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Out of New Zealand: molecular identification of the highly invasive freshwater mollusk *Potamopyrgus antipodarum* (Gray, 1843) in South America

Gonzalo A Collado^{1,2}

Abstract

Background: The New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) is among the most widespread non-indigenous mollusk in the world. Based on a comprehensive phylogenetic analysis, the invasion of this species to central Chile, which is also the first record of this species from South America, is reported.

Results: Molecular analysis identified four populations of *P. antipodarum* in central Chile, Parque O'Higgins and Estero La Dehesa in Santiago city, and Estero Consuelo and the Chalinga River in Salamanca, a town located in a different basin. No sequence divergence was found among populations in the cytochrome c oxidase subunit I (COI) gene. Morphological and reproductive evidence is in agreement with these findings.

Conclusions: This is the first record of *P. antipodarum* in the Neotropical region. All populations contained only females with embryos or juvenile snails in their brood pouches suggesting that they are viable and well established. It is important to prevent the spread of *P. antipodarum* to other localities in Chile and other South American countries.

Keywords: Biological invasions; Caenogastropoda; Chile; COI gene; Tateidae

Background

The widespread introduction of non-native species has been considered as one of the major threats to biodiversity (Lodge and Shrader-Frechette 2003). The mud snail *Potamopyrgus antipodarum* is a caenogastropod originated from New Zealand and adjacent islands (Winterbourn 1970, 1972). This snail has become among the most widespread non-indigenous aquatic invertebrates in the world (Butkus et al. 2012). Several transport methods have been reported as responsible for propagation of this global exotic species, which include both active and passive dispersal (Alonso and Castro-Diez 2008). This species has invaded brackish and freshwater habitats in several countries in Europe, Australia, Asia, and North America (e.g. Ponder 1988; Bowler 1991; Shimada and Urabe 2003; Radea et al. 2008; Butkus et al. 2012; Hamada et al. 2013).

Potamopyrgus antipodarum is a minute snail highly variable in size, shape and ornamentation. Adults range from 3 to 6 mm in length in USA, but they reach 11 mm in their native habitat (Richards 2002). Winterbourn (1970) reported considerable variation in the shell ornamentation of the species in its native range, even within a single population. Shell polymorphism in *P. antipodarum* would be influenced by environmental and genetics bases (Winterbourn 1970; Haase 2003). Recently, Butkus et al. (2012) reported regular (smooth) and carinate morphotypes from Lake Viikokšni, suggesting two independent invasion events. However, this should be taken with caution since the presence of a keel-like ridge can be a phenotypically plastic trait.

Potamopyrgus antipodarum is a generalist species, feeding on aquatic plants, green algae and detritus (Haynes and Taylor 1984), being able to tolerate a broad range of physicochemical aquatic conditions (Dorgelo 1987; Proctor et al. 2007; Poirier 2013). In the rivers of Wyoming, USA, the species dominates secondary production, even reaching

Correspondence: gcollado@ubiobio.cl

¹Departamento de Ciencias Básicas, Facultad de Ciencias, Universidad del Bío-Bío, Avda. Andrés Bello s/n, Casilla 447, Chillán, Chile

²Fundación Chile Natura, Santiago, Chile

one of the highest values of productivity ever reported for a stream invertebrate (Hall et al. 2006). Zaranko et al. (1997) reported its densities in Lake Ontario being as high as 5,600 snails per square meter, which is a value close to that found in native populations ($4,000/\text{m}^2$, see Collier et al. 1998). However, in other invaded habitats, *P. antipodarum* can achieve densities as high as 500,000 snails per square meter (Hall et al. 2003; Richards 2002; Richards et al. 2001), and even more ($800,000/\text{m}^2$, see Dorgelo 1987).

