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Corynosoma australe Johnston, 1937 and *C. cetaceum* Johnston & Best, 1942 (Acanthocephala: Polymorphidae) from marine mammals and fishes in Argentinian waters: allozyme markers and taxonomic status

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Abstract

Genetic and morphological studies were carried out on acanthocephalans belonging to *Corynosoma* Lühe, 1904 and referable to the species *C. cetaceum* Johnston & Best, 1942 and *C. australe* Johnston, 1937, which were recovered from both definitive and intermediate hosts in Argentinian waters. The aims were to estimate the level of genetic differentiation between the two taxa at any stage of their life-cycle, to provide genetic (allozyme) markers for their recognition and to analyse the systematic status of both taxa. Acanthocephalans were collected from the stomach and intestine of *Arctocephalus australis* (Zimmerman), the intestine of *Mirounga leonina* (Linnaeus) and the stomach of *Pontoporia blainvillei* Gervais & D'Orbigny (definitive hosts) in Argentinian waters. Alternative alleles at all the 13 enzymatic loci studied were observed for *C. australe* and *C. cetaceum*. The specimens from the stomach of both *P. blainvillei* and *A. australis* were identified, on the basis of the great number of diagnostic loci found, as *C. cetaceum*; those from intestine of both *A. australis* and *M. leonina* as *C. australe*. A high level of genetic differentiation ($D_{Nei}=\infty$: $I_{Nei}=0.00$) between the two taxa was found, suggesting a generic distinction between the two species. Cystacanths of the two species from the body-cavity of the fish *Cynoscion guatucupa* (Cuvier) collected from the same geographical area were identified genetically. Morphological patterns, such as the number of hooks and hook rows on the proboscis, the distribution of somatic and genital armature, and other morphometric and meristic differences, in addition to ecological data, enabled the identification of these two species at cystacanth, juvenile and adult stages. However, a number of morphological and morphometric features of the Argentinian material were different to those of *C. australe* and *C. cetaceum* described from other regions of the world.

Introduction

Corynosoma Lühe, 1904 (Acanthocephala: Polymorphidae) presently comprises numerous species which utilise pinnipeds, cetaceans and fish-eating

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birds as definitive hosts, and crustaceans and fishes as intermediate hosts (Delyamure, 1968). Despite their wide distribution among vertebrates, the systematic status of several species is still not clear. Currently, there is a long list of synonymies and misidentifications (see e.g. Amin, 1985), including the type-species, *C. strumosum* (Rudolphi, 1802) Lühe, 1904, whose description has recently been amended (Nickol et al., 2002a). This is probably due to two main reasons: (1) the systematics of this genus is presently based on a few variable morphological features (such as the number of hook rows and of hooks per row on the proboscis, and the distribution patterns of somatic and genital spines) and general morphometry; and (2) several sources of intraspecific variability within populations of *Corynosoma* spp. (such as the effect of parasite age and size, host-induced effects and geographical influence) which migth affect morphological features (George-Nascimento & Marin, 1992; Aznar et al., 1999a). Similarly, confusion has been reported between genera of the Family Polymorphidae Meyer, 1931 (Schmidt, 1973, 1975; Amin, 1992; Aznar et al., 1999a; Nickol et al., 1999), which arose for the same reasons as problems at the specific level.

Records of adult *Corynosoma* in marine mammals from the South-West Atlantic Ocean present a similar state of taxonomic uncertanty. Indeed, along the Argentinian coast, Morini & Boero (1960) recorded *C. otariae* Morini & Boero, 1960, based upon six specimens from the South American sea lion *Otaria flavescens* (Shaw), which was differentiated from the original description of *C. australe* Johnston, 1937 from the Australian sea lion *Neophoca cinerea* (Péron) in Australian waters (Johnston, 1937) by the similar size of the sexes, the number of proboscis hook rows (20 instead of 18), a larger body and embriophore size, and the distribution of the somatic armature in both sexes. However, Zdzitowiecki (1989), comparing the description of Morini & Boero (1960) with his redescription of *C. australe* (Zdzitowiecki, 1984a), synonymised *C. otariae* with *C. australe* without any mention of the differences reported by Morini & Boero (1960). Later, George-Nascimento & Marin (1992) were unable to identify at the specific level specimens from *O. flavescens* and the South American fur seal *Arctocephalus australis* Zimmerman on the Uruguayan coast; later specimens from *A. australis* off Uruguay were identified as *C. australe* by Aznar et al. (2004). *C. australe* was also recently recorded from a cetacean, the dusky dolphin *Lagenorhynchus obscurus* (Gray), also from Argentinian waters (Dans et al., 1999).

