



## Research paper

# Distributional patterns of endemic southern South American freshwater aeglids (Crustacea: Decapoda: Anomura: Aeglididae)

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## ABSTRACT

The biogeographical and phylogenetic patterns of *Aegla* Leach, 1820 were analysed integrating track and cladistic biogeographic methods. We obtained 73 individual tracks, 10 generalised tracks and three nodes. Two taxon-area cladograms were constructed based on previous phylogenetic trees published for *Aegla* and Brooks Parsimony Analysis (BPA) was applied to the presence-absence matrices of generalised tracks (rows) vs components (columns). Four and three equally most parsimonious trees were obtained and two strict consensus cladograms, respectively. The consensus cladogram shown here has a basal separation among three areas: Argentinean-Chilean Patagonian areas, Cuyan ecoregion in central-western Argentina, and the remaining areas in Argentina, Uruguay, Bolivia and Brazil. Within the latter, north-western Argentina, south-western Bolivian and Uruguay ecoregions were nested within several southern Brazilian areas. Our results support a close relationship between the Parana dominion of the Neotropical region and the Subantarctic subregion of the Andean region, which might be related to a temperate climate prevailing in southern South America before being disrupted by cooling and aridification conditions and to geo-climatic events that occurred since the Mesozoic. The Yungas biogeographic province was also supported by the distribution of *Aegla*. Nodes were all located in southern Brazil, coinciding with the hydrological processes of headwaters and drainages that occurred due to the Serra do Mar uplift. Some species of *Aegla* previously classified as a single species might constitute species complexes.

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## 1. Introduction

The panbiogeographic approach is implemented through track analysis (Croizat 1958, 1964; Morrone 2015b). It emphasises the relevance of the spatial or geographical dimensions (places and localities) for understanding of evolutionary patterns and processes of biotic distributions developed in the past (Craw et al. 1999). This is

aimed at recognizing primary biogeographical homology, which represents a hypothesis about a common biotic history based on distributional congruence, formulated without any phylogenetic information (Morrone 2009, 2014b). Over the last decade track analysis has been used to assess diverse ranges of taxa in a wide variety of habitats (Fernandez et al. 2012; Ferretti et al. 2012, 2014; Mayén-Estrada and Aguilar-Aguilar 2012; Mercado-Salas et al. 2012; Heads 2014; del Río et al. 2015; Ramírez-Barahona 2015; Silva and Gallo 2016). This analysis consists of three basic steps: plotting collection localities for each species on maps and connecting them according to their geographical proximity with straight lines named individual tracks (IT), obtaining generalized tracks (GT) based on the significant superposition of two or more different IT, and identifying nodes in the areas where two or more GT intersect (Morrone 2015b).

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Generalised tracks are understood as ancestral biotas formerly widespread and subsequently fragmented by tectonic or climatic changes (Craw et al. 1999; Morrone 2009). Their interpretation has been controversial and is based on vicariance and/or dispersal frameworks (Morrone 2015b). Nodes represent compound or complex areas characterised by their endemism, high diversity, dynamic distributional boundaries between different biotas, disjunction, divergence of monophyletic groups, convergence and parallelism (polyphyly), ecological (e.g. altitudinal) anomalies (i.e., absence of taxa), incongruence and recombination of characters, the occurrence of specimens difficult to identify and unusual hybrids (Heads 2004). These areas may be considered as hotspots and priority areas for conservation (Álvarez Mondragón and Morrone 2004). Track analysis is a fundamental first step for other more elaborate analysis (Morrone 2015b). Cladistic biogeography uses phylogenetic hypotheses to falsify the distributional patterns described in a previous panbiogeographic study. Both analyses can be treated as complementary within an integrative approach (Morrone and Crisci 1995; Lomolino et al. 2010).

*Aegla* Leach, 1820 is the only taxon of the infraorder Anomura (Decapoda) that is entirely restricted to freshwater habitats. The family Aeglidae includes three genera, two of them from marine deposits: *Haumuriaegla* from New Zealand, and *Protaegla* from Mexico (Feldmann 1984; Feldmann et al. 1998). *Aegla* is the only extant genus of Aeglidae. These organisms are the southernmost freshwater “crabs”, being found in waterbodies of Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay (Martin and Abele 1986; Pérez-Losada et al. 2004; Fig. 1). This area possesses an amazing diversity of landscape characteristics and freshwater limnotopes. For example, the range of altitude is almost 7000 m (the peak of the Aconcagua Mountain is 6962 m a.s.l.), whereas variation in air temperature is almost 34 °C and latitudes span 30° from the Tropic of Capricorn southward. The extent of some endorheic and exorheic systems is vast in this region, e.g. the Paraná-Plata drainage basin is the second largest South American fluvial system. The lacustrine Chilean and endorheic Subandean regions are other important freshwater limnotopes of southern South America. In these sites, the species of *Aegla* have rather relatively small distributional areas restricted to one drainage basin or a few adjacent basins, showing high levels of endemism and representing an excellent group for panbiogeographic and cladistic biogeographic studies (Morrone 1996). Nonetheless, some species have wide distributions (e.g. *A. platensis* and *A. uruguayana*) and their different populations may form non-monophyletic groups, constituting cryptic species (Marchiori et al. 2014, 2015). The habitat of most species of *Aegla* is epigeous, being found in rivers, lakes and streams up to ~4000 m altitude in north-western Argentinean and Chilean cordillera, but some of them are found in caves of Brazil (Fernandes et al. 2013) and up to 320 m depth in Chilean rivers and lakes (Jara 1977; Bond-Buckup and Buckup 1994). In these environments, some troglitic (e.g. *A. cavernicola* and *A. leptochela*) or trogliphilic species (e.g. *A. schmitti* and *A. marginata*) are highly endemic (Fernandes et al. 2013). *Aegla* is the most severely threatened taxon of all South American freshwater decapod crustaceans, with 70% of the species under some level of threat and 20% critically endangered (Santos et al. 2017). This is associated to their high endemism, restricted area of occupancy and severely fragmented spatial distribution with reproductively isolated subpopulations (Bueno et al. 2016). Besides, the sources of threats to conservation of aeglids derive mainly from habitat degradation (Bueno et al. 2016; Santos et al. 2017).

The origin, distribution and diversification of *Aegla* have been discussed in some previous studies. About its origin, two alternative hypotheses have postulated either an entrance through the Atlantic coast of South America (Schmitt 1942; Ringuet 1949;

Morrone and Lopretto 1994) or a Chilean ingression (Ortmann 1902; Feldmann 1984; Pérez-Losada et al. 2004). Currently, the best supported hypothesis about the entrance of *Aegla* ancestors in South America is the Pacific-origin, based on fossil (Feldmann 1984) and molecular evidence (Pérez-Losada et al. 2004). Pérez-Losada et al. (2004) at a global scale attributed the current geographic distributional patterns of *Aegla* to vicariance processes linked to the orogenic phases that occurred during the formation of the Andean chain. On the other hand, Oyanedel et al. (2011) at a local scale associated the current geographic distributional patterns of *Aegla* to dispersal movements that took place during the extension/coalescence of fluvial drainages and to the existence of multiple island glacial refuges. Collins et al. (2011) at a regional scale postulated that the current distribution of *Aegla* may have been influenced by modifications in the land geography and the formation of continental aquatic environments in southern South America. Other authors have related the current distribution of *Aegla* to local environmental variables at regional and macroecological levels (Miserendino 2001; Tumini et al. 2016).