Because frequently there are no obvious morphological characters to distinguish different components of invertebrate fauna, DNA barcoding and molecular phylogenetic analysis are increasingly used to identify aquatic invaders in a variety of taxa (e.g. Geller et al. 1997; Facon et al. 2003; Albrecht et al. 2009; Duggan et al. 2012;

Porco et al. 2013; Wetterer 2014). In 2010, an investigation of the small freshwater gastropod of the superfamily Rissoidae Gray, 1847 *sensu lato* of Chile was initiated by the author, sampling snails from a number of locations. In a previous morphological work, Collado et al. (2011a) assigned snails from the Chalinga River and Estero Consuelo to the genus *Heleobia* Stimpson, 1865 following Biese (1944, 1947). Here, I perform a comprehensive phylogenetic analysis to evidence that these snails actually represent the non-native species *P. antipodarum*. I also report the occurrence of this species in other two watersheds from central Chile, Estero La Dehesa east of Santiago, and a spring located within the Parque O'Higgins, also in this city. Additionally, I evaluate the reproductive performance of populations studied.

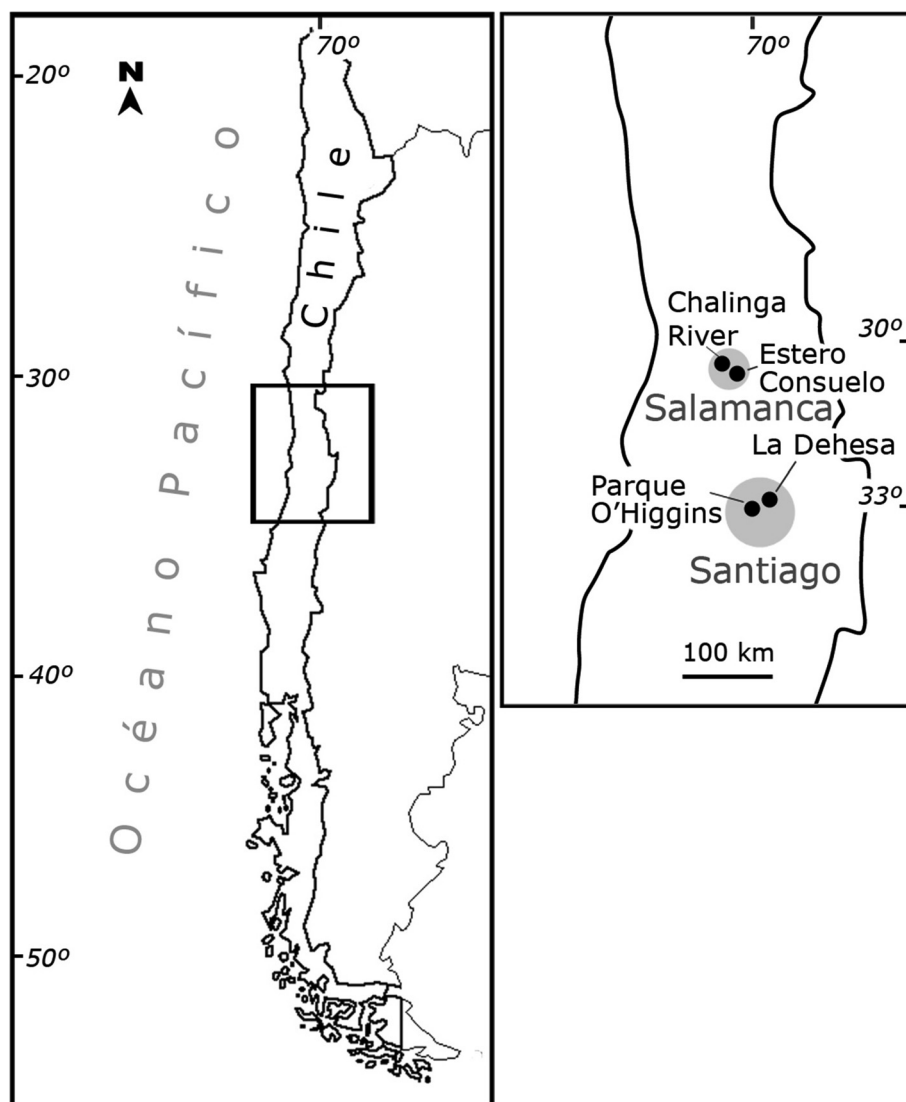


Figure 1 Sampling sites of *Potamopyrgus antipodarum* in central Chile (black dots).

