix inflata Daday (1902)	0	0	1	0	0	0
Macrothrix laticornis Jurine (1820)	0	0	1	0	0	0
Macrothrix odontocephala Daday (1902)	0	0	1	0	0	0
Macrothrix palearis Harding (1955)	1	0	0	0	0	0
Family Chydoridae						
Alona affinis Leydig (1860)	0	0	1	0	0	0
A. cambouei De Guerne & Richard, 1893	1	0	0	0	0	0
A. guttata Sars (1862)	0	0	1	0	0	0
A. intermedia Sars (1862)	0	0	0	0	0	0
A. poppei Richard (1897)	0	0	0	1	0	0
A. pulchella King (1853)	0	0	0	1	0	0
A. quadrangularis Müller (1776)	0	0	0	1	0	0
Alonella clathratula Sars (1862)	1	0	0	0	1	0
A. excisa Fisher (1854)	0	0	0	0	1	0
Camptocercus rectirostris Schoedler (1862)	0	0	1	1	1	0
Chydorus sphaericus Müller (1775)	1	0	1	1	1	0

Continuation

	Northern Chile (18º-27°S)	North-Central Chile (27º-30°S)	Central Chile (30º-38°S)	Northern Patagonia (38º-41°S)	Central Patagonia (40º-51°S)	Southern Patagonia (51º-55°S)
Leydigia leydigi Schoedler (1863)	0	0	1	1	0	0
Paralona nigra Sars (1862)	0	0	1	1	0	0
Pleuroxus aduncus Jurine (1820)	0	0	1	1	0	0
P. scopulifer Ekman (1900)	0	0	1	0	0	0
Class Maxillopoda						
Subclass Copepoda						
Order Calanoida						
Family Centropagidae						
Boeckella bergi Richard (1897)	0	0	1	0	0	0
B. brasilensis Lubbock (1855)	0	0	0	0	1	0
B. brevicaudata Brady (1875)	0	0	0	0	1	1
B. calcaris Harding (1955)	1	0	0	0	0	0
B. gibbosa Brehm (1935)	0	0	1	1	0	0
B. gracilipes Daday (1901)	1	0	1	1	1	0
B. gracilis Daday (1902)	1	0	1	1	0	0
B. meteoris Kiefer (1928)	0	0	1	0	1	0
B. michaelseni Mrázek (1901)	0	0	0	0	1	0
B. occidentalis Marsh (1906)	1	0	0	0	0	0
B. poopoensis Marsh (1906)	1	0	0	0	0	0
B. poppei Mrázek (1901)	0	0	0	0	1	1
Parabroteas sarsi Ekman (1905)	0	0	0	0	1	1
Family Diaptomidae						
Tumeodiaptomus diabolicus Dussart (1979)	0	0	1	1	0	0
Order Cyclopoida						
Family Cyclopidae						
Acanthocyclops michaelseni Mrázek (1901)	0	0	0	0	0	1
A. vernalis Fisher (1853)	0	0	0	1	0	0
Diacyclops andinus Locascio de Mitrovich & Menu-Marque (2001)	1	0	0	0	0	0
Eucyclops ensifer Kiefer (1927)	0	0	0	0	1	0
E. serrulatus Fisher (1851)	0	0	1	1	1	0
Macrocyclops albidus Jurine (1820)	0	0	1	1	0	0
Mesocyclops araucanus Löffler (1962)	0	0	0	1	1	0
M. longisetus Thiebaud (1912)	0	0	1	0	0	0
Metacyclops mendocinus Wierzejski (1892)	0	0	1	1	0	0
Microcyclops anceps Richard (1897)	0	0	1	0	0	0
Paracyclops fimbriatus chiltoni Thomson (1882)	0	0	1	1	0	0
Tropocyclops prasinus meridionales Kiefer (1927)	0	0	1	1	1	0
Class: Malacostraca						
Subclass: Peracarida						
Order: Amphipoda						
Family: Hyalellidae						
Hyalella chiloensis González & Watling (2001)	0	0	1	0	1	0
H. costera González & Watling (2001)	1	1	1	1	0	0
H. curvispina Schoemaker (1942)	0	0	0	0	0	1
H. fossamanchini Cavalieri (1959)	1	0	0	0	0	0
H. franciscae González & Watling (2003)	0	0	0	0	1	1
H. kochi González & Watling (2001)	1	0	0	0	0	0
H. patagonica Cuningham (1871)	0	0	1	1	1	1
H. simplex Schellenberg (1943)	0	0	0	1	0	1