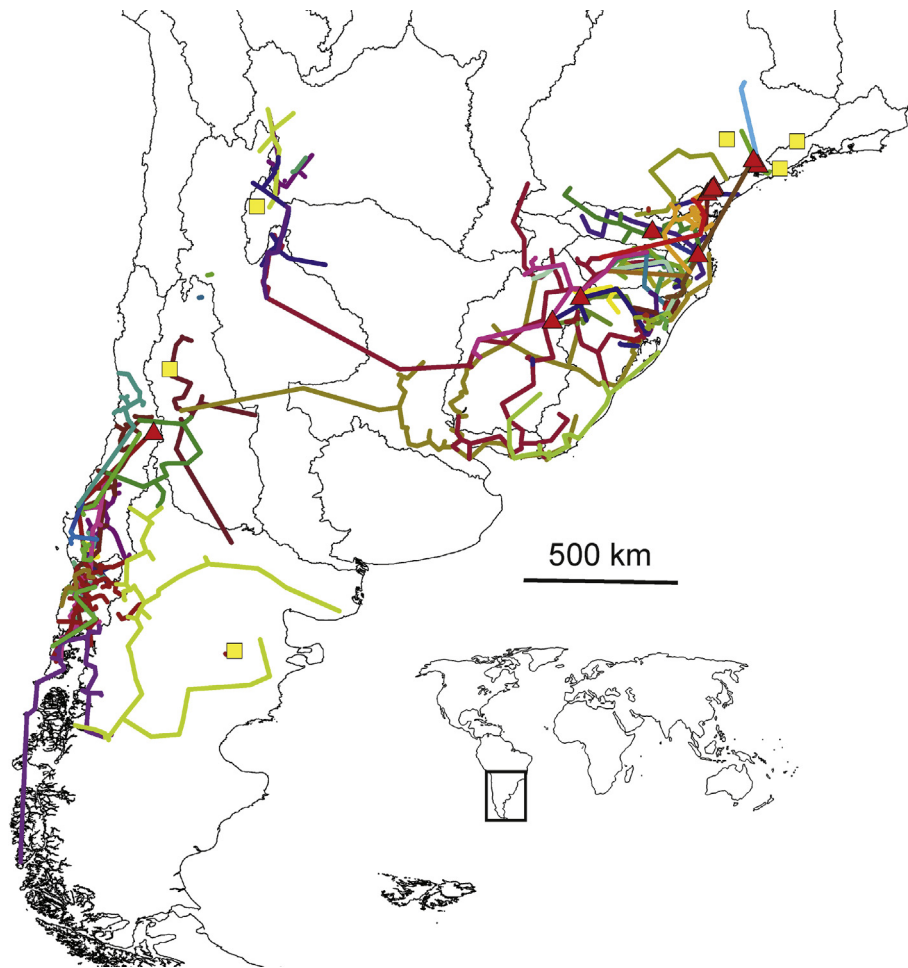
There is a paucity of data on the distribution of *Aegla* in relation to track and cladistic biogeographic analyses. Besides, new species of *Aegla* have been described recently and several studies about morphology, evolution, phylogeny, conservation, ecology and physiology, among others, have been done (see Appendix A and references cited herein). Here, we analyse the distribution of *Aegla* in southern South America to address: (i) that the relationship between its biogeographical and phylogenetic features can be clarified by the application of track and cladistic biogeographic analyses and (ii) that both widespread species and species complexes of *Aegla* are of more concern than previously acknowledged.

## 2. Material and methods

### 2.1. Study area and data sources

The study area comprises aquatic systems of a vast region of southern South America, which extends approximately from 20° to 50°S (3500 km in a straight line distance). This area corresponds to the distributional range of all the species of *Aegla* known to the present (Fig. 1).

The updated number of the formally recognised species and subspecies of *Aegla* is 85, based on recent descriptions (Santos et al. 2009, 2010, 2012, 2013, 2014, 2015; Bond-Buckup et al. 2010a, 2010b; Moraes et al. 2016, 2017; Bueno et al. 2017). Moreover, there are 10 species from Argentina and Brazil assumed either as new species or putative new species. The assumed new Brazilian species previously published but not described yet are three: *Aegla* spp. n. 2–4 (Fernandes et al. 2013). Besides, the assumed new Argentinean species previously published but not described yet are two: *Aegla* spp. n. 5–6 (Barber et al. 2012). On the other hand, the putative new species include the Brazilian *Aegla* sp. n. 1 (Moraes et al. 2016) and four Argentinean *Aegla* spp. n. 7–10 (Tumini et al., in preparation). The diagnostic characters of the population considered as putative new species did not match with any currently described species. The occurrence of all the species of *Aegla* was obtained from 1172 sites. In Brazil we had registered 58 species in 412 localities (Appendix B.1), in Argentina 20 species in 237 localities (Appendix B.2), in Chile 19 species in 389 localities (Appendix B.3), in Uruguay five species in 127 localities (Appendix B.4), in Bolivia two species in four localities (Appendix B.5) and in Paraguay a single species in three localities (Appendix B.6). Some species were shared among the different countries. Specimens of the nominal and putative new species of Argentina were collected in rivers and streams during several collecting campaigns carried out from 2001 to 2014 and deposited in the Crustacean Collection of the Laboratorio de



**Fig. 1.** Map showing the study area for *Aegla* in southern South America, the freshwater ecoregions of [Abell et al. \(2008\)](#), and the individual tracks constructed for the species with two or more occurrence data. The individual data points of the species with an exclusive locality of occurrence are also included (triangles: species with a single sample site that supported a generalised track; and squares: species with a single sample site that did not support any generalised track). The inset shows the location of the study area in a world map.

Macrocrustáceos of the Instituto Nacional de Limnología (INALI-CONICET-UNL), Santa Fe, Argentina. The identification key of [Bond-Buckup and Buckup \(1994\)](#) and the diagnosis of [Bond-Buckup et al. \(2010\)](#) were used to identify the species. Besides, we based the taxonomic delimitation of the Argentinean populations on morphogeometric and phylogeographic analyses not published yet (Tumini et al., in preparation; Loretán et al., in preparation). These distributional data were supplemented with information from Argentinean (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; Museo de La Plata, La Plata; Museo Provincial de Ciencias Naturales “Florentino Ameghino”, Santa Fe; Museo Provincial de Ciencias Naturales y Antropología “Prof. Antonio Serrano”, Paraná; and Crustacean Collection of the Instituto Miguel Lillo, Tucumán), Brazilian (Crustacean Laboratory of the Universidade Federal do Rio Grande do Sul, UFRGS, Porto Alegre) and German (Senckenberg Museum, Frankfurt) museum collections. Moreover, we made a thorough literature review for the whole Aegliidae family in its entire distributional range ([Appendix A](#)). For field data, values for geographic coordinates were recorded at each site using digital equipment (Garmin Dakota 20, Kansas City, Missouri). For non-georeferenced data obtained from museums or literature, localities for each species were based on a combination of the information sources and latitude and longitude coordinates were obtained from Google Earth version 7.1.5.1557.

## 2.2. Data analysis

### 2.2.1. Track analysis

Initially we plotted the collection localities using ARCGIS 10.1. Then, we draw the IT manually for each species with two or more occurrence data applying the minimum spanning tree method ([Craw et al. 1999](#); [Morrone 2009, 2015b](#)). It consists in connecting by a straight line two occurrence localities by choosing the nearest pair; then, the nearest locality to any of them is united, and so on. Thus, the sum of all the segments connecting the localities is minimal in the resulting IT ([Morrone 2009](#)). This method has been considered as the first formalisation to construct tracks ([Page 1987](#); [Craw 1988](#); [Morrone 2004](#)) and it has been the most widely applied ([Morrone 2015b](#)). Individual tracks were then superimposed manually and, when they showed substantial topological agreement, the resulting summary lines were considered generalised tracks. We assumed that a species supports a given GT even if a small fraction of its localities (<30%) fell outside the area defined by that track. Whenever the IT of a species fell in a higher fraction outside the area defined by a given GT, we considered this species as part of such generalised track if this fraction did not support any other GT (i.e., did not superimpose with another IT). Widespread species were not considered to be part of a GT when a great fraction of their localities (>70%) fell outside such generalised track. These

species contributed to the GT (although they did not define them), thus they were not excluded from the analysis. Finally, we identified the nodes where areas were part of two or more GT.

Despite the genetic, geometric morphometric and phylogeographic evidence for some cryptic species of *Aegla* (Marchiori et al. 2014, 2015; Crivellaro et al. 2017; Zimmermann et al. 2018), we treat them as single species as they have not been taxonomically recognised as more than one species up to now. The species of *Aegla* are generally highly endemic (Morrone 1996), so we assume that widespread species which contributed to more than one GT would be more likely to constitute species complexes (cryptic/ring/sister/flock species: Knowlton 1986; Fegan and Prior 2005; Giri and José de Paggi 2006; Bickford et al. 2007; Silva de Oliveira et al. 2012; Jörger and Schrödl 2013; Lecointre et al. 2013; Alcaide et al. 2014; Davis et al. 2016).

As biogeographical units, we used the freshwater ecoregions of Abell et al. (2008) corresponding to the study area in southern South America (Fig. 1). Their ecoregion maps represent a useful tool for large-scale conservation strategies and for providing a global-scale information base for increasing freshwater biogeographic knowledge. These ecoregions were defined on the basis of freshwater fish biogeography and broad-scale ecological processes, and have played an important role in setting conservation priorities of *Aegla* in southern South America (Pérez-Losada et al. 2009).