Methods

In this study, four localities in two regions from central Chile, Región de Coquimbo and Región Metropolitana, were sampled from prospective sites for snail collection (Figure 1). In Región de Coquimbo, two watersheds were sampled, both in the town of Salamanca, the Chalinga River (31° 46' 15.61" S; 70° 59' 05.09" W), which is a small, intermittent watercourse north of the town, and Estero Consuelo (31° 46' 48.61" S; 70° 57' 37.33" W), a stream east of the town. In Región Metropolitana, two watersheds were sampled in Santiago city; Estero La Dehesa (33° 22' 02.00" S; 70° 31' 15.00" W), a stream located in the eastern suburbs of the city, and Parque O'Higgins (33° 28' 06.22" S; 70° 39' 38.31" W), an urban park that offers recreation, fishing, and open green space to residents and whose southern section includes a spring that flows about 300 m into an small artificial lagoon. In this spring, *P. antipodarum* co-occur with a snail species of the genus *Physa* Draparnaud, 1801, platyhelminthes, and other invertebrates. The snails were obtained from macrophytes of the spring using a sieve and preserved in absolute ethanol prior to molecular and morphological analyses. The snails were photographed at the same magnification with a Motic SMZ-168 Stereo Microscope (Motic, Richmond, BC, Canada) with a Moticom 2000 (Motic, Xiamen, China) integrated digital camera. The shell of adult snails was broken and the mantle tissue was removed to determine the sex by the presence/absence of a penis. In the case of the females, the oviduct wall was dissected to determine the

presence of embryos or juveniles. The measurements of animals were performed under a stereo microscope. The author is authorized to the removal of animals from watersheds in Chile (Resolution N° 3285, Subsecretaría de Pesca y Acuicultura, Ministerio de Economía, Fomento y Turismo, República de Chile). Voucher specimens of *P. antipodarum* were deposited in the Colección Malacológica del Servicio Agrícola y Ganadero de Chile (CMSAG 3651 and 3652).

A small piece of tissue from the mantle and gill was cut off from the snails to extract genomic DNA using the cetyl trimethylammonium bromide (CTAB) method (Winnepennickx et al. 1993). A fragment of the mitochondrial gene, cytochrome *c* oxidase subunit I (COI) was amplified by polymerase chain reaction (PCR) using the primers LCO1490 (5'-GGTCAACAAATCATAAA GATATTGG-3') and HCO2198 (5'-TAAACTTCAGG GTGACCAAAAAATCA-3') (Folmer et al. 1994); PCR conditions were the same as those in Collado et al. (2011b). Amplified products were sequenced by Macrogen Inc., South Korea. The sequences were edited and aligned with BioEdit (Hall 2001) using default parameters. Phylogenetic analyses were performed using maximum parsimony (MP) and Bayesian inference (BI) methods. The MP analysis was carried out with the program PAUP* 4.0 (Swofford 2003) using a heuristic search with the tree bisection and reconnection branch swapping algorithm and the addition of random sequences. Character states were treated as unordered, assuming equal weight. The statistical confidence of the nodes was evaluated using 100

Table 1 Classification and GenBank accession numbers for the rissooidean taxa studied

