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Morphological and molecular evidence on the existence of a single estuarine and rocky intertidal acanthocephalan species of *Profilicollis* Meyer, 1931 (Acanthocephala: Polymorphidae) along the Atlantic and Pacific coasts of southern South America

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Abstract *Profilicollis chasmagnathi* Holcman-Spector, Mañé-Garzón & Dei-Cas, 1977 (Acanthocephala: Polymorphidae) has been reported to parasitise different grapsid species as intermediate hosts along the South Atlantic shores, i.e. *Cyrtograpsus angulatus* (Dana) and *Neohelice granulata* (Dana) in Uruguay and *Cyrtograpsus altimanus* (Rathbun) in Argentina. Larvae of a similar acanthocephalan described as *Profilicollis antarcticus* Zdzitowiecki, 1985 were recorded in the crab *Hemigrapsus crenulatus* (Milne-Edwards) from an estuarine habitat on the Southeast Pacific shore in Chile. Earlier studies have questioned the specific assignation of the Chilean estuarine populations of *Profilicollis* Meyer, 1931. The aim of this study was to re-examine the identification of these acanthocephalans by means of morphological and molecular analyses of cystacanths of *Profilicollis* spp. gathered from *C. angulatus*, *N. granulata*, *C. altimanus* and *H. crenulatus*. Our analyses showed that a single species of *Profilicollis*, *P. chasmagnathi*, parasitises these four crab species. The assessment of specimens from the South Shetlands Islands, the type-locality of *P. antarcticus*, is needed before formally proposing that *P. antarcticus* is a junior subjective synonym of *P. chasmagnathi*.

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Introduction

The genus *Profilicollis* Meyer, 1931 (Acanthocephala: Polymorphidae) includes acanthocephalans characterised by having a long neck, fully ovoid proboscis in both sexes and eggs with concentric membranes, and that use decapods and seabirds as intermediate and definitive hosts, respectively (Nickol et al., 1999). This genus has a confused and instable taxonomy mainly due to the high morphologically similarity and poor understanding of the biology and distribution of its species.

The genus encompasses nine species, of which three have been recorded in South America,

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Profilicollis altmani (Perry, 1942), *P. antarcticus* Zdzitowiecki, 1985 and *P. chasmagnathi* (Holcman-Spector, Mañé-Garzón & Dei-Cas, 1977). *Profilicollis altmani* was reported parasitising marine decapods such as the mole crabs *Emerita* spp. and seagulls of the family Laridae in both Atlantic and Pacific shores (Amin, 2013; Goulding & Cohen, 2014; Rodríguez & D'Elía, 2016; Rodríguez et al., 2016). *Profilicollis antarcticus* is distributed in the Southeast Pacific coast using as intermediate host the grapsid crab *Hemigrapsus crenulatus* (Milne-Edwards), typical inhabitant of estuarine systems and as definitive hosts the kelp gull *Larus dominicanus* (Lichtenstein), the imperial shag *Phalacrocorax atriceps* (King) and the snowy sheathbill *Chionis albus* Gmelin; in the last host an immature female was found (Zdzitowiecki, 1985; Torres et al., 1991; Rodríguez et al., 2016). *Profilicollis chasmagnathi* has been recorded in the estuarine crabs *Neohelice granulata* (Dana) and *Cyrtograpsus angulatus* (Dana) as intermediate hosts (Holcman-Spector et al., 1977; Martorelli, 1989; Alda et al., 2011; La Sala et al., 2012) and diverse birds such as the white-faced ibis *Plegadis chihi* (Vieillot), the red-gartered coot *Fulica armillata* Vieillot, the white-tufted grebe *Rollandia rolland* (Quoy & Gaimard) and the seagulls *Larus atlanticus* Olrog and *L. dominicanus* as definitive hosts (Vizcaino, 1989; Martorelli, 1989; Diaz et al., 2011; La Sala et al., 2013); the acanthocephalan species is known from the southwestern Atlantic coast (Holcman-Spector et al., 1977; Diaz et al., 2011).