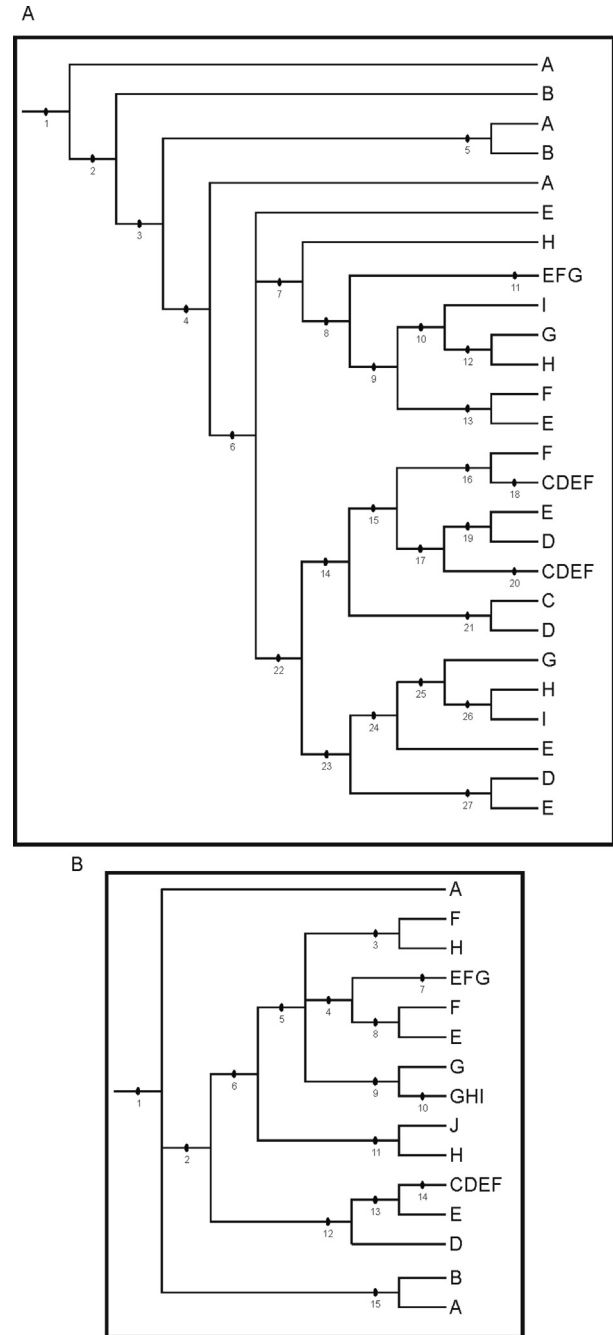
### 2.2.2. Cladistic biogeographic analysis

After the track analysis, we undertook a cladistic biogeographic analysis. Pérez-Losada et al. (2004) combined diverse methods based on heuristic approaches to conduct a phylogenetic analysis sequencing one nuclear and four mitochondrial genes of 64 species of *Aegla*. They obtained two similar consensus trees, each with five clades, namely A to E. Afterwards, Moraes et al. (2016) analysed a partial fragment of a mitochondrial gen of 34 species of *Aegla*, including six disjunctive populations of *A. paulensis* form a species complex (i.e., *A. japi*, *A. jaragua*, *A. jundiai*, *A. lancinhas*, *A. rosanae* and *A. vanini*). They obtained a consensus tree with these seven species grouped jointly to the species that composed the clade C previously proposed by Pérez-Losada et al. (2004). We based our cladistic biogeographic analysis in the Bayesian and maximum likelihood Aeglidae phylogenetic tree published by Pérez-Losada et al. (2004, 770) and the phylogenetic tree of Moraes et al. (2016) to obtain two taxon-area cladograms respectively, adding to the terminal species the GT that these taxa constituted in the panbiogeographic approach that we have performed here (Appendix C). The GT in each taxon-area cladogram were coded as characters, while each node was considered as hypothetical ancestor and classified as a component (Fig. 2A and B). Based on them, we made two presence-absence matrices of GT (rows) vs cladogram components (columns). If a given component was present in a clade, it was coded as “1” (Table 1A and B). We applied a Brooks Parsimony Analysis (BPA: Wiley 1988; Goyenechea et al. 2001). BPA uses data from phylogenetic hypotheses in a parsimony analysis to reconstruct either biogeographic relationships of areas or co-evolutionary relationships among species inhabiting the same area. We analysed the matrices with TNT (Goloboff et al. 2008) to obtain the most parsimonious trees and the strict consensus cladograms, respectively.

## 3. Results

### 3.1. Track analysis

We obtained 74 individual tracks, while 19 species with only one occurrence locality could not be represented by an IT: *Aegla ringueleti* and *Aegla* spp. n. 5 and 7 from Argentina; *A. charon*,



**Fig. 2.** Area cladograms obtained based on the phylogenetic trees published by: A. Pérez-Losada et al. (2004, 770); and B. Moraes et al. (2016). Components are numbered from 1 to 27 and from 1 to 15, respectively. Generalised tracks are represented by the letters A to J.

*A. georginae*, *A. japi*, *A. jaragua*, *A. leptochela*, *A. ludwigi*, *A. meloi*, *A. microphthalma*, *A. perobae*, *A. pomerana*, *A. rosanae*, *A. vanini* and *Aegla* spp. n. 2–4 from Brazil; and *A. intermedia* from Chile (Fig. 1). The overlap of 63 of these IT plus the individual records of 13 species allowed the identification of 10 GT which spanned over 15 ecoregions (Fig. 3). No generalised tracks were recovered for Paraguay and central and north-eastern Argentina. The GT and the biogeographical units (ecoregions) that correspond to each one are briefly characterised as follows:

GTA. Argentina–Chile Patagonia track. It extends along the South Andean Pacific Slopes, Patagonia and Valdivian Lakes



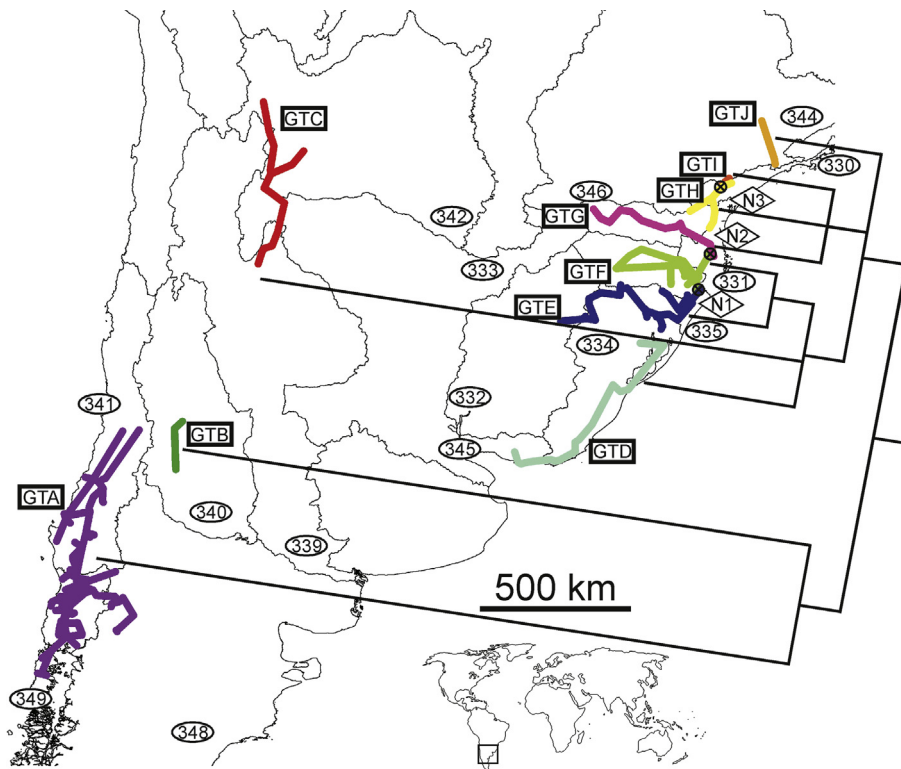
**Table 1**

Presence-absence matrices based on the generalised tracks included in each component (basal node of a clade) of the area cladograms obtained from the phylogenetic trees of: A. Pérez-Losada et al. (2004, 770); and B. Moraes et al. (2016). A hypothetical ancestral area coded by the absence of any components (all zeros) was included to root the cladograms.

A.																											
Generalised tracks	Components																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
root	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C	1	1	1	1	0	1	0	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0
D	1	1	1	1	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1
E	1	1	1	1	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1
F	1	1	1	1	0	1	1	1	1	0	1	0	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0
G	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0
H	1	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0
I	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0
J	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0

B.															
Generalised tracks	Components														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
root	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
B	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0
D	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0
E	1	1	0	1	1	1	1	1	0	0	0	1	1	1	0
F	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0
G	1	1	0	1	1	1	1	0	1	1	0	0	0	0	0
H	1	1	1	0	1	1	0	0	1	1	1	0	0	0	0
I	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0
J	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0



**Fig. 3.** Map showing the ten generalised tracks (GTA-J) and three nodes (N1-3) in the ecoregions, superimposed to the area cladogram (represented by branches) obtained through the cladistic biogeographic analysis. Numbers correspond to each ecoregion considered in the study: 330) Ribeira de Iguape, 331) Southeastern Mata Atlantica, 332) Lower Uruguay, 333) Upper Uruguay, 334) Laguna dos Patos, 335) Tramandai Mampituba, 339) Mar Chiquita Salinas Grandes, 340) Cuyan Desaguadero, 341) South Andean Pacific Slopes, 342) Chaco, 344) Upper Parana, 345) Lower Parana, 346) Iguassu, 348) Patagonia and 349) Valdivian Lakes. The inset shows the location of the study area in a world map.

ecoregions. It is supported by 19 species: *A. abtao*, *A. alacalufi*, *A. araucaniensis*, *A. bahamondei*, *A. cholchol*, *A. concepcionensis*, *A. denticulata*, *A. expansa*, *A. hueicollensis*, *A. intermedia*, *A. laevis*, *A. manni*, *A. neuquensis*, *A. occidentalis*, *A. papudo*, *A. pewenchaie*, *A. riolimayana*, *A. rostrata* and *A. spectabilis*.