Family	Species	GenBank accession	Source
Barleeiidae	<i>Barleeia oldroydi</i> (Bartsch 1920)	JX970602	Wilke et al. (2013)
Amnicolidae	<i>Amnicola limosa</i> (Say, 1817)	AF213348	Wilke et al. (2000a)
Assimineidae	<i>Assiminea grayana</i> Fleming, 1828	HQ623170	Wilke et al. (2013)
Beddomeia group	<i>Beddomeia paludinella</i> (Reeve, 1857)	JX970603	
Bithyniidae	<i>Bithynia tentaculata</i> (Linnaeus, 1758)	JX970605	
Bythinellidae	<i>Bythinella austriaca</i> (Frauenfeld, 1856)	AF213349	Wilke et al. (2000a)
Iravadiidae	<i>Clenchiella</i> sp.	JX970606	Wilke et al. (2013)
Cochliopidae	<i>Heleobops carrikeri</i> Davis and McKee, 1989	AF213347	Wilke et al. (2000a)
Falsicingulidae	<i>Falsicingula athera</i> Bartsch, 1936	HQ623172	Wilke et al. (2013)
Hydrobiidae	<i>Hydrobia acuta</i> (Draparnaud, 1805)	AF278808	Wilke et al. (2000b)
Lithoglyphidae	<i>Lithoglyphus naticoides</i> (Pfeiffer, 1828)	AF367642	Wilke et al. (2001)
Moitessieriidae	<i>Moitessieria</i> cf. <i>puteana</i> Coutagne, 1883	AF367635	
Pomatiopsidae s.s.	<i>Pomatiopsis lapidaria</i> (Say, 1817)	AF367636	
Rissooideae	<i>Setia turriculata</i> Monterosato, 1884	AF253084	Davis et al. (1998)
Stenothyridae	<i>Stenothyra</i> cf. <i>glabra</i> A. Adams, 1861	HQ623177	Wilke et al. (2013)
Tateidae	<i>Tatea huonensis</i> (Tenison-Woods, 1876)	JX970619	Wilke et al. (2013)
Hydrobiidae	<i>Ascorhis tasmanica</i> Martens, 1858	AF129329	Hershler et al. (1999)
Truncatellidae	<i>Geomelania inornata</i> Chitty, 1853	AF367629	Wilke et al. (2001)

Table 2 GenBank accession numbers for the taxa studied of the family Tateidae

Species	GenBank accession number	Source
<i>Fluviopupa</i> sp.	JX970615	Wilke et al. (2013)
<i>Halopyrgus pupoides</i> (Hutton, 1882)	JX970616	
<i>Hemistomia winstonefi</i> (Haase and Bouchet, 1998)	JX970617	
<i>Obtusopyrgus alpines</i> Haase, 2008	AY631088	
<i>Opacuincola delira</i> Haase, 2008	AY631090	
<i>Potamolithus ribeirensis</i> Pilsbry, 1911	JX970618	Wilke et al. (2013)
<i>Potamopyrgus antipodarum</i> (Gray, 1843)	EU573983	Ponder et al. (2008)
	AB703675	Hamada et al. (2013)
	AB703676	
	AB703677	
	AY631101	Haase (2005)
	AY631102	
<i>Potamopyrgus estuarinus</i> (Winterbourn, 1971)	AY631103	
	AY631104	
<i>Potamopyrgus kaitunuparaoa</i> Haase, 2008	AY631105	
	AY631106	
<i>Potamopyrgus oppidanus</i> Haase, 2008	AY631112	
<i>Sororipyrgus kutukutu</i> Haase, 2008	AY631108	
<i>Catapyrgus matapango</i> Haase, 2008	AY631072	
<i>Hadopyrgus ngataana</i> Haase, 2008	AY631073	
<i>Leptopyrgus melbourni</i> Haase, 2008	AY631075	
<i>Rakiurapyrgus cresswelli</i> (Climo, 1974)	AY631081	
<i>Meridiopyrgus muaupoko</i> Haase, 2008	AY631083	
<i>Paxillostium nanum</i> Gardner, 1970	AY631111	
<i>Halopyrgus pagodulus</i> Haase, 2008	AY631113	
<i>Tongapyrgus kohitatea</i> Haase, 2008	AY631124	
<i>Tatea huonensis</i> (Tenison-Woods, 1876)	JX970619	Wilke et al. (2013)
<i>Tatea rufilabris</i> (A. Adams, 1862)	EU151940	Colgan and da Costa ^a
<i>Edgbastonia alanwillsi</i> Ponder et al. 2008	EU580440	Ponder et al. (2008)
Spring from Parque O'Higgins	KJ616603	Present study
	KJ616604	Present study
	KJ616605	Present study
	KJ616606	Present study
Chalinga River	KJ616607	Present study
	KJ616608	Present study
	KJ616609	Present study
	KJ616610	Present study

Table 2 GenBank accession numbers for the taxa studied of the family Tateidae (Continued)

Estero Consuelo	KJ616611	Present study
	KJ616612	Present study
	KJ616613	Present study
	KJ616614	Present study
Estero La Dehesa	KJ616615	Present study
	KJ616616	Present study
	KJ616617	Present study
	KJ616618	Present study

^aUnpublished data.

bootstrap pseudoreplicates (Felsenstein 1985). The BI was performed with MrBayes v. 3.1.2 (Ronquist and Huelsenbeck 2003) after selecting the best evolutionary model in jModelTest (Posada 2008). The analysis was run three times for 3 million generations, sampling trees every 1,000 generations and using a burn-in period of 10%.