C. cetaceum has commonly been reported as a parasite of the franciscana *Pontoporia blainvillei* Gervais & D'Orbigny off the Uruguayan (Schmidt & Dailey, 1971; Kagei et al., 1976; Aznar et al., 1994a) and Argentinian coasts (Aznar et al., 1994a, b), and from the short beaked common dolphin *Delphinus delphis* Linnaeus off Argentina (Aznar et al., 2002a). Unidentified species of this genus have also been reported from *P. blainvillei* (see Dailey & Brownell, 1972). A geographical comparison of samples of *C. cetaceum* showed several differences (such as the number of hooks per row on the proboscis and the distribution patterns of the somatic spines) between South American and South Australian specimens (Aznar et al., 1999a). The generic status of *C. cetaceum* has also been a matter of controversy (see Schmidt & Dailey; 1971; Smales, 1986; Aznar et al., 1999a). This taxon was transferred to *Polymorphus* Lühe, 1911, due to the absence of genital spines in both sexes, but was reinstated as *C. cetaceum* by Aznar et al. (1999a); however its generic status remains unresolved (García-Varela et al., 2005).

Records of cystacanths belonging to *Corynosoma* from fishes off Argentina are: *C. australe* (see Zdzitowiecki, 1989; Sardella et al., 1995; Tanzola et al., 1997; Cremonte & Sardella, 1997; Tanzola & Guagliardo, 2000; Timi, 2003); and *C. hammani* (Linstow, 1892) (see Tanzola et al., 1997; Tanzola & Guagliardo, 2000). Unidentified cystacanths of *Corynosoma* have also been reported (Szidat, 1949, 1969; Suriano, 1966; Ivanov, 1996; Sardella & Timi, 1996; Sardella et al., 1998). From the numerous reports listed above, it is clear that the systematic status of material of *Corynosoma* at the cystacanth stage in the South-West Atlantic Ocean also remains uncertain.

On the other hand, genetic markers obtained from multilocus allozyme electrophoresis have been demonstrated to be a useful tool for answering questions related to the systematics of several parasites and for detecting various cryptic or sibling species, as well as establishing genetic relationships between congeneric taxa of endoparasites (Andrews & Chilton, 1999), including those from marine mammals (Nascetti et al., 1986, 1993; Mattiucci

et al., 1997, 2001, 2003). Allozyme markers have also previously been applied to the systematics of other acanthocephalan species (De Buron et al., 1986; Aho et al., 1992; Väinöla et al., 1994). Molecular-genetic studies on acanthocephalans of the genus *Corynosoma* have recently been carried out by García-Varela et al. (2005).

In the present work, morphological and genetic studies were carried out on acanthocephalans referable to the morphospecies *C. australe* (an uncontroversial taxon) and *C. cetaceum* (a problematical species) recovered from definitive and intermediate hosts in Argentinian waters. The aims of the study were: to estimate the level of genetic differentiation between the two taxa at any stage of their life-cycle, to provide genetic (allozyme) markers for their recognition and to analyse the systematic status of both taxa.

Materials and methods

Acanthocephalans were obtained from the following definitive hosts: the South American fur seal *Arctocephalus australis* (Zimmerman) found dead along Claromecó beach and San Clemente del Tuyú, Buenos Aires Province; the southern elephant seal *Mirounga leonina* (Linnaeus) found dead at San Clemente del Tuyú; and the franciscana *Pontoporia blainvillei*, an accidental by-catch, at Mar del Plata (details of the collection data are given in Table 1).