GTB. Cuyan track. It extends along the Cuyan Desaguadero ecoregion. It is supported by two species: *A. affinis* and *A. scamosa*.

GTC. North-western Argentina - south-western Bolivia track. It extends along the Mar Chiquita Salinas Grandes, Chaco and Lower Parana ecoregions. It is supported by six species: *A. humahuaca*, *A. intercalata*, *A. jujuyana*, *A. saltensis*, *A. sanlorenzo* and *A. septentrionalis*.

GTD. Uruguay–Brazil track. It extends along the Laguna dos Patos and Lower Parana ecoregions. It is supported by four species: *A. prado*, *A. uruguayana*, *A. obstipa* and *A. violacea*.

GTE. Rio Grande track. It extends along the Southeastern Mata Atlantica, Lower Uruguay, Upper Uruguay, Laguna dos Patos and Tramandai Mampituba ecoregions. It is supported by 16 species: *A. franciscana*, *A. georginae*, *A. grisella*, *A. inconspicua*, *A. inermis*, *A. itacolomiensis*, *A. leptodactyla*, *A. ligulata*, *A. longirostri*, *A. ludwigi*, *A. manuinflata*, *A. plana*, *A. renana*, *A. rossiana*, *A. serrana* and *A. spinipalma*.

GTF. Santa Catarina track. It extends along the Southeastern Mata Atlantica and Upper Uruguay ecoregions. It is supported by seven species: *A. brevipalma*, *A. jarai*, *A. leachi*, *A. oblata*, *A. odebrectii*, *A. pomerana* and *A. spinosa*.

GTG. Santa Catarina - Paraná track. It extends along the South-eastern Mata Atlantica and Iguassu ecoregions. It is supported by four species: *A. meloi*, *A. muelleri*, *A. parana* and *A. parva*.

GTH. Paraná - São Paulo track. It extends along the Ribeira de Iguape, Southeastern Mata Atlantica, Upper Parana and Iguassu ecoregions. It is supported by five species: *A. cavernicola*, *A. lancinhas*, *A. marginata*, *A. schmitti* and *A. strinatii*.

GTI. South São Paulo track. It extends along the Ribeira de Iguape ecoregion. It is supported by seven species: *A. charon*, *A. leptochela*, *A. microphthalmia*, *A. quilombola* and *Aegla* spp. n. 2–4. This GT was based on the IT of *A. quilombola* jointly to six individual points located very close geographically. We have joined all these species in the same GT assuming that in the near future further localities of occurrence may be identified for the species with an exclusive individual point of occurrence.

GTJ. North São Paulo track. It extends along the Upper Parana ecoregion. It is supported by six species: *A. franca*, *A. japi*, *A. jaragua*, *A. jundiai*, *A. paulensis* and *Aegla* sp. n. 1.

The overlap of these GT allowed identifying three nodes, all located in southeastern Brazil (Fig. 3). Node N1, in the limits of the Rio Grande do Sul and Santa Catarina states, was defined by the generalised tracks Rio Grande (GTE) and Santa Catarina (GTF). Node N2, in the Santa Catarina state, was defined by the generalised tracks Santa Catarina (GTF) and Santa Catarina - Paraná (GTG). Node N3, in the São Paulo state, was defined by the generalised tracks Paraná - São Paulo (GTH) and South São Paulo (GTI).

The remaining species of *Aegla* which did not conform any GT were classified into the following distributional patterns:

Widespread species distributed in several generalised tracks. *Aegla platensis*, distributed in northern Argentina, Uruguay, southern Brazil and southeastern Paraguay, contributed to the generalised tracks GTC, GTD, GTE and GTF; and *A. camargoii*, from southeastern Brazil, contributed to the generalised tracks GTE, GTF and GTG.

Widespread species that did not support any GT. *Aegla singularis* is distributed in north-eastern Argentina, north-western Uruguay and southern Brazil. Its individual track contributes to the generalised track GTF, but did not define it because the extension of its IT was very wide, reaching other ecoregions far from the core of the superimposed IT that defined the generalised track GTF.

Species with individual tracks that did not superimpose among them, not even with any of the other species analysed in this study. In Argentina, *Aegla* sp. n. 6 in Patagonia, *Aegla* spp. n. 8–9 in north-western and, *Aegla* sp. n. 10 in north-eastern. In Brazil, *Aegla castro*, *A. lata* and *A. loyolai*. In central-northern Uruguay, *A. carinata*.

Species with an exclusive occurrence locality which did not support any GT. *Aegla ringueleti* in north-western Argentina; *Aegla* sp. n. 5 and *Aegla* sp. n. 7 in Patagonia and central-western Argentina, respectively; and *Aegla perobae*, *A. rosanae* and *A. vanini* distributed in southeastern Brazil.

### 3.2. Cladistic biogeographic analysis

The area cladograms obtained from the phylogenetic trees of Pérez-Losada et al. (2004, 770) and Moraes et al. (2016) had 27 and 15 components, respectively (i.e., nodes of each clade; Fig. 2A and B). While on the basis of the presence-absence matrices of GT vs cladogram components (Table 1A and B), four and three equally most parsimonious trees were obtained respectively and two strict consensus cladograms (one for each analysis). Notwithstanding both consensus cladograms showed the same relationships, we have chosen the one from Moraes et al. (2016) as it includes the GTJ as a sister area of some Argentinean, Uruguayan, Bolivian and Brazilian areas. This generalised track was supported by six species as follows. One species previously not found in its restricted area of occurrence (i.e., *A. franca*), three new species described by Moraes et al. (2016; i.e., *A. japi*, *A. jaragua* and *A. jundiai*), the redescribed and regeoreferenced Brazilian “crab” *A. paulensis* and one putative new species proposed by these authors (i.e., *Aegla* sp. n. 1). With the exception of *A. paulensis*, the remaining five species that supported the GTJ were not included in the phylogenetic analysis of Pérez-Losada et al. (2004). Moreover, the occurrence localities of this species were uploaded and redefined by Moraes et al. (2016), improving the information available. We show this consensus cladogram herein (Fig. 3). It has a basal separation among three areas: Argentinean-Chilean Patagonia (GTA), Cuyan in central-western Argentina (GTB), and the remaining areas in Argentina, Uruguay, Bolivia and Brazil (GTC-J). The species that shaped the generalised tracks GTA and GTB were linked to the remaining species that were part of the others GT. First, they were related with the Upper Parana ecoregion in the northernmost zone of southern Brazil (GTJ). Then, the remaining Brazilian species that were further north were grouped together (GTG-GTI), whereas the Uruguayan and the southernmost Brazilian species (GTD) were related to the north-western Argentinean - south-western Bolivian species (GTC). Finally, the remaining Brazilian species were grouped together (GTE-GTF; Fig. 3).

## 4. Discussion

Using a track analysis, we found that the Patagonian and central-western Argentinean species of *Aegla* were related in two different ways to the Patagonian Chilean species and to the southern Brazilian species, supporting the separation of the Neotropical and Andean regions. On the other hand, the north-western Argentinean - south-western Bolivian species of *Aegla* were related to the Uruguayan - southernmost Brazilian species. Additionally, the nodes found in southern Brazil define this area as a site of biogeographic convergence and great conservation concern of *Aegla*. Moreover, some species which contributed to more than one GT probably constitute species complexes.

Heads (2004) postulated that the relevance of a track analysis lies on the identification of nodes, not on the delimitation or verification of any area; however, we found support to the separation of the Neotropical and Andean regions described previously for South

America (Morrone 2014a, 2015a). These relationships are coincident with the results obtained by Pérez-Losada et al. (2004). Their phylogenetic analysis showed that *Aegla* comprises two clades: a basal western clade formed by southern Argentinean and Chilean species; and another more recent central-eastern clade which includes species from northern Argentina, Uruguay and Brazil. Besides, we find an arrangement for the species of *Aegla* in north-western Argentina - south-western Bolivia that supports the Yungas biogeographic province previously defined by Morrone (2014a).