As Chilean rissooidean snails have been assigned to different families (Collado et al. 2011a), original sequences were aligned with sequences of snails obtained from GenBank covering a wide range of taxa within this superfamily (see Wilke et al. 2013) (Table 1). After ascertaining the family of the Chilean snails, original sequences were aligned with sequences of different genera within the particular family to determine the genus and species to which the snails belong, in this case *P. antipodarum*. Original sequences were deposited in GenBank (Table 2).

Results

The snails collected in central Chile have ovate to conical shell shape, smooth, with a deep suture, and with up to six whorls (Figure 2). The aperture is oval, sometimes thickened, and with a thin brown operculum. The external shell morphology of these snails is consistent with the drawings and photographs of *P. antipodarum* shown in other studies (Winterbourn 1970, 1972; Gangloff 1998; Butkus et al. 2012; Poirier 2013). All the snails examined in the present study were females. The largest snail belonged to the population from Estero La Dehesa (Table 3). The presence of embryos or juveniles in the breeding pouches was detected in every studied population (Figure 3). In a previous study, Collado and Méndez (2011) demonstrated that the species treated as *Heleobia choapaensis* (Biese, 1944) from Estero Consuelo was ovoviviparous.

A COI fragment of 639 bp was amplified in the snail sampled in the present study. No sequence variation was found within the four populations. The MP and BI analyses indicated that these snails fell in a clade integrated by snails that belong to the family Tateidae Thiele, 1925 (Figure 4). In both analyses, the Tateidae node was highly supported. A subsequent phylogenetic analysis included

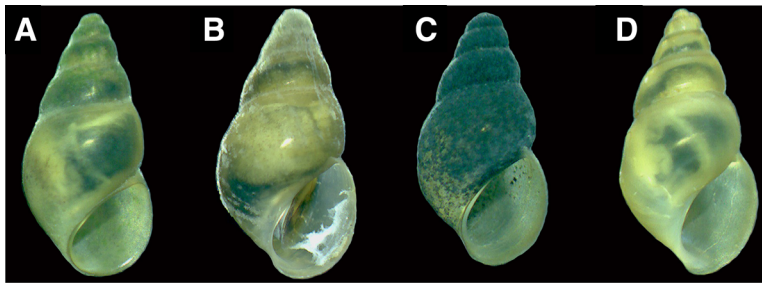


Figure 2 Living representative adult snails of *Potamopyrgus antipodarum* in central Chile. Shell length and shell width are given in millimeters. (A) Parque O'Higgins (3.8 × 2.1) (B) Estero La Dehesa (4.0 × 2.1). (C) Estero Consuelo (2.9 × 1.5). (D) Chalinga River (2.9 × 1.6).

20 species of this family (Table 2) using *Ascorhis tasmanica* as an outgroup (see also Wilke et al. 2013 for the sister group of the Tateidae). In this analysis, the matrix was composed of 638 nucleotide sites. The relationships among these species were well resolved by the MP and BI analyses (selected model: TPM2uf + I + G). Both analyses located the snails studied here within the genus *Potamopyrgus* (MP: 96% bootstrap support), specifically within the clade composed by the sequences of the species *P. antipodarum* (MP: 100% bootstrap support). The same systematic position was inferred in the BI analysis (1.00 posterior probability) (Figure 5).

The haplotype of the invader tateid snails from Chile was identical with the haplotype of the European invader from West India Dock, London (GenBank: EU573983) (Ponder et al. 2008), Chitose River in Japan (GenBank: AB703675) (Hamada et al. 2013), and those obtained in Lake Superior, USA (GenBank: GQ996433) and Lake Alexandrina, New Zealand (GenBank: GQ996432) (Neiman et al. 2010, personal communication).