Balboa et al. (2009) recorded *Profilicollis* sp. in *H. crenulatus* from estuarine system in the southeast Pacific coast of Chile and noted that the cystacanths found in this crab are very similar to those of *P. chasmagnathi* recovered from specimens of *N. granulata* (syn. *Chasmagnathus granulatus* Dana) in Uruguay by Holcman-Spector et al. (1977). In regard to this fact, it is relevant to note that the description of *P. antarcticus* from the southern Pacific coast was done without comparison with *P. chasmagnathi* from the southwest Atlantic coast. Although *P. antarcticus* and *P. chasmagnathi* were described as parasitising distinct species of crabs of the family Varunidae inhabiting estuarine and rocky intertidal environments, environmental conditions inhabited by these crabs, are similar, and this is an important factor for infections of the intermediate hosts (Steinauer et al., 2007; Rodríguez et al., 2016). The aim of this study was to test if *P. antarcticus* and *P. chasmagnathi*

represent a single species by analysing morphological and molecular evidence.

Materials and methods

Sampling and morphological study

During April 2009 and January 2016 four varunid crab species were collected by hand at four systems at the Southern Atlantic (SA) and Southern Pacific (SP) oceans. The crabs *Cyrtograpsus angulatus* and *Neohelice granulata* (Varunidae) were collected at José Ignacio coastal lagoon (34.8°S, 54.7°W) and Solis Grande stream (34.8°S, 55.4°W) in Uruguay; *Cyrtograpsus altimanus* (Varunidae) was collected at Punta Cuevas (42.4°S, 65.2°W) Puerto Madryn in Argentina (SA); and *Hemigrapsus crenulatus* (Varunidae) was collected at the mouth of the River Valdivia (39.8°S, 73.4°W) in Chile (SP). Crabs were transported alive to the laboratory, and examined for the presence of cystacanths. Parasites were placed in distilled water to force the osmotic eversion of the proboscis. Twenty-three cystacanths were fixed in 10% formalin for morphological analysis that follows the nomenclature of Holcman-Spector et al. (1977) and Balboa et al. (2009). Other specimens were preserved in 96% ethanol for molecular analysis.

Molecular data and phylogenetic analysis

Genetic comparisons and phylogenetic analyses were based on DNA sequences of the mitochondrial cytochrome *c* oxidase subunit 1 (*cox*1) gene. Sequences were gathered from 19 individuals of *Profilicollis* recovered from estuarine and rocky intertidal crabs as follows: Atlantic coast, *C. altimanus* (n = 3), *C. angulatus* (n = 9) and *N. granulata* (n = 3). Four sequences generated by Rodríguez et al. (2016) for cystacanths ex *H. crenulatus* (n = 3) from the Pacific coast, were also downloaded from GenBank. Sequences were generated using the universal primers of by Folmer et al. (1994) and the protocol outlined in Rodríguez & D'Elía (2016); the new DNA sequences were edited using CodonCode (Codon-Code, Dedham, Massachusetts, USA) and deposited in the GenBank database (KY292510–KY292524).

To enlarge the taxonomic and geographical coverage of *Profilicollis*, these 18 sequences were integrated into a matrix with 18 sequences of *P. altmani* from the

North Atlantic (NA), South Atlantic (SA), North Pacific (NP) and South Pacific (SP), and *Profilicollis botulus* (Van Cleave, 1916), downloaded from GenBank (accession numbers are given in terminal labels of Fig. 1); these sequences were published by Goulding & Cohen (2014), Rodríguez & D'Elía (2016) and Rodríguez et al. (2016). In total, 36 sequences of *Profilicollis* were analysed using *Polymorphus minutus*, *Profilicollis botulus* and *Arhytmorhynchus brevis* which are considered closely related to *Profilicollis* (see García-Varela et al., 2013) as the outgroup.