The observed distributional pattern of *Aegla* in the Neotropical and Andean regions can be compared with the modern distribution of the conifer genus *Araucaria* in southern South America and with the climatic phenomena that shaped it in the Triassic. In this regard, Ledru and Stevenson (2012) postulated that the phases of expansion and retraction of *Araucaria* in southern South America provide a good bio-indicator for detecting changes in freshwater systems. They exposed that in Brazil and Chile, the location of the current *Araucaria* forest is defined by the intensity and frequency of a drastic drop in temperature observed between 85000 and 60000 years ago, characterised by ice expansion and lowering of sea level by 70 m.

Several authors have discussed the relationship between the Subantarctic subregion of the Andean region, comprising the Juan Fernández Islands in the Pacific Ocean, central-southern Chile and Argentina and the Falkland-Malvinas Islands; and the Parana dominion of the Neotropical region, placed in north-eastern Argentina, southeastern Brazil and eastern Paraguay (Kuschel 1960; Maury et al. 1996; Morrone 2006). The association between them could be related to a temperate climate prevailing in southern South America during the Paleogene. These conditions allowed the existence of a continuous cloud forest extending further south than today, stretching to the northern part of the Antarctic Peninsula (Morrone and Lopretto 1994). This area was disrupted by cooling and aridification conditions that began in the Oligocene and Miocene. At those times, ancestral Aeglidae radiated into aquatic habitats (Feldmann 1984). Thereafter, they could move (dispersal) or became restricted (vicariance) to the high altitudes where some species are currently found; in fact, *Aegla* is the dominant decapod at the highest altitudes in southern South America (Tumini et al. 2016). The process of aeglid species differentiation began in those original populations and the current high degree of endemism is a result of the loss of connectivity of the environments (Collins et al. 2011). The relationship between the Subantarctic and Parana subregions is also supported by taxa currently distributed disjunctively in these areas: the weevil families Belidae (Vanin 1976) and Nemomychidae (Kuschel and May 1997) and also by an opilionid species (Maury et al. 1996).

The disjunct distribution of *Aegla* supposes an uncertain origin for the group and there are alternative hypotheses in relation to their ingressions into southern South America, which postulate either an Atlantic (Schmitt 1942; Ringuelet 1949; Morrone and Lopretto 1994) or a Pacific ingression (Feldmann 1984; Ortmann 1902; Pérez-Losada et al. 2004). Schmitt (1942) explained that there were two general forms of rostra developed in the species of *Aegla*, which define distinct and distinguishable geographic distributions linked to an Atlantic or a Pacific type. Feldmann (1986) considered this classification as probably not important enough to emphasise; however, he classified the shape of the rostrum of *Haumuriaegla glaessneri*, the earliest known representative of the Aeglidae, as Atlantic in form contrasting his previous Pacific origin assumption for the group (Feldmann 1984).

Panbiogeography assumes that vicariance and range expansion are the primary biogeographical processes needed to explain general biotic distributions (Morrone 2015b) and nodes may represent areas of biogeographic convergence (Heads 2004). On the other

hand, under a dispersalist approach nodes may represent centres of origin or barriers to chance dispersal with organisms able to randomly cross barriers and occupy new areas where they adapt and evolve into new species (Morrone 2015b). Besides, Hummer and Hancock (2015) considered that the centre of origin of a group should correspond to the area of greatest richness. As biotic history is reticulate (Brooks 2004), we should not reduce our explanations exclusively to dispersal or vicariance, but integrate both processes into a single model that allows us to understand the evolution of *Aegla* distributions. Incorporating the dating of the lineages would be very useful to achieve the identification of cenocrons, namely biotic subsets within a biota by their common biotic origin and evolutionary history (Morrone 2009). Fossil data may also be used (Morrone 2009) to allow us to refine hypotheses on dispersal and vicariance and to distinguish cases of pseudo-congruence (Donoghue and Moore 2003). In the absence of a complete dated phylogenetic hypothesis, we think that the Atlantic or Pacific origin of *Aegla* remains as an open question.

Pérez-Losada et al. (2009) assessed the distribution and genetic diversity of *Aegla* with conservation purposes. They identified the ecoregions Laguna dos Patos Basin, Southeastern Mata Atlantica (southeastern Brazil), South Andean Pacific Slopes (central Chile), Valdivian Lakes (southern Chile) and Lower Parana (northern Argentina and southern Uruguay–Paraguay) as priority areas for conservation. These areas were also relevant in our study, as we obtained GT in all of them and nodes were found in the Southeastern Mata Atlantica ecoregion. We did not find GT or nodes in Paraguay, which could be probably due to the low number of geographical records available there. Coinciding with the location of the three nodes identified in our study, Pérez-Losada et al. (2009) found that southern Brazil supports the highest indices of diversity and endemism of *Aegla*. The complexity of this region can be explained by the capture and breakup of headwaters between drainages that occurred due to the final uplift of the Serra do Mar. Crivellaro et al. (2017) suggest that fluvial geomorphology has an important role in shaping patterns of *Aegla* species richness. In agreement with the assumptions of Pérez-Losada et al. (2009), we believe that these events modified the upper course of the eastern tributaries of the Paraná and Uruguay rivers in the Paleocene and the short intermountain rivers flowing eastward where *Aegla* occurred, contributing to their diversification (Santos et al. 2012, 2013 2014). In this sense, the axis formed by the rivers Paraguay, Paraná and Uruguay might have been the main dispersal corridor from where aeglids from the Amazon and Atlantic forests invaded southern continental systems since the upper Miocene (Collins et al. 2011). Moreover, several geo-climatic events affected in different ways and degrees the Neotropical region since the Mesozoic (e.g. continental drift between South America and Africa, uplift of the Andes mountains, climate changes, marine incursions, megadome uplifts, and rifting). These phenomena marked changes in the Amazon, Magdalena, La Plata and Orinoco basin flows, as well as the paleo-drainages of smaller rivers of the eastern margin of the South America Platform (Potter 1997; Ribeiro 2006), consequently influencing *Aegla* distributional patterns (Collins et al. 2011).

Besides the history-driven distributional pattern hypothesis, there are assumptions based on relevant environmental factors. In this regard, Miserendino (2001) showed at a regional level that the local distribution of *A. neuquensis* was affected by environmental variables of Andean Patagonian rivers and streams. In addition, Tumini et al. (2016) evidenced at a macroecological level the influence of several environmental factors as determinants of the current macro-distribution of *Aegla* in Argentina.

As the species of *Aegla* are generally highly endemic (Morrone 1996), we assume that widespread species and those which

contribute to more than one GT would be more likely to constitute species complexes (cryptic/ring/sister/flock species), suggesting a non-monophyletic origin for these taxa. This is based on the statement that among the non-morphological/genetic criteria used to define species in complexes, the distributional patterns of taxa are included (Knowlton 1986) and they are characterised for being limited or restricted (Bickford et al. 2007; Davis et al. 2016). This is particularly important for groups with poor dispersal abilities (Jörger and Schrödl 2013), as aeglids are (Crivellaro et al. 2017).

The monophyletic origin of some species of *Aegla* has been controversial. Pérez-Losada et al. (2004) postulated, based on a phylogenetic analysis that populations of *A. cholchol*, *A. franciscana*, *A. jarai*, *A. marginata*, *A. parana* and *A. platensis* did not form exclusive groups and qualified as different species. Further, Zimmermann et al. (2018) assessed through a phylogeographic analysis, genetic diversity in populations of *A. platensis* from Argentina and Brazil. Moraes et al. (2017) based their study on morphological data to confirm a paraphyletic relationship between populations previously all known as *A. marginata* and described a new species. Giri and Collins (2014) observed a clinal pattern throughout the distribution of *A. uruguayana*, which could be attributed to genetic drift. Marchiori et al. (2014, 2015), based on genetic divergences and differentiation in carapace shape, suggested that *A. longirostri* and *A. platensis* may represent cryptic species. Even Crivellaro et al. (2017) showed through phylogenetic and phylogeographic analyses that *A. longirostri* represents a complex of cryptic species. Moraes et al. (2016) used morphological and molecular data to show that six disjunct populations of *A. paulensis* form a species complex.