Discussion

The morphological survey, reproductive features, and the COI gene markers data showed that the populations surveyed in central Chile belong to the highly invasive clonal snail *P. antipodarum*. Although several native hydrobioid species have been named or assigned to the genus *Potamopyrgus* Stimpson, 1865 on the South American continent (Pilsbry 1911, 1944, 1952; Doello Jurado 1916; Haas 1938, 1949, 1952; Lima and Pereira de Souza 1990), at

present all of them are allocated in different genera (Gaillard 1973; Gaillard and de Castellanos 1976; Hershler and Thompson 1992; Wesselingh 2000; Pons da Silva 2003). Thus until now, there was no evidence of the presence of the genus *Potamopyrgus* neither in Chile nor any other South American country.

In the present study, only a single haplotype was identified in the four Chilean localities, although this may be not conclusive because only four snails were sequenced in each location. In North America, Dybdahl and Drown (2011) found four genotypes of *P. antipodarum* from the whole USA. Different haplotypes of this species were also identified in Japan as a consequence of more than one colonization event (Hamada et al. 2013). At present, it is impossible to know the origin and exact time of the arrival of *P. antipodarum* to Chile considering that the



Figure 3 Adult ovoviviparous female (<5 mm) of *Potamopyrgus antipodarum* from Estero La Dehesa, Santiago, Chile. The pallial oviduct brood pouch was dissected to show several shelled juveniles.

Table 3 Number of snails collected, and size of specimens used in the present study; all specimens collected were females

Locality	Specimens observed	Shell size of the smallest specimen (length-wide)	Shell size of the largest specimen (length-wide)
Parque O'Higgins	20	3.5 × 1.7 mm	4.4 × 2.2 mm
Estero La Dehesa	15	2.8 × 1.5 mm	5.1 × 2.6 mm
Chalinga River	39	2.7 × 1.4 mm	4.2 × 1.9 mm
Estero Consuelo	24	2.5 × 1.3 mm	4.4 × 1.9 mm