In order to avoid the use of the term 'juvenile' for any non-adult specimen, acanthocephalans recovered from fish hosts are referred to as 'cystacanths', those worms from the definitive host which have not reached sexual maturity are denoted as 'juveniles' and mature specimens as 'adults'.

Cystacanths were collected from eight specimens of striped weakfish *Cynoscion guatucupa* (Cuvier) caught by fishermen using trawl nets and landed at the Mar del Plata harbour (Table 1).

The gastrointestinal tracts of the definitive hosts were frozen prior to dissection and parasitological examination. Acanthocephalans were collected from the stomach and/or intestine of their definitive hosts, washed in saline solution and a subsample frozen in distilled water in Eppendorf-like tubes, then stored at −70 °C for genetic analysis. The same procedure was applied to living cystacanths collected from body-cavity of fish. For morphological analysis, thawed and living specimens were extended in distilled water for several hours prior to fixation, then fixed in 4% formaldehyde, stored in 70% alcohol, cleared in lactophenol and examined under a light microscope. The number of proboscis hook rows were counted from transverse sections of the distal end of the

Table 1. Collection data for the samples of *Corynosoma* spp. studied from the Argentinian coast.

Hosts	Collecting site	Date of collection	Nh	*C. australe*			*C. cetaceum*			n_{MAE}	
				Stomach	Intestine	Body-cavity	Stomach	Intestine	Body-cavity	*C. australe*	*C. cetaceum*
A. australis	Claromecó (38°22′S, 60°16′W)	September, 1999	1	–	5,231	–	47	63	–	–	–
A. australis	San Clemente del Tuyú (36°30′S, 56°20′W)	August, 2000	1	–	150*	–	6	–	–	37	5
M. leonina	San Clemente del Tuyú (36°30′S, 56°20′W)	August, 2000	1	–	51	–	–	–	–	22	–
P. blainvillei	Mar del Plata (38°08′S, 57°32′W)	August, 1999	1	–	–	–	1,961	–	–	–	28
C. guatucupa	Mar del Plata (38°08′S, 57°32′W)	May, 2000	8	–	–	87	–	–	74	17	17

Nh, number of hosts examined. *, not all parasites counted. n_{MAE}, specimens studied by multilocus allozyme electrophoresis.

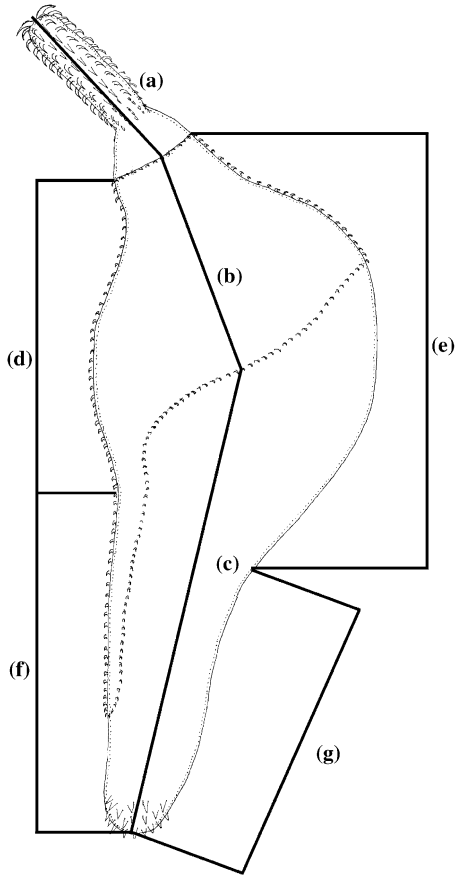


Fig. 1. Scheme of measurements for specimens of *Corynosoma*: a + b + c, total length; b + c, trunk length; d, ventral fore-trunk length; e, dorsal fore-trunk length; f, ventral hind-trunk length; g, dorsal hind-trunk length.

proboscis mounted in apical view. General measurements were taken on specimens mounted in lateral position, as shown in Figure 1. Somatic spines were measured on the dorsal posterior border of the trunk armature. Drawings were made using a drawing tube. Measurements of embryophores are based on fully-developed embryophores (with an identifiable acanthor inside). Measurements are given in millimetres, unless otherwise indicated, as the mean followed by range in parentheses. Only those morphological features showing differences with previous descriptions of both species are provided.