Continuation

	Northern Chile (18º-27°S)	North-Central Chile (27º-30°S)	Central Chile (30º-38°S)	Northern Patagonia (38º-41°S)	Central Patagonia (40º-51°S)	Southern Patagonia (51º-55°S)
Subclass Eucarida						
Order: Decapoda						
Family: Parastacidae						
Samastacus spinifrons Philippi (1882)	0	0	1	1	1	0
Parastacus pugnax Poeppig (1835)	0	0	1	0	0	0
P. nicoleti Philippi (1882)	0	0	0	1	0	0
Virilastacus araucanius Faxon (1914)	0	0	1	1	0	0
V. rucapihuelensis Rudolph & Crandall (2005)	0	0	0	1	0	0
V. retamali Rudolph & Crandall (2007)	0	0	0	1	1	0
Family: Palaemonidae						
Cryphiops caementarius Molina (1782)	1	1	1	0	0	0
Sub-order: Anomura						
Family: Aeglidae						
Aegla abtao Schmitt (1942)	0	0	0	1	1	0
A. affinis Schmitt (1942)	0	0	1	0	0	0
A. alacalufi Jara & López (1981)	0	0	0	0	1	0
A. araucaniensis Jara (1980)	0	0	0	1	1	0
A. bahamondei Jara (1982)	0	0	1	0	0	0
A. concepcionensis Schmitt (1942)	0	0	1	0	0	0
A. cholchol Jara (1999)	0	0	0	1	0	0
A. denticulata denticulada Nicolet (1842)	0	0	1	0	1	0
A. denticulata lacustris Jara (1989)	0	0	0	1	0	0
A. expansa Jara (1992)	0	0	1	0	0	0
A. hueicollensis Jara (1999)	0	0	0	1	0	0
A. laevis laevis Schmitt (1942)	0	0	1	0	0	0
A. laevis talcahuano Schmitt (1942)	0	0	1	0	0	0
A. manni Jara (1980)	0	0	0	1	0	0
A. neuquensis Schmitt (1942)	0	0	0	0	1	0
A. occidentalis Jara *et al.* (2003)	0	0	1	1	0	0
A. papudo Schmitt (1942)	0	0	1	0	0	0
A. pewenchae Jara (1994)	0	0	1	1	0	0
A. rostrata Jara (1977)	0	0	0	1	0	0
A. spectabilis Jara (1986)	0	0	0	1	0	0

Central Patagonia, and this is relatively similar to Southern Patagonia. This grouping is separated from both of the two northern regions of Chile (Fig. 6). For cladocerans, there was a main grouping of Central Chile with Northern and Central Patagonia, and in decreasing order of similarity, Southern Patagonia, and Northern and North-Central Chile (Fig. 7). Finally, for copepods we found two main groupings (Central Chile-Northern Patagonia and Central-Southern Patagonia), that is distinct from the closely similar Northern and North-Central Chile (Fig. 8).

The parsimony endemicity analysis generated an exclusive cladogram with 111 steps, a consistency index of 0.84, and a retention index of 0.58. The bootstrap values obtained varied between 0.55 and 0.98 for different areas of endemism (Fig. 9). The cladogram depicts two main endemism areas represented by Central and Southern Patagonia and by Northern, North-Central and Central Chile and Northern Patagonia (Fig. 9).

DISCUSSION

The results for all crustacean species and for the grouping of Branchiopoda and Copepoda showed a gradual difference between Patagonian species and species located in northern regions, and are in agreement with the panbiogeographical analysis for centropagid copepods of Menu-Marque *et al.* (2000), who found widespread species in combination with

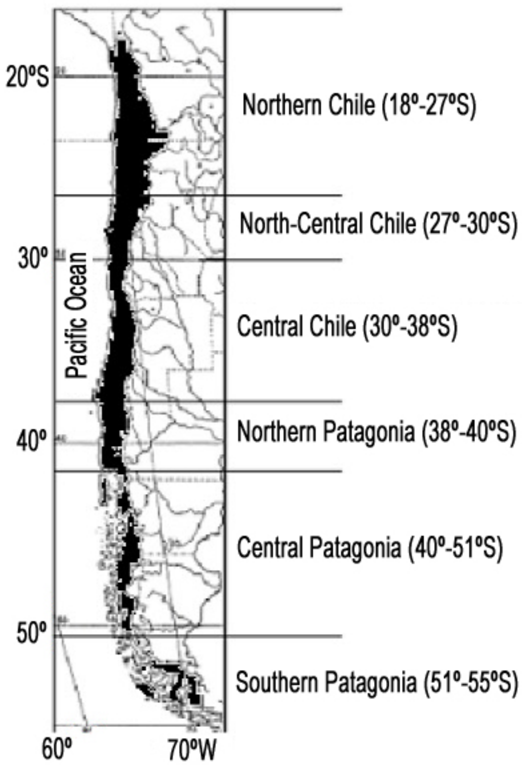

Figure 1. Map of continental Chilean territory showing the hydrographical areas utilized by the author.