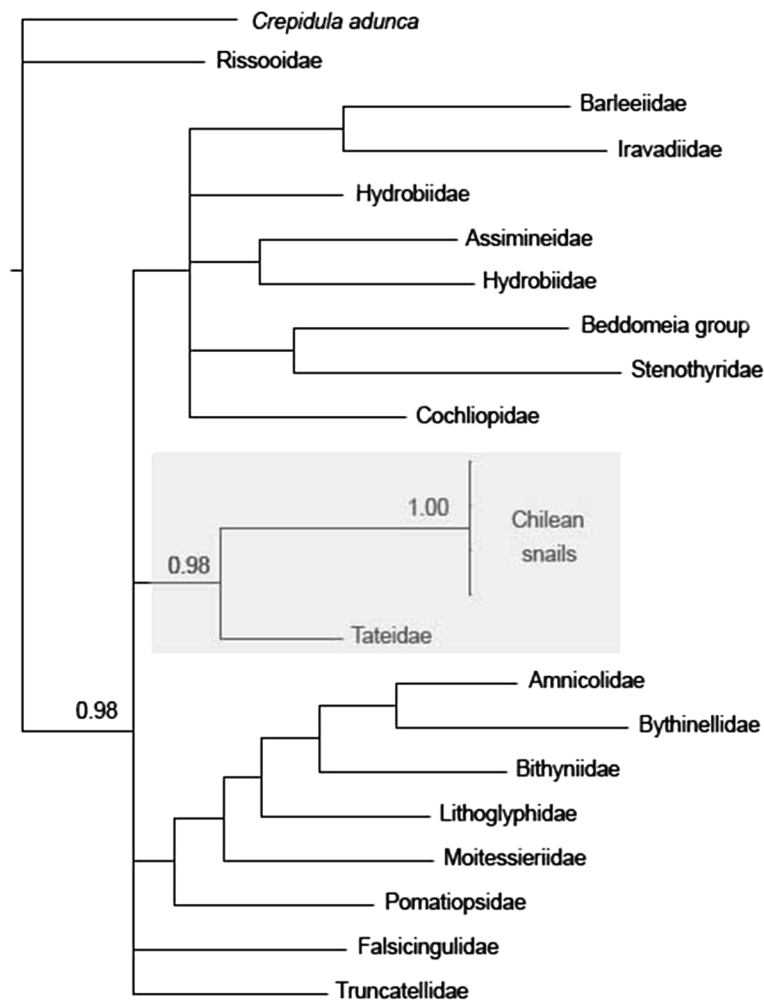


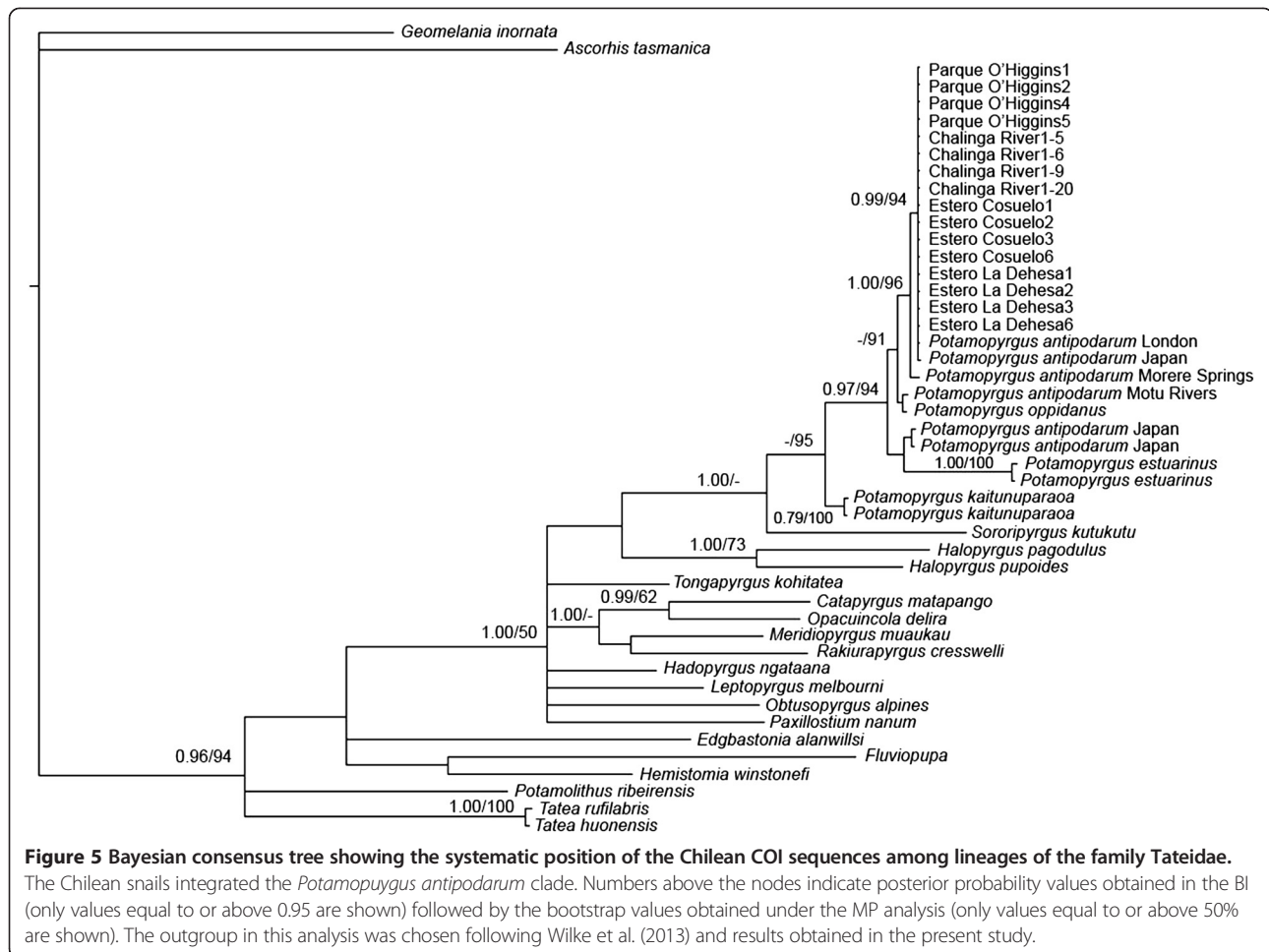
Figure 4 Bayesian consensus tree of rissooidean snails based on COI gene sequences. The phylogenetic position of the Chilean snails is shown in the gray box. The taxa represent the families (or family-level assignments) within the rissooidean (see Wilke et al. 2013). Numbers above the nodes indicate posterior probability values obtained in the BI (only values equal to or above 0.95 are shown). The outgroup in this analysis was chosen following Wilke et al. (2013).

same haplotype is found in Japan, England, New Zealand, and USA (Ponder et al. 2008; Neiman et al. 2010; Hamada et al. 2013, present study). A microsatellite analysis could reveal more informative results due to the higher mutation rates than COI gene.