Sequences were aligned in Clustal as implemented in MEGA 7 (Tamura et al., 2013) using the default parameter values. Observed genetic distances (uncorrected p-distance model) were calculated in MEGA 7. Phylogenetic relationships were inferred *via* Maximum likelihood analyses (ML) conducted in IQ-Tree (Nguyen et al., 2015), using its online implementation W-IQ-TREE at http:/iqtree.cibiv.univie.ac.at (Trifinopoulus et al., 2016). The implemented model of nucleotide substitution (TPM3u + G4) was selected also with IQ-Tree. Support for clades found in the most likely tree was estimated *via* the SH-aLRT test
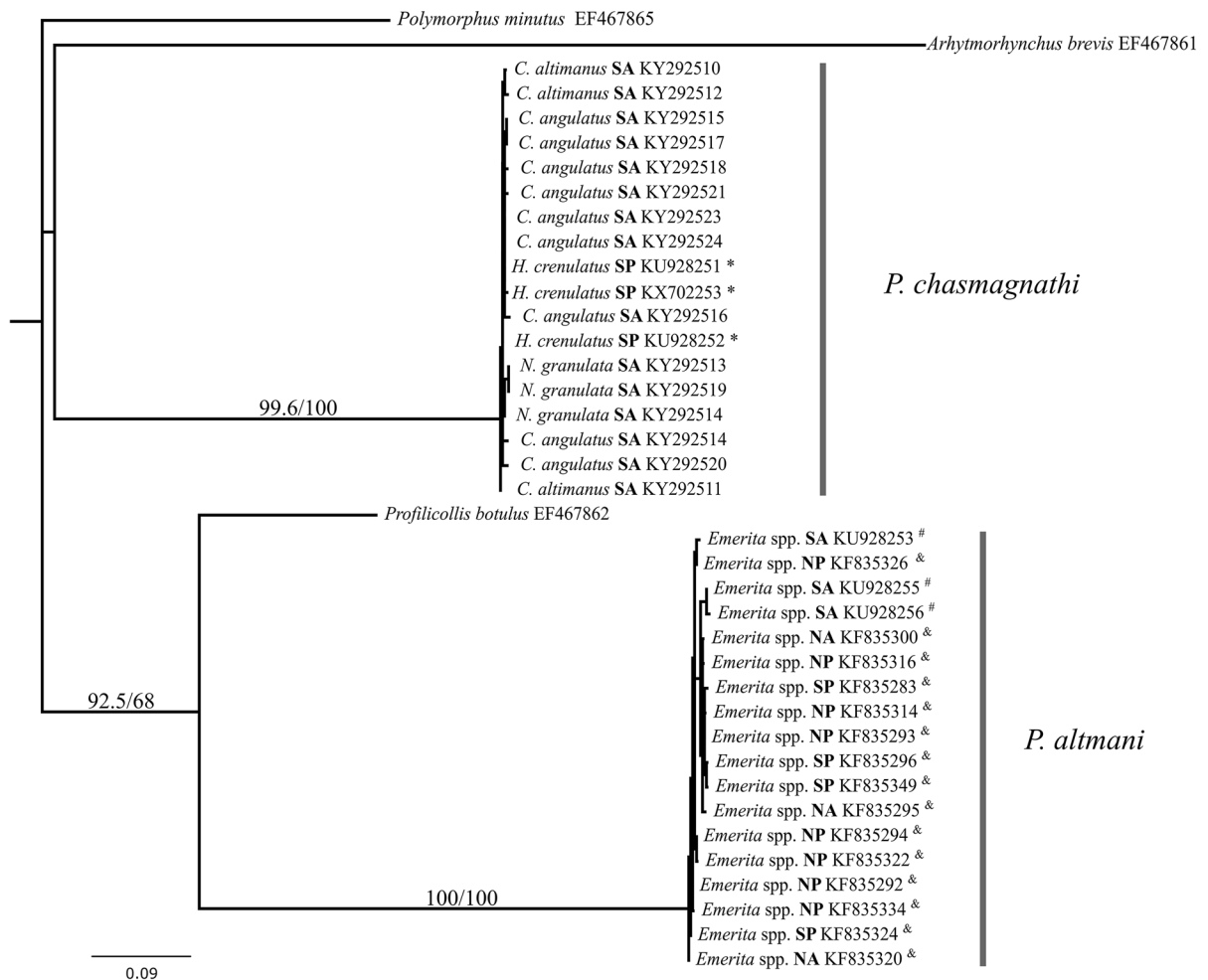