Voucher specimens are deposited in the Colección Zoología Invertebrados del Museo de La Plata (Helmintos). ***Corynosoma australe***: 5 adult males (Coll. No. 5405) and 5 adult females (Coll. No. 5405) from the intestine of *Arctocephalus australis*; 3 adult males (Coll. No. 5406) and 3 adult females (Coll. No. 5406) from the intestine of *Mirounga leonina*; 5 cystacanth males (Coll. No. 5407) and 5 cystacanth females (Coll. No. 5407) from the body-cavity of *Cynoscion guatucupa*. ***Corynosoma cetaceum***: 5 adult males (Coll. No. 5408) and 5 adult females (Coll. No. 5408) from stomach of *Pontoporia blainvillei*; 5 juvenile males (Coll. No. 5409) and 5 juvenile females from stomach and intestine of *A. australis*; 5 cystacanth males (Coll. No. 5410) and 5 cystacanth females (Coll. No. 5410) from the body-cavity of *Cynoscion guatucupa.*

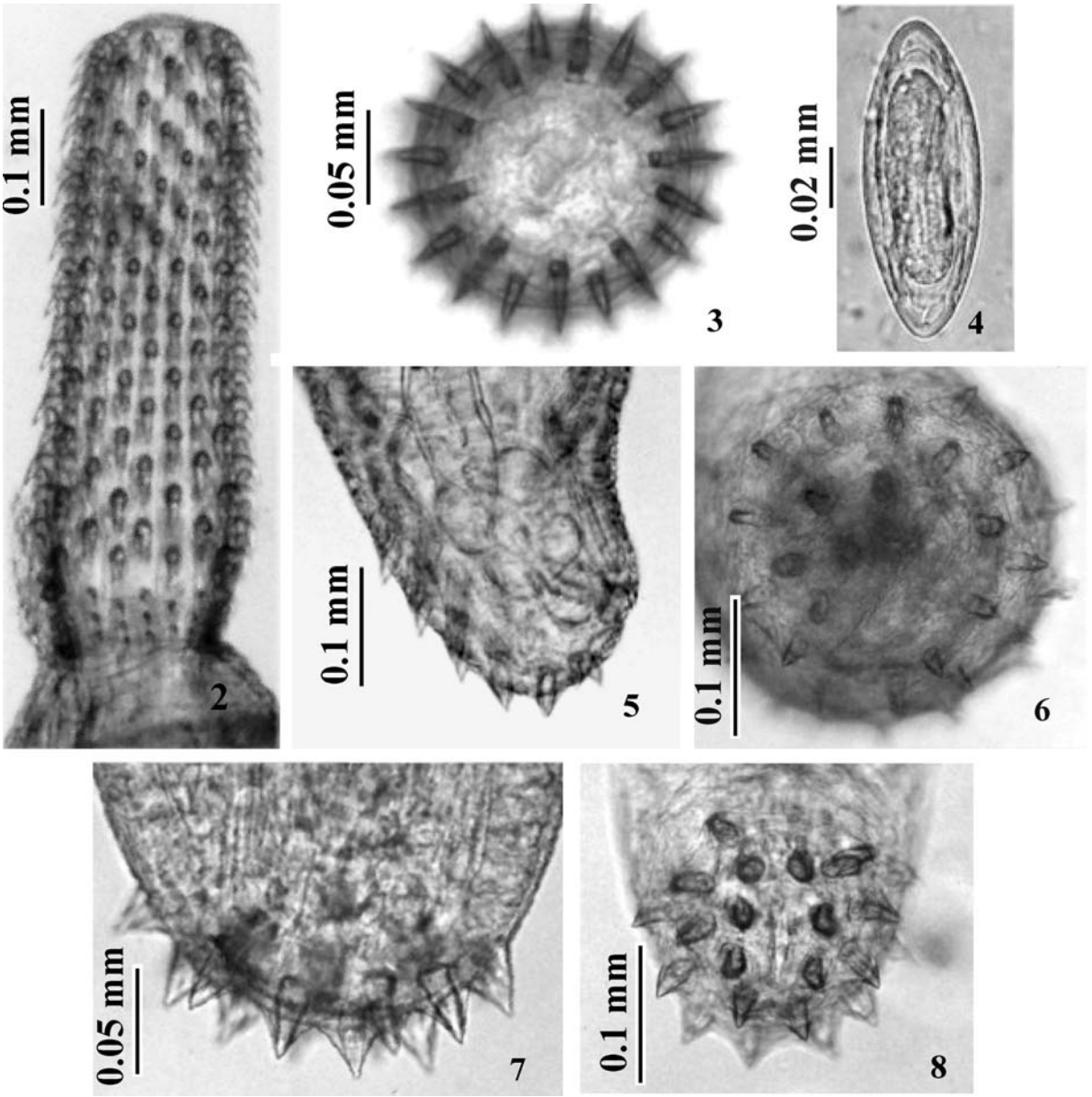
Genetic analysis was performed on 92 acanthocephalans (see Table 1) as follows: 42 from *A. australis*, 22 from *M. leonina* and 28 from *P. blainvillei*. Thirty-four cystacanths from *C. guatucupa* were also analysed. Acanthocephalans were kept frozen at −70 °C, then transported in dry ice to Rome for genetic analysis. Standard horizontal starch gel electrophoresis was performed at 5 °C and 7–9 cm V/cm for 4–5 hr, according to Mattiucci et al. (1997). Single specimens were crushed in distilled water. The following enzymes (listed by their code number) were tested: malate dehydrogenase (*Mdh-1*) E.C. 1.1.1.37; malic enzyme (*Me*) E.C. 1.1.1.40; 6-phosphogluconate dehydrogenase (*6Pgdh*) E.C. 1.1.1.44; glyceraldehyde-3-phosphate dehydrogenase (*Gapdh*) E.C. 1.2.1.12; superoxide dismutase (*Sod-1*) E.C. 