In our study, *A. cholchol* in Chile supported GTA, whereas in Brazil *A. franciscana* and *A. longirostri* supported GTE and *A. jarai* the GTF. The occurrence data points of the populations of these species showed a very tight distribution in relation to each corresponding GT, supporting their classification as each mentioned taxon. *Aegla marginata* and *A. parana* in Brazil supported GTH and GTG, respectively, showing most of their populations a very tight distribution in relation to each GT. However, three occurrence localities of these species were far from their distributional core and did not fit to each GT. These localities correspond to: a record of *A. marginata* at Chapecó in south-western Santa Catarina state (Boos et al. 2012) located 400 km approx. in a straight line distance south-western from the southernmost population cited for the species (north-eastern Santa Catarina state); and two records of *A. parana* at Quatro Pontes, western Paraná state (Bond-Buckup and Buckup 1994), located 156 km approx. in a straight line distance north-western from the westernmost population (south-western Paraná state). These far localities could be indicating species complexes. Assigning the species level to these populations merits further exploration. *Aegla platensis* and *A. uruguayana* showed the widest distributional areas. *Aegla platensis* showed a widespread distribution in northern Argentina, Uruguay, southern Brazil and southeastern Paraguay, belonging to several tracks (GTC, GTD, GTE and GTF). This could be suggesting support to the assertion of previous studies as a species complex. On the other hand, *A. uruguayana* shows a widespread distribution in north-eastern, central and central-western Argentina, southern and northern Uruguay and southern Brazil. This species supports the single track GTD since its distribution overlaps throughout the IT of *A. prado* at eastern Uruguay–southeastern Brazil. However, most part of the IT segments of *A. uruguayana* were not superimposed with the IT segments of *A. prado*, not even with any other IT of *Aegla*. This supports the idea that *A. uruguayana* may probably be a species complex, which warrants further investigation.

*Aegla camargoi* in southern Brazil and *A. singularis* in north-eastern Argentina, northern Uruguay and southern Brazil have

not been classified as species complexes by previous studies; however, *A. camargoi* contributes to GTE, GTF and GTG, whereas *A. singularis* contributes to GTF. Nevertheless, the last species did not define the GTF as most of the segments of its IT reach other ecoregions far from the core of this GT. Although these observations may contribute to classify the species as part of a species complex, the diversity among populations merits further exploration through genetic, morphological and/or natural history analyses.

Most species of *Aegla* have epigeal habits being found in lakes, streams and rivers (Bond-Buckup and Buckup 1994). However, there are seven species which are obligate cave-dwelling species (troglitic) and other two species that are facultative (trogliphilic). Six of the seven troglitic species (i.e., *A. charon*, *A. leptochela*, *A. microphthalmia* and *Aegla* spp. n. 2–4) supported the GTI. The remaining troglitic species, *A. cavernicola*, and one trogliphilic species, *A. strinatii*, supported the GTH. All these species are endemic to the Alto Ribeira located in the Ribeira do Iguape Hydrographic Basin, southeastern Brazil (Rocha et al. 2010; Fernandes et al. 2013; Bueno et al. 2017). In these environments, two additional trogliphilic species (*A. marginata* and *A. schmitti*) were found in sympatry with some of the seven troglitic species. Fernandes et al. (2013) explained that individuals of these two species may transit freely between the surface and cave environments and are able to establish self-sustained populations in both habitats. The same applies to the trogliphilic populations of *A. rostrata* found in caves ranging from 0.6 to 320 m depth in southern Chilean rivers and lakes (Jara 1977), which supported the GTA. Fernandes et al. (2013) affirmed that southeastern Brazilian troglitic species are highly endemic and have allopatric distribution as their occurrence localities are restricted exclusively to each type locality. In this regard, Bueno et al. (2017) characterised the distributional pattern of the stygobitic *A. charon* as highly endemic, since their known area of occupancy is limited to subterranean habitat of the type locality and no other species of aeglid was found inhabiting the same cave. Although subterranean dispersal would be limited by underground stratigraphic barriers and the low vagility of juveniles, Fernandes et al. (2013) expected that some of the troglitic species could indeed migrate through subterranean routes. Indeed, the troglitic species *A. cavernicola* supports this assumption, as it has been recorded at two sites (160 km in a straight line distance away) and could be represented by an IT in our study. Complementing, Bueno et al. (2010) even considered that there is still great potential for discovering new species and new populations of the known species inhabiting yet unexplored epigeal and subterranean habitats in the southeastern Brazilian Alto Ribeira. These assumptions justify the grouping we did for the seven troglitic species in the same GT (South São Paulo track - GTI).

## 5. Conclusions

Notwithstanding the panbiogeographic approach has had critiques regarding its effectiveness (Heads 2014; Morrone 2015b), our findings suggest that it may represent a useful tool for detecting general patterns of dispersal-vicariance and help identifying areas for biodiversity conservation (nodes). Our analysis contributes to widen the knowledge of *Aegla* as a unique group among decapod Crustacea, allowing a better understanding about its distributional patterns and biogeographic history. A study like this provides a framework for future works on biogeography and conservation of *Aegla* and represents a contribution for expanding the knowledge of the biogeographic history of the freshwater environments of southern South America. Further studies should be aimed at providing more detailed and updated analysis within species complexes and troglitic species as well as setting more detailed



researches about others relevant taxonomical, ecological, phylogenetic, historical and evolutionary aspects of *Aegla*, including all the nominal and putative new species employed in our study.

The amount of data analysed here is very high and there is no other study made on *Aegla* with these characteristics. In this sense, Echeverry and Morrone (2010) affirmed that it is desirable to have as many distributional data as possible to obtain well supported historical patterns. Although our analyses included almost all of the described species as well as some new and putative new species, there are still key regions that need to be screened, as Patagonia, north-eastern Argentina, Bolivia and Paraguay.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.jcz.2018.06.004>.