Fig. 1 Genealogical relationships of haplotypes of the *cox*1 gene of specimens of the genus *Profilicollis* recovered in a Maximum Likelihood analysis (Ln = -2643.278). Support values, only given for species and multispecies clades, correspond to SH-aLRT test and ultrabootstrap proportions. Intermediate hosts and ocean (NA, North Atlantic; SA, South Atlantic; NP, North Pacific; SP, South Pacific) are indicated at terminal labels for *P. chasmagnathi* and *P. altmani*. GenBank accession numbers are also given at the terminal labels; those signaled with an (&) were taken from Goulding & Cohen (2014), those with (#) were generated by Rodríguez & D'Elía (2016), those with (*) were generated by Rodríguez et al. (2016); sequence gathered in this study lack symbols

(Guindon et al., 2010) and with 1,000 ultrafast bootstrap pseudoreplications (BL).

Results

The morphological assessment of the cystacanths collected at the Atlantic coast of Uruguay and Argentina and at the Chilean Pacific coast showed that they are similar. Cystacanths from the four crab species exhibit the same oval shape of the proboscis, as well as the number of longitudinal rows of hooks and hooks per row (16–20 rows with 7–9 hooks per row; see Table 1). Regarding the metrical data, the acanthocephalan samples from *C. altimanus* collected in Argentina and *H. crenulatus* collected in Chile resembled each other more than they resembled the samples from *C. angulatus* and *N. granulata* collected in Uruguay (Table 1). For instance, cystacanths from *C. altimanus* and *H. crenulatus* share similar morphometric values for proboscis length and width, as well as for the number and length of hooks (7–8; Table 1). However, cystacanths recovered from *H. crenulatus* (Chile) possess a wider receptacle and longer neck than all other cystacanths.

The phylogenetic analysis indicated that none of the cystacanths recovered from the varunid crabs in this study belongs to the species *P. altmani*, previously reported from *Emerita* spp. crabs (Goulding & Cohen, 2014; Rodríguez & D'Elía, 2016) (Fig. 1). Haplotypes of *Profilicollis* extracted from all four estuarine and rocky intertidal crab species fell into a highly supported (pp = 1) clade (Fig. 1) for which the oldest available name is *P. chasmagnathi*. This clade showed low genetic variation; the p-distance among its haplotypes ranged between 0 and 0.01 (mean 0.005). Haplotypes from cystacanths did not form monophyletic groups corresponding to the host crab species. In addition, the genetic variation of *P. chasmagnathi* lacks geographical structure. Two cystacanths from *H. crenulatus* (SP) and two cystacanths from *C. angulatus* (SA) shared the same haplotype. Similarly, another haplotype was found in cystacanths from *N. granulata* from two different sites (NA) In contrast, the most divergent haplotypes of *P. chasmagnathi* were found in crabs of *C. angulatus* from José Ignacio lake and Solis Grande stream, Uruguay (NA) and another divergent haplotype was found in *C. altimanus* from Argentina and *C. angulatus* from Uruguay (NA;

Fig. 1). The average genetic p-distance between the clades of *P. chasmagnathi* and *P. altmani* was 0.25.

Discussion

Currently, several taxonomic studies of parasites, including acanthocephalans, integrate morphological and molecular evidence (e.g. Pinacho-Pinacho et al., 2012, Alcantar-Escalera et al., 2013; Tkach et al., 2013). However, the transition to an integrative taxonomy (*sensu* Dayrat, 2005) is far from being reached in parasite taxonomy. In particular this approach would prove to be useful in studies of groups with highly similar morphologically species, such as polymorphid acanthocephalans.