1.15.1.1; aspartate amino transferase (*Aat-2*) E.C. 2.6.1.1; adenylate kinase (*Adk-1*) E.C. 2.7.4.3; acid phosphatase (*Acph*) E.C.3.1.3.2; leucine aminopeptidase (*Lap-1, Lap-2*) E.C. 3.4.11; peptidase (Leu-Leu) (*Pep B*) E.C. 3.4.11; peptidase Leu-Ala (*Pep C-1*) E.C. 3.4.11; and glucose phosphate isomerase (*Gpi*) E.C. 5.3.1.9. The buffer systems and staining procedures used were those detailed in Mattiucci et al. (1997). Isozymes were numbered in order of decreasing mobility from the most anodal one. Allozymes were named with numbers indicating their mobility (in mm, standardised conditions) relative to the most common allele, designated as *100*, found in a reference population (i.e. a population of *Corynosoma australe* collected from *A. australis* in Argentinean waters).

The statistical significance of departures from the Hardy-Weinberg (H-W) equilibrium was estimated using chi-square test (χ^2). The genetic divergence was estimated using the following indices: standard genetic Distance and Identity (D_{Nei} and I_{Nei}, Nei, 1972). Population genetic analysis was performed using BIOSYS software (Swofford & Selander, 1989).

***Corynosoma australe* Johnston, 1937**

Description (Figures 2–8*)*

With characteristics of previous descriptions of this species. Hooks arranged in 18–20 rows (usually 18). Each row comprises 12–14 hooks, 9–11 anterior hooks (usually 10) with well-developed, posteriorly directed roots and 2–4 (usually 3) small basal hooks with small, anteriorly directed roots. Following combinations of anterior/basal hooks were observed: 9/3, 9/4, 10/2, 10/3, 10/4, 11/2 and 11/3, usually 10/3. Up to 4 different combinations were recorded in single individual.