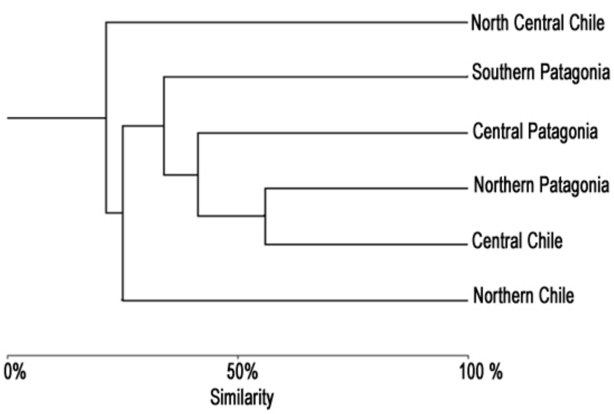

Figure 2. Dendrogram of all inland water crustaceans considered in the present study.

species showing a very restricted geographical distribution. One possible factor would be the high dispersal capability of Branchiopoda and Copepoda (Menu-Marque *et al.,* 2000; De los Ríos-Escalante, 2010). Malacostracans are different: in the present study we found a marked difference between Patagonian species and Northern species in agreement with the panbiogeographical analyses of the amphipod genus *Hyalella* (De los Ríos-Escalante *et al.,* 2012),

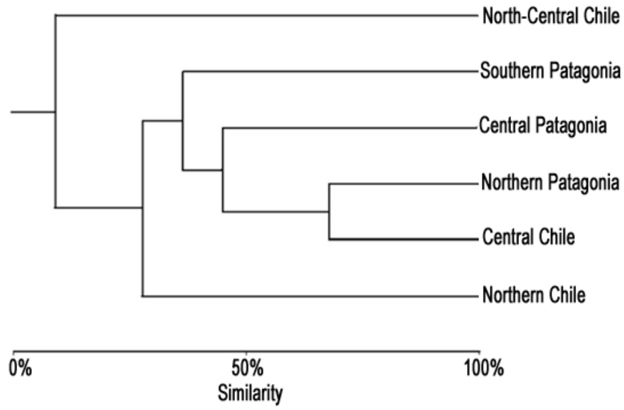

Figure 3. Dendrogram of inland water crustaceans zooplanktonic (Branchiopoda and Copepoda) considered in the present study.

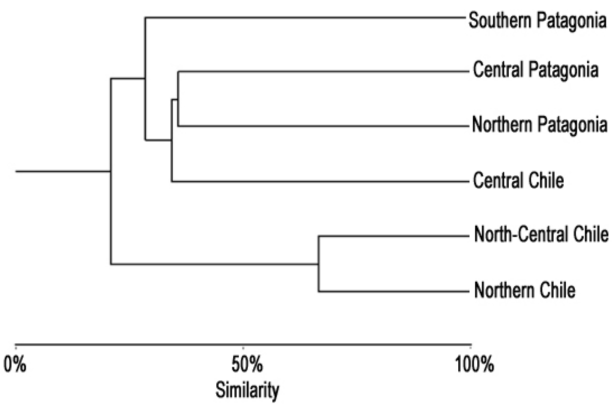

Figure 4. Dendrogram of inland water Malacostraca considered in the present study.

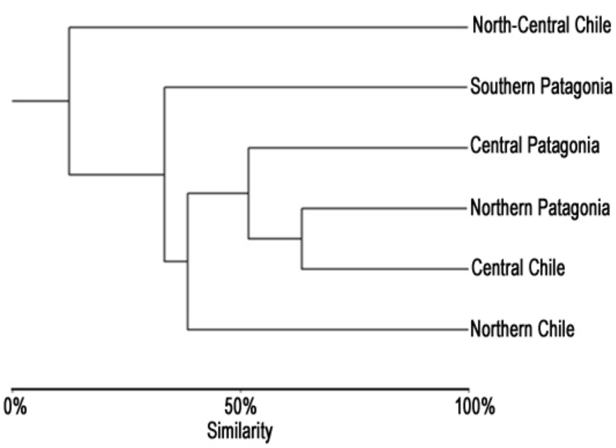

Figure 5. Dendrogram of inland water Decapoda considered in the present study.

and of inland water decapods (Morrone & Lopretto, 1994). A similar zoogeographical pattern was observed in the genus *Aegla* (Perez-Lozada *et al.,*