Profilicollis antarcticus was originally described based on specimens recovered from the seabird *Chionis albus* at the South Shetland Islands, 120 km north of the Antarctic Peninsula (Zdzitowiecki, 1985). Remarkably, the description of *P. antarcticus* was done without comparison with the previously described *P. chasmagnathi* from the southwest Atlantic coast (Holcman-Spector et al., 1977; Zdzitowiecki, 1985). Subsequently, specimens recovered from individuals of *L. dominicanus* and *P. atriceps* off the coast of Chile were assigned to *P. antarcticus* (see Torres et al., 1991). Later, Pulgar et al. (1995) registered cystacanths in Chilean specimens of the crab *H. crenulatus* referred to as *P. antarcticus.* In addition, the distribution of *P. antarcticus* was enlarged as it was mentioned for the intertidal New Zealand crabs *Helice crassa* Dana, *H. crenulatus* and *Macrophthalmus hirtipes* (Heller) as well as the definitive bird hosts *Haematopus finschi* Martens and *Limosa lapponica* (Linnaeus) (Brockerhoff & Smales, 2002). Finally, Balboa et al. (2009) noted that cystacanths recovered from the crab *H. crenulatus* at Chilean South Pacific estuaries, referred to as *P. antarcticus*, were very similar to those of *P. chasmagnathi* from Uruguay leaving open the question about the correct assignation of the Chilean specimens to *P. antarcticus* and by extension the distinction of *P. antarcticus* and *P. chasmagnathi*. Comparing the morphology of our samples of cystacanths and those referred as *P. antarcticus* by Brockerhoff & Smales (2002) from New Zealand, *Profilicollis chasmagnathi* by Holcman-Spector et al. (1977) from Uruguay, and *Profilicollis* sp. by Balboa et al. (2009) from Chile, we

Table 1 Morphometrics data and shape of the proboscis of cystacanths referred to as *Profilicollis antarcticus*, *P. chasmagnathi* and *Profilicollis* sp. by Balboa et al. ([2009](#)) and *P. chasmagnathi* from four varunid crab species collected in Uruguay, Argentina and Chile

Source	Balboa et al. (2009)			Present study			
Country	Uruguay	New Zeland	Chile	Uruguay	Uruguay	Argentina	Chile
Referred to as	P. chasmagnathi	P. antarcticus	Profilicollis sp.	P. chasmagnathi	P. chasmagnathi	P. chasmagnathi	P. antarcticus
Host	N. granulata	H. crassa	H. crenulatus	C. angulatus (n = 6)	N. granulata (n = 7)	C. altimanus (n = 4)	H. crenulatus (n = 6)
Total body length	3,980–6,780	3,055–4,530 (3,786)	4,700–7,000 (5,853)	3,500–6,600 (5,322)	4,870–6,550 (5,716)	3,150–4,700 (3775)	5,250–6,022 (5,541)
Maximum body width	560–830	–	900–1,320	500–795 (698)	587–810 (705)	750–950 (850)	893–1,320 (1,007)
Proboscis shape	Ovoid	Ovoid	Ovoid	Ovoid	Ovoid	Ovoid	Ovoid
Proboscis length	440–680	398–537 (473)	500–700 (626)	440–695 (593)	455–665 (567)	550–600 (575)	547–606 (580)
Proboscis width	260–500	316–417 (371)	290–550 (464)	250–485 (398)	245–551 (383)	400–450 (413)	477–593 (540)
Proboscis receptacle length	2,000–3,450	1,495–1,639 (1,548)	2,300–3,000 (2,738)	2,200–3,250 (2,733)	2,100–3,520 (2,803)	1,500–2,300 (1,825)	1,704–2,041 (1,835)
Proboscis receptacle width	150–270	225–269 (242)	320–420 (366)	150–280 (222)	165–280 (219)	100–650 (268)	524–668 (582)
Neck length	550–1,670	716–1,225 (958)	820–1,120 (970)	820–1,420 (1,147)	630–1,500 (1,078)	800–1,800 (1,375)	1,173–1,723 (1,374)
Neck width	220–420	291–448 (448)	250–467 (382)	325–460 (389)	245–462 (354)	400–500 (425)	312–427 (383)
No. of hook rows	16–20	22	16–22	18–20	16–20	16–19	16–18
No. of hooks per row	8–9	6–8	8–9	8–9	8–9	7–8	7–8
Apical hooks length	–	30–66 (51)	28–35 (32)	24–32 (28)	25–32 (29)	40–50 (46)	22–37 (28)
Medium hooks length	–	35–66 (53)	30–40 (34)	27–36 (31)	27–35 (32)	40–45 (41)	41–48 (45)
End hooks length	–	45–67 (59)	40–45 (43)	36–40 (39)	38–42 (40)	45–55 (50)	41–56 (51)