Figures 2–8. Corynosoma australe Johnston, 1937, adults from the stomach of *Arctocephalus australis*. 2. Detail of the proboscis, lateral view. 3. Detail of the proboscis showing 19 rows of hooks, apical view. 4. Embryophore. 5. Posterior end of female showing genital spines, lateral view. 6. Posterior end of female showing genital spines, apical view. 7. Posterior end of male showing genital spines, lateral view. 8. Posterior end of male showing genital spines, apical view.

Cystacanths from fish hosts with characteristics of adults, but smaller in size, although proboscis is almost of same size as adults; with developing genitalia. Measurements are given in Table 2.

Male (based on 12 adults and 6 cystacanths). Ventrally somatic armature covers 80.2 (77.7–88.3)% of trunk length in adults and 80.8 (78–83.5)% in cystacanths. Genital opening surrounded by 3 irregular rows of 18–34 triangular genital spines, larger than somatic spines.

Female (based on 10 adults and 6 cystacanths). Ventrally somatic armature covers 89.2 (84.6–100)% of trunk length in adults and 87.4 (85–89)% in cystacanths. Genital opening surrounded by irregular rows of 18–35 triangular genital spines shifted to ventral side, shorter and wider than somatic spines and smaller than those of males. In some specimens genital and somatic spines are contiguous in ventral region but clearly distinguishable.

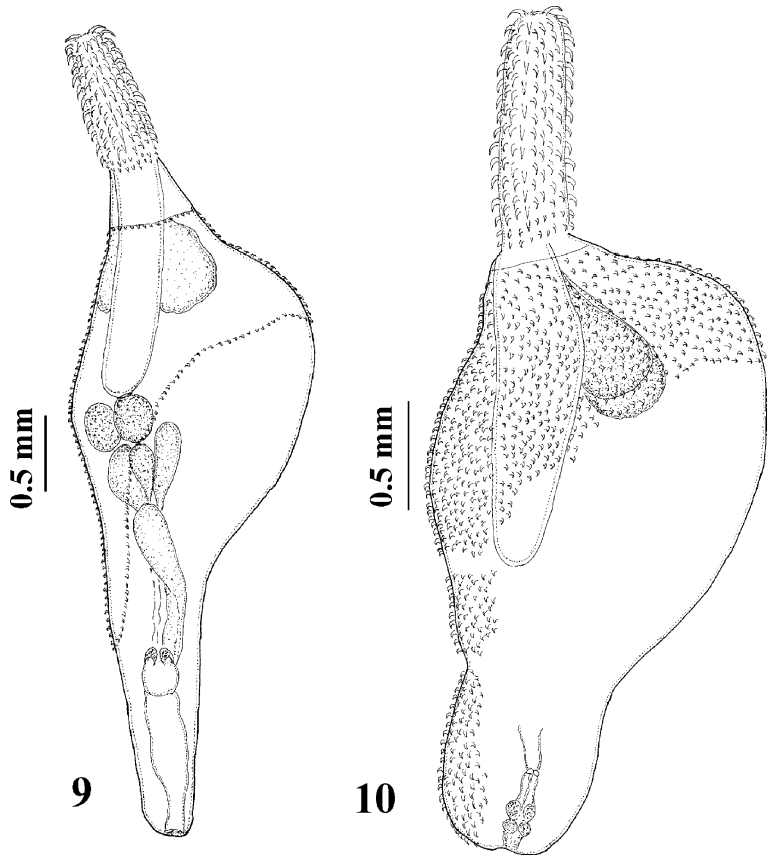
New definitive host: *Mirounga leonina* Linnaeus.
New intermediate host: *Cynoscion guatucupa* (Cuvier).
New localities: Mar del Plata (38°08′S, 57°32′W) and San Clemente del Tuyú (36°30′S, 56°20′W), Argentina.