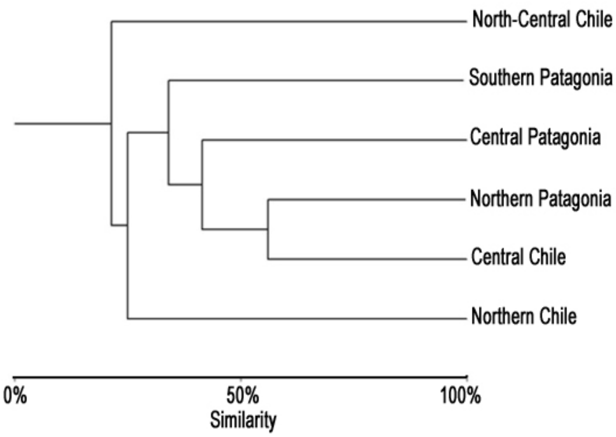

Figure 6. Dendogram of inland water Amphipoda considered in the present study.

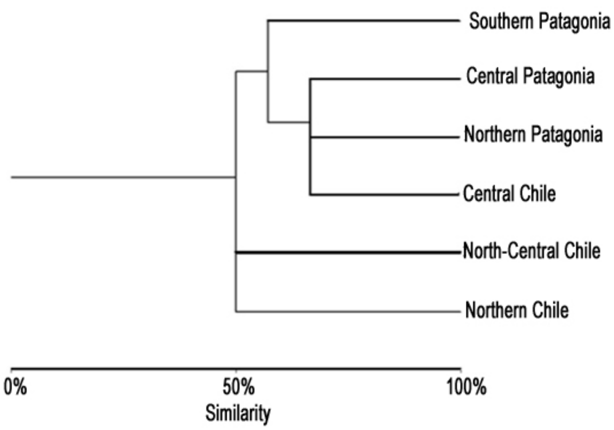

Figure 7. Dendogram of inland water Cladocera considered in the present study.

2002, 2004, 2009). This difference may be explained in part by the presence in Patagonia, of Southern South American and Subantarctic species (Pugh *et al.*, 2002; Dos Santos *et al.*, 2008).

An important factor here is that Southern Patagonia has a few subtropical species combined with Subantarctic species (Pugh *et al.*, 2002; Dos Santos *et al.*, 2008), whereas Northern Chile exemplifies a different faunal region (Menu-Marque *et al.*, 2000; Morrone, 2006; De los Ríos-Escalante *et al.*, 2012). In addition, in Chile, the Andes mountains represent a barrier that limits or prevents species dispersal between the two sides of the mountains and explains the marked differences in species reported from zones including Andean mountains (Morrone, 2006), compared to Southern Patagonia, where the mountains have practically disappeared and where it is possible to find many common species (Menu-Marque *et al.*, 2000). Following this scenario, may help to explain the marked differences in species reported in western and eastern South America (Soto & Zúñiga, 1991; Morrone & Lopretto, 1994; Menu-Marque *et al.*, 2000; Oyanedel *et al.*, 2008).

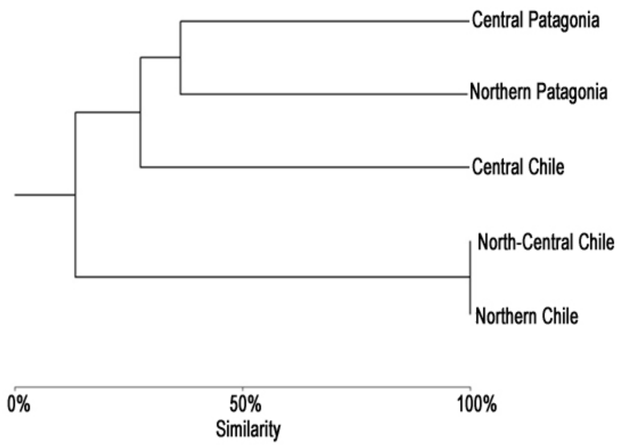

Figure 8. Dendogram of inland water Copepoda considered in the present study.

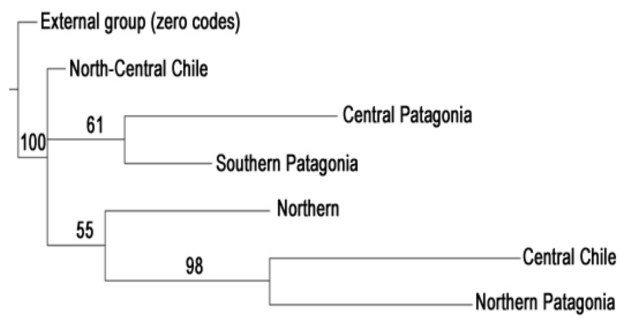

Figure 9. Cladogram obtained from the parsimony analysis of endemicity of Chilean inland water crustaceans. Bootstrap values are indicated on the nodes.

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