observed that they show overlapping character traits (Table 1). For instance, neck width, rows and hooks showed similar morphometric data; even if the values were not the same, the ranges are overlapping. Also, cystacanths gathered from *C. altimanus* (Argentina) and *H crenulatus* (Chile) share more characters than cystacanths from *C. angulatus* and *N. granulata* (both from Uruguay) that share other characters among them (Table 1). These differences could be attributable to intraspecific variation, due to selective pressure by host (Near, 2002; Huyse & Littlewood, 2007). As mentioned above, *P. antarcticus* was described from an adult specimen, and no cystacanth description exists from the Antarctic Peninsula; as such, we cannot compare estuarine southern South American specimens, belonging to *Profilicollis chasmagnathi*, with typical *P. antarcticus*.

The results of this study, integrating morphological and molecular data, suggest that cystacanths recovered from the estuarine and rocky intertidal crab species *C. angulatus*, *N. granulata*, *C. altimanus* and *H. crenulatus* along the Southern Atlantic and Southern Pacific American coasts belong to a single species and not to two as previously considered. Given the rule of priority, the taxonomic name that corresponds to this bioceanic-distributed species is *P. chasmagnathi*. We have not analysed specimens from the South Shetland Islands referable to *P. antarcticus*, and as such, we cannot formally suggest that *P. antarcticus* is a junior synonym of *P. chasmagnathi*. In addition, future studies should examine if molecular evidence corroborates the existence of *P. chasmagnathi* in New Zealand.

The molecular analysis showed that *P. chasmagnathi* exhibits a low level of genetic variation and that this variation is not structured geographically or in relation to intermediate host crab species. Lack of phylogeographical and/or host related structure was also reported for the co-generic and co-distributed *P. altmani* (see Goulding & Cohen, 2014; Rodriguez & D'Elía, 2016). The cause molding this pattern may relate to the high mobility of the definitive avian hosts of the species of *Profilicollis*, including the seagulls *L. atlanticus*, *L. dominicanus*, *Chroicocephalus maculipennis* Lichtenstein, *Leucophaeus pipixcan* (Wagler) and *Leucophaeus modestus* (Tschudi), which with their large migrations ranges may contribute to the wide geographical distribution and lack of geographical structure of these parasite species (see La Sala et al., 2013; Goulding & Cohen, 2014; Rodríguez et al., 2016).

In summary, we have shown that along estuaries and rocky intertidal systems of the Pacific and Atlantic coasts of southern South America there is one acanthocephalan species, *P. chasmagnathi*, which parasitises four estuarine crab species. This result is similar to what has been found for the acanthocephalan *P. altmani*, which was determined to be the single species in the sandy marine coast along North and South America (Goulding & Cohen, 2014; Rodriguez & D'Elía, 2016; Rodríguez et al., 2016). Thus our study and the previous studies of *P. altmani* have narrowed the number of species of *Profilicollis* recognised from southern South America to only two species. Both acanthocephalan species are segregated by distinct habitats and the intermediate hosts that inhabit them; sandy beaches for *P. altmani* and estuaries and rocky intertidal environments for *P. chasmagnathi*, which in turn results in strict parasite-environment links.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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