***Corynosoma cetaceum* Johnston & Best, 1942**
Syn. *Polymorphus arctocephali* Smales, 1986

Table 2. Measurements (mm) of *Corynosoma australis* from *Arctocephalus australis* and *Cynoscion guatucupa.*

Host	*A. australis*		*C. guatucupa*	
	male (n = 12)	female (n = 10)	male (n = 6)	female (n = 6)
Total length	4.60 (4.20–5.40)	4.91(4.22–5.50)	2.82 (2.56–3.18)	3.20 (3.02–3.42)
Maximum width	1.43 (1.30–1.62)	1.59 (1.34–1.90)	0.85 (0.76–0.96)	0.94 (0.80–1.14)
Proboscis length	0.63 (0.58–0.72)	0.68 (0.60–0.74)	0.63 (0.58–0.68)	0.67 (0.60–0.74)
Proboscis width	0.22 (0.21–0.24)	0.23 (0.22–0.25)	0.21 (0.18–0.23)	0.22 (0.15–0.28)
Neck length	0.19 (0.16–0.24)	0.20 (0.15–0.26)	0.22 (0.19–0.24)	0.23 (0.20–0.27)
Neck maximum width	0.40 (0.36–0.46)	0.44 (0.38–0.50)	0.34 (0.26–0.42)	0.31 (0.26–0.42)
Trunk length	3.69 (3.42–4.30)	3.94 (3.30–4.66)	1.87 (1.64–2.18)	2.30 (2.18–2.42)
Fore-trunk ventral length	1.62 (1.40–1.90)	1.77 (1.38–2.30)	1.06 (0.96–1.14)	1.18 (0.90–1.48)
Fore-trunk dorsal length	2.21 (2.00–2.60)	2.41 (1.94–3.00)	1.29 (1.14–1.40)	1.40 (1.10–1.60)
Hind-trunk ventral length	1.90 (1.67–2.16)	1.93 (1.72–2.26)	0.88 (0.82–0.98)	1.11 (0.86–1.44)
Hind-trunk dorsal length	1.51 (1.30–1.78)	1.47(1.20–1.66)	0.74 (0.60–0.82)	0.89 (0.74–0.96)
Hind-trunk width at mid-length	0.55 (0.50–0.62)	0.72 (0.58–0.86)	0.37 (0.30–0.42)	0.43 (0.34–0.54)
Somatic spine length*	40 (30–50)	40 (36–46)	38 (31–42)	43 (40–46)
Somatic spine width*	8 (6–10)	9 (6–10)	7 (6–7)	8
Genital spine length*	45 (42–48)	31 (25–38)	46 (44–48)	36 (31–40)
Genital spine width*	22 (17–29)	11 (8–15)	25 (21–27)	9 (8–10)
Proboscis receptacle length	0.82 (0.74–0.92)	0.94 (0.84–1.04)	0.93 (0.86–1.02)	1.20 (1.10–1.30)
Proboscis receptacle width	0.16 (0.14–0.20)	0.18 (0.16–0.20)	0.21 (0.16–0.26)	0.20 (0.14–0.28)
Lemnisc length	0.67 (0.56–0.74)	0.69 (0.56–0.80)	0.47 (0.38–0.56)	0.47 (0.40–0.56)
Lemnisc width	0.47 (0.42–0.52)	0.49 (0.36–0.60)	0.27 (0.24–0.30)	0.27 (0.20–0.32)
Right testis length	0.54 (0.44–0.70)	–	0.12 (0.10–0.14)	–
Right testis width	0.34 (0.26–0.42)	–	0.09 (0.08–0.12)	–
Left testis length	0.54 (0.40–0.66)	–	0.11 (0.10–0.14)	–
Left testis width	0.34 (0.28–0.42)	–	0.09 (0.08–0.12)	–
Everted bursa length	0.57 (0.42–0.72)	–	–	–
Everted bursa width	0.56 (0.52–0.62)	–	–	–
Embryophore length*	–	103 (92–115)	–	–
Embryophore width*	–	33 (27–42)	–	–

*In micrometres.



Figures 9–10. *Corynosoma cetaceum* Johnston & Best, 1942, cystacanths from the body-cavity of *Cynoscion guatucupa*. 9. Male, lateral view. 10. Female, lateral view.