It has been suggested that at high densities *P. antipodarum* may compete with native macroinvertebrates for food or space (Kerans et al. 2005) and alter the nutrient cycles, especially nitrogen and carbon (Hall et al. 2003), with significant effects on higher and lower trophic levels (Kerans et al. 2005). *Potamopyrgus antipodarum* is extremely abundant in the spring from Parque O'Higgins, where it reaches thousands of animals per square meter (unpublished data). The snails also are relatively abundant in the other localities, except in Estero La Dehesa, where in one hour of sampling using a sieve, only 15 snails were obtained. This, together with the observation of viable

breeding snails and similar size range reported in other invaded regions, suggest that the populations of these animals are well established in central Chile. It is unknown whether the species is more widespread in this country.

Ovoviviparity seems to be an important factor for successful invasions. With this type of reproductive strategy (Winterbourn 1970; Ponder 1988), *P. antipodarum* females brood embryos in a brood pouch and release from 20 to 120 free crawling juveniles (Cheng and LeClair 2011). Native *P. antipodarum* populations contain both abundant parthenogenetic females and sexual females and males at a relatively lower proportion (Winterbourn 1970). However, non-native populations mostly consist of parthenogenetic females, males being rare or absent (Gangloff 1998; Butkus et al. 2012). Thus, colonization may have occurred from the introduction of a single female (Proctor et al. 2007; Cheng and LeClair 2011;



Poirier 2013). Like *P. antipodarum*, the exotic ovoviviparous snail *Sinotaia quadrata* (Benson 1842) (Viviparidae Gray, 1847) was also introduced into South America and is now established in Argentina (Ovando and Cuezco 2012).

Potential natural vectors of *P. antipodarum* include fish, birds, water flow, and floating algae or macrophytes (Vareille-Morel 1983; Ribi 1986; Zaranko et al. 1997; Proctor et al. 2007). Regarding transport by animals, these snails can survive passage through the digestive system of fish and birds (Haynes et al. 1985; Ribi 1986). Non-natural vectors include ship ballast water, freshwater tanks, aquaculture products, aquatic ornamental plants, domestic livestock, firefighting machinery, recreational watercraft and trailers, transport of mud, and sport fishing equipment (Ribi 1986; Bowler 1991; Richards et al. 2001; Proctor et al. 2007; Ponder et al. 2008; Alonso and Castro-Diez 2008); it is unknown how the species came to Chile.

The NZ Mudsail Management Plan Working Group in USA was established in 2003 to prevent and delay the spread of the introduced *P. antipodarum* to new areas into the United States (Proctor et al. 2007). Some of the

objectives proposed were identify foci, pathways and vectors of *P. antipodarum*, develop methods of detecting new populations of this species and develop strategies to control introduced populations. In Chile, exotic freshwater snails have increased in recent times; the main route of introduction has probably been freshwater commercial aquarium trade (Jackson and Jackson 2009; Letelier et al. 2007). The procedures proposed by Proctor et al. (2007) may be implemented in Chile as a control measure against these species and *P. antipodarum*.

Conclusions

The phylogenetic analysis of COI gene supports the inclusion of the snail sequences from Parque O'Higgins, Estero La Dehesa, Estero Consuelo, and the Chalinga River in central Chile into the *Potamopyrgus antipodarum* lineage. Thus, the snails studied belong to the family Tateidae. In all locations, sexually mature females were found. Ecological studies are needed to understand the impact of this invasive species on aquatic ecosystems in Chile.

Competing interests

The author declares that he has no competing interests. The author declares that he has no financial competing interests. The author declares that he has no non-financial competing interests.

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