## References

- Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S.C., Bussing, W., Stiassny, M.L.J., Skelton, P., Allen, G.R., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., Higgins, J.V., Heibel, T.J., Wikramanayake, E., Olson, D., López, H.L., Reis, R.E., Lundberg, J.G., Pérez, M.H.S., Petry, P., 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience* 58, 403–414.
- Alcaide, M., Scordato, E.S.C., Price, T.D., Irwin, D.E., 2014. Genomic divergence in a ring species complex. *Nature* 511, 83–94.
- Álvarez Mondragón, E., Morrone, J.J., 2004. Propuesta de áreas para la conservación de aves de México, empleando herramientas panbiogeográficas e índices de complementariedad. *Interciencia* 29, 112–120.
- Barber, B.R., Xu, J., Pérez-Losada, M., Jara, C.G., Crandall, K.A., 2012. Conflicting evolutionary patterns due to mitochondrial introgression and multilocus phylogeography of the Patagonian freshwater crab *Aegla neuquensis*. *PLoS One* 7, e37105.
- Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Mier, R., Winker, K., Ingram, K.K., Das, I., 2007. Cryptic species as a window on diversity and conservation. *Trends Ecol. Evol.* 22, 148–155.
- Bond-Buckup, G., Buckup, L., 1994. A Família Aeglidae (Crustacea, Decapoda, Anomura). Museu de Zoologia da Universidade de São Paulo, São Paulo.
- Bond-Buckup, G., Jara, C.G., Buckup, L., Bueno, A.A.P., Pérez-Losada, M., Crandall, K.A., 2010a. Description of a new species of Aeglidae, and new records of related species from river basins in Argentina (Crustacea, Anomura). *Zootaxa* 2343, 18–30.
- Bond-Buckup, G., Jara, C.G., Buckup, L., Pérez-Losada, M., Bueno, A.A.P., Crandall, K.A., Santos, S., 2010b. New species and new records of endemic freshwater crabs from the Atlantic forest in southern Brazil (Anomura: Aeglidae). *J. Crust. Biol.* 30, 495–502.
- Boos, H., Bond-Buckup, G., Buckup, L., Araujo, P.B., Magalhães, C., Almerão, M.P., dos Santos, R.A., Mantelatto, F.L., 2012. Checklist of the Crustacea from the state of Santa Catarina, Brazil. *Check List* 8, 1020–1046.
- Brooks, D.R., 2004. Reticulations in historical biogeography: the triumph of time over space in evolution. In: Lomolino, M.V., Heaney, L.R. (Eds.), *Frontiers of Biogeography: New Directions in the Geography of Nature*. Sinauer Associates Inc., Massachusetts, pp. 111–124.
- Bueno, S.L.S., Camargo, A.L., Takano, B.F., Cohen, F.P.A., 2010. Crustáceos eglídeos (*Aegla* sp.): uma história única na América do Sul. *O Carste*. Belo Horizonte 22, 8–11.
- Bueno, S.L.S., Shimizu, R.M., Moraes, J.C.B., 2016. A remarkable anomuran: the taxon *Aegla* Leach, 1820. Taxonomic remarks, distribution, biology, diversity and conservation. In: Kawai, T., Cumberlidge, N. (Eds.), *A Global Overview of the Conservation of Freshwater Decapod Crustaceans*. Springer, Switzerland, pp. 23–64.
- Bueno, S.L.S., Camargo, A.L., Moraes, J.C.B., 2017. A new species of stygobitic aeglid from lentic subterranean waters in southeastern Brazil, with an unusual morphological trait: short pleopods in adult males. *Nauplius* 25, e201700021.
- Collins, P.A., Giri, F., Williner, V., 2011. Biogeography of the freshwater decapods in the La Plata basin, South America. *J. Crust. Biol.* 31, 179–191.
- Craw, R.C., 1988. Panbiogeography: method and synthesis in biogeography. In: Myers, A.A., Giller, P.S. (Eds.), *Analytical Biogeography: an Integrated Approach to the Study of Animal and Plant Distributions*. Chapman and Hall, London and New York, pp. 405–435.
- Craw, R.C., Grehan, J.R., Heads, M.J., 1999. Panbiogeography: Tracking the History of Life. Oxford University Press, New York.
- Crivellaro, M.S., Zimmermann, B.L., Bartholomei-Santos, M.L., Crandall, K.A., Pérez-Losada, M., Bond-Buckup, G., Santos, S., 2017. Looks can be deceiving: species delimitation reveals hidden diversity in the freshwater crab *Aegla longirostri* (Decapoda: Anomura). *Zool. J. Linn. Soc.* <https://doi.org/10.1093/zoolinnean/zlx030>.
- Croizat, L., 1958. Panbiogeography. author, Caracas.
- Croizat, L., 1964. Space, Time, Form: the Biological Synthesis. author, Caracas.
- Davis, M.A., Douglas, M.R., Collyer, M.L., Douglas, M.E., 2016. Deconstructing a species-complex: geometric morphometric and molecular analyses define species in the western rattlesnake (*Crotalus viridis*). *PLoS One* 11, e0146166.
- del Rio, M.G., Morrone, J.J., Lanteri, A.A., 2015. Evolutionary biogeography of south American weevils of the tribe Naupactini (Coleoptera: Curculionidae). *J. Biogeogr.* 42, 1293–1304.
- Donoghue, M.J., Moore, B.R., 2003. Toward an integrative historical biogeography. *Integr. Comp. Biol.* 43, 261–270.
- Echeverry, A., Morrone, J.J., 2010. Parsimony analysis of endemicity as a panbiogeographical tool: an analysis of Caribbean plant taxa. *Biol. J. Linn. Soc.* 101, 961–976.
- Fegan, M., Prior, P., 2005. How complex is the "Ralstonia solanacearum species complex"? In: Allen, C., Prior, P., Hayward, A.C. (Eds.), *Bacterial Wilt Disease and the Ralstonia solanacearum Species Complex*. APS Press, Saint Paul, pp. 449–461.
- Feldmann, R.M., 1984. *Haumuriaegla glaessneri* n. gen. and sp. (Decapoda; Anomura; Aeglidae) from Haumurian (late Cretaceous) rocks near Cheviot, New Zealand. *New Zeal. J. Geol. Geop.* 27, 379–385.
- Feldmann, R.M., 1986. Paleogeography of two decapod taxa in the Southern Hemisphere: global conclusions with sparse data. In: Gore, R.H., Heck, K.L. (Eds.), *Crustacean Biogeography*. Balkema, Rotterdam and Boston, pp. 5–19.
- Feldmann, R.M., Vega, F.J., Applegate, S.P., Bishop, G.A., 1998. Early Cretaceous arthropods from the Tlayúa Formation at Tepexi de Rodríguez, Puebla, México. *J. Paleontol.* 72, 79–90.
- Fernandes, C.S., Bueno, S.L.S., Bichuette, M.E., 2013. Distribution of cave-dwelling *Aegla* spp. (Decapoda: Anomura: Aeglidae) from the Alto Ribeira Karstic area in southeastern Brazil. *J. Crust. Biol.* 33, 567–575.
- Fernandez, J.C.C., Peixinho, S., Hajdu, E., 2012. Phylogeny and an integrated biogeography of *Acanthotetilla* Burton, 1959 (Demospongiae: Spirophorida: Tetillidae): two-way traffic on the peri-African track. *Zootaxa* 3402, 1–23.
- Ferretti, N., González, A., Pérez-Milles, F., 2012. Historical biogeography of mygalomorph spiders from the peripampasic orogenic arc based on track analysis and PAE as a panbiogeographical tool. *Syst. Biodivers.* 10, 179–193.
- Ferretti, N., González, A., Pérez-Milles, F., 2014. Identification of priority areas for conservation in Argentina: quantitative biogeography insights from mygalomorph spiders (Araneae: Mygalomorphae). *J. Insect Conserv.* 18, 1087–1096.
- Giri, F., Collins, P.A., 2014. Clinal variation in carapace shape in the South American freshwater crab, *Aegla uruguayana* (Anomura: Aeglidae). *Biol. J. Linn. Soc.* 113, 914–930.
- Giri, F., José de Paggi, S., 2006. Geometric morphometric and biometric analysis for the systematic elucidation of *Brachionus caudatus* Barrois and Daday, 1894 (Rotifera Monogononta Brachionidae) forms. *Zool. Anz.* 244, 171–180.
- Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24, 774–786.
- Goyenechea, I., Flores Vilella, O., Morrone, J.J., 2001. Introducción a los fundamentos y métodos de la biogeografía cladística. In: Llorente-Bousquets, J., Morrone, J.J. (Eds.), *Introducción a la biogeografía en Latinoamérica: teorías, conceptos, métodos y aplicaciones*. Las prensas de Ciencias, Facultad de Ciencias. UNAM, México City, pp. 225–243.
- Heads, M., 2004. What is a node? *J. Biogeogr.* 31, 1883–1891.
- Heads, M., 2014. Panbiogeography, its critics, and the case of the ratite birds. *Aust. Syst. Bot.* 27, 241–256.
- Hummer, K.E., Hancock, J.F., 2015. Vavilovian centers of plant diversity: implications and impacts. *Hortscience* 50, 780–783.
- Jara, C.G., 1977. *Aegla rostrata* n. sp., (Decapoda, Aeglidae), nuevo crustáceo dulceacuicola del Sur de Chile. *Stud. Neotrop. Fauna* E 12, 165–176.
- Jörger, K.M., Schrödl, M., 2013. How to describe a cryptic species? Practical challenges of molecular taxonomy. *Front. Zool.* 10, 59.
- Knowlton, N., 1986. Cryptic and sibling species among the Decapod Crustacea. *J. Crust. Biol.* 6, 356–363.
- Kuschel, G., 1960. Terrestrial zoology in southern Chile. *Proc. Roy. Soc. Lond.* 152, 540–550.
- Kuschel, G., May, B.M., 1997. A new genus and species of Nemonychidae (Coleoptera) associated with *Araucaria angustifolia* in Brazil. *N. Z. J. Entomol.* 20, 15–22.
- Lecoindre, G., Améziane, N., Boisselier, M.-C., Bonillo, C., Busson, F., Causse, R., Chenail, A., Couloux, A., Coutanceau, J.-P., Cruaud, C., Udekem d'Acoz, C. d., De Ridder, C., Denys, G., Dattai, A., Duhamel, G., Eléaume, M., Féral, J.-P., Gallut, C.,

- Havermans, C., Held, C., Hemery, L., Lautrédu, A.-C., Martin, P., Ozouf-Costaz, C., Pierrat, B., Pruvost, P., Puillandre, N., Samadi, S., Saucède, T., Schubart, C., David, B., 2013. Is the species flock concept operational? The antarctic shelf case. *PLoS One* 8, e68787.
- Ledru, M.-P., Stevenson, J., 2012. The rise and fall of the genus *Araucaria*: a southern hemisphere climatic connection. In: Haberle, S.J., David, B. (Eds.), *Peopled Landscapes. Archaeological and Biogeographic Approaches to Landscapes*. ANU E Press, Canberra, pp. 241–253.
- Lomolino, M.V., Riddle, B.R., Whittaker, R.J., Brown, J.H., 2010. *Biogeography*, fourth ed. Sinauer Associates Inc., Sunderland, Massachusetts.
- Marchiori, A.B., Bartholomei-Santos, M.L., Santos, S., 2014. Intraspecific variation in *Aegla longirostri* (Crustacea: Decapoda: Anomura) revealed by geometric morphometrics: evidence for ongoing speciation? *Biol. J. Linn. Soc.* 112, 31–39.
- Marchiori, A.B., Fornel, R., Santos, S., 2015. Morphometric variation in allopatric populations of *Aegla platensis* (Crustacea: Decapoda: Anomura): possible evidence for cryptic speciation. *Zoomorphology* 134, 45–53.
- Martin, J.W., Abele, L.G., 1986. Phylogenetic relationships of the genus *Aegla* (Decapoda: Anomura: Aegliidae), with comments on anomuran phylogeny. *J. Crust. Biol.* 6, 576–616.
- Maury, E.A., Pinto-da-Rocha, R., Morrone, J.J., 1996. Distribution of *Acropsopilio chilensis* Silvestri, 1904, in southern South America (Opiliones, Palpatores, Caddidae). *Biogeographica* 72, 127–132.
- Mayén-Estrada, R., Aguilar-Aguilar, R., 2012. Track analysis and geographic distribution of some *Lagenophrys* Stein, 1852 (Protozoa: Ciliophora: Peritrichia) species. *J. Nat. Hist.* 46, 249–263.
- Mercado-Salas, N.F., Pozo, C., Morrone, J.J., Suárez-Morales, E., 2012. Distribution patterns of the American species of the freshwater genus *Eucyclops* (Copepoda: Cyclopoida). *J. Crust. Biol.* 32, 457–464.
- Miserendino, M.L., 2001. Macroinvertebrate assemblages in Andean Patagonian rivers and streams: environmental relationships. *Hydrobiologia* 444, 147–158.
- Moraes, J.C.B., Tavares, M., Bueno, S.L.S., 2017. Taxonomic review of *Aegla marginata* Bond-Buckup & Buckup, 1994 (Decapoda, Anomura, Aegliidae) with description of a new species. *Zootaxa* 4323, 519–533.
- Moraes, J.C.B., Terossi, M., Buranelli, R.C., Tavares, M., Mantelatto, F.L., Bueno, S.L.S., 2016. Morphological and molecular data reveal the cryptic diversity among populations of *Aegla paulensis* (Decapoda, Anomura, Aegliidae), with descriptions of four new species and comments on dispersal routes and conservation status. *Zootaxa* 4193, 001–048.
- Morrone, J.J., 1996. On the geographical distribution of *Aegla* Leach: identification of areas of endemism (Decapoda: Aegliidae). *Biogeographica* 72, 113–119.
- Morrone, J.J., 2004. Panbiogeografía, componentes bióticos y zonas de transición. *Rev. Bras. Entomol.* 48, 149–162.
- Morrone, J.J., 2006. Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annu. Rev. Entomol.* 51, 467–494.
- Morrone, J.J., 2009. *Evolutionary Biogeography: an Integrative Approach with Case Studies*. Columbia University Press, New York.
- Morrone, J.J., 2014a. Biogeographical regionalisation of the Neotropical region. *Zootaxa* 3782, 1–110.
- Morrone, J.J., 2014b. Parsimony analysis of endemism (PAE) revisited. *J. Biogeogr.* 41, 842–854.
- Morrone, J.J., 2015a. Biogeographical regionalisation of the Andean region. *Zootaxa* 3936, 207–236.
- Morrone, J.J., 2015b. Track analysis beyond panbiogeography. *J. Biogeogr.* 42, 413–425.
- Morrone, J.J., Crisci, J.V., 1995. Historical biogeography: introduction to methods. *Annu. Rev. Ecol. Systemat.* 26, 373–401.
- Morrone, J.J., Lopretto, E.C., 1994. Distributional patterns of freshwater Decapoda (Crustacea: Malacostraca) in southern South America: a panbiogeographic approach. *J. Biogeogr.* 21, 97–109.
- Ortmann, A.E., 1902. The geographical distribution of freshwater decapods and its bearing upon ancient geography. *Proc. Am. Phil. Soc.* 41, 267–400.
- Oyanedel, A., Valdovinos, C., Sandoval, N., Moya, C., Kiessling, G., Salvo, J., Olmos, V., 2011. The southernmost freshwater anomurans of the world: geographic distribution and new records of Patagonian aeglids (Decapoda: Aegliidae). *J. Crust. Biol.* 31, 396–400.
- Page, R.D.M., 1987. Graphs and generalised tracks: quantifying Croizat's panbiogeography. *Syst. Zool.* 36, 1–17.
- Pérez-Losada, M., Bond-Buckup, G., Jara, C.G., Crandall, K.A., 2004. Molecular systematics and biogeography of the southern South American freshwater "crabs" *Aegla* (Decapoda: Anomura: Aegliidae) using multiple heuristic tree search approaches. *Syst. Biol.* 53, 767–780.
- Pérez-Losada, M., Bond-Buckup, G., Jara, C.G., Crandall, K.A., 2009. Conservation assessment of southern South American freshwater ecoregions on the basis of the distribution and genetic diversity of crabs from the genus *Aegla*. *Conserv. Biol.* 23, 692–702.
- Potter, P.E., 1997. The Mesozoic and Cenozoic paleodrainage of South America: a natural history. *J. South Am. Earth Sci.* 10, 331–344.
- Ramírez-Barahona, S., 2015. Geographic differentiation of tree ferns (Cyatheales) in Tropical America. *Am. Fern J.* 105, 73–85.
- Ribeiro, A.C., 2006. Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: an example of faunal evolution associated with a divergent continental margin. *Neotrop. Ichthyol.* 4, 225–246.
- Ringuelet, R.A., 1949. Los anomuros del género *Aegla* del noroeste de la República Argentina. *Rev. Mus. La Plata Zool* 6, 1–45.
- Rocha, S.S., Shimizu, R.M., Bueno, S.L.S., 2010. Reproductive biology in females of *Aegla strinatii* (Decapoda: Anomura: Aegliidae). *J. Crust. Biol.* 30, 589–596.
- Santos, S., Bond-Buckup, G., Buckup, L., Bartholomei-Santos, M.L., Pérez-Losada, M., Jara, C.G., Crandall, K.A., 2015. Three new species of Aegliidae (*Aegla*, Leach, 1820) from Paraná state, Brazil. *J. Crust. Biol.* 6, 839–849.
- Santos, S., Bond-Buckup, G., Buckup, L., Loureiro, T.G., Gonçalves, A.S., Verdi, A., 2014. The Aegliidae of Uruguay (Decapoda, Anomura), with the description of a new species of *Aegla*. In: Yeo, D.C.J., Cumberlidge, N., Klaus, S. (Eds.), *Advances in Freshwater Decapod Systematics and Biology*. Crustaceana Monographs, Boston, pp. 195–205.
- Santos, S., Bond-Buckup, G., Buckup, L., Pérez-Losada, M., Finley, M., Crandall, K.A., 2012. Three new species of *Aegla* (Anomura) freshwater crabs from the Upper Uruguay river hydrographic basin in Brazil. *J. Crust. Biol.* 32, 529–540.
- Santos, S., Bond-Buckup, G., Gonçalves, A.S., Bartholomei-Santos, M.L., Buckup, L., Jara, C.G., 2017. Diversity and conservation status of *Aegla* spp. (Anomura, Aegliidae): an update. *Nauplius* 25, e2017011.
- Santos, S., Bond-Buckup, G., Pérez-Losada, M., Bartholomei-Santos, M.L., Buckup, L., 2009. *Aegla manuiflata*, a new species of freshwater anomuran (Decapoda: Anomura: Aegliidae) from Brazil, determined by morphological and molecular characters. *Zootaxa* 2088, 31–40.
- Santos, S., Bond-Buckup, G., Pérez-Losada, M., Jara, C.G., Crandall, K.A., Buckup, L., 2010. New records and description of a new species of Aegliidae (Crustacea: Anomura) from river basins in southern Brazil. *Nauplius* 18, 79–86.
- Santos, S., Jara, C.G., Bartholomei-Santos, M.L., Pérez-Losada, M., Crandall, K.A., 2013. New species and records of the genus *Aegla* Leach, 1820 (Crustacea, Anomura, Aegliidae) from the west-central region of Rio Grande do Sul, Brazil. *Nauplius* 21, 211–223.
- Schmitt, W.L., 1942. The species of *Aegla*, endemic South American fresh-water Crustaceans. *Proc. U. S. Natl. Mus.* 91, 431–525.
- Silva de Oliveira, D.A., Decraemer, W., Holovachov, O., Burr, J., Tandingan de Ley, I., De Ley, P., Moens, T., Derycke, S., 2012. An integrative approach to characterize cryptic species in the *Thoracostoma trachygaster* Hope, 1967 complex (Nematozoa: Leptosomatidae). *Zool. J. Linn. Soc.* 164, 18–35.
- Silva, H.M.A., Gallo, V., 2016. Distributional patterns of enchodontoid fishes in the Late Cretaceous. *Cretac. Res.* 65, 223–231.
- Tumini, G., Giri, F., Williner, V., Collins, P.A., 2016. The importance of biogeographical history and extant environmental conditions as drivers of freshwater decapod distribution in southern South America. *Freshw. Biol.* 61, 715–728.
- Vanin, S.A., 1976. Taxonomic revision of the south American Belidae (Coleoptera). *Arq. Zool* 28, 1–75.
- Wiley, E.O., 1988. Parsimony analysis and vicariance biogeography. *Syst. Biol.* 37, 271–290.
- Zimmermann, B.L., Crivellaro, M.S., Hauschild, C.B., Bartholomei-Santos, M.L., Crandall, K.A., Pérez-Losada, M., Giri, F., Collins, P.A., Santos, S., 2018. Phylogeography reveals unexpectedly low genetic diversity in a widely distributed species: the case of the freshwater crab *Aegla platensis* (Decapoda: Anomura). *Biol. J. Linn. Soc.* 123, 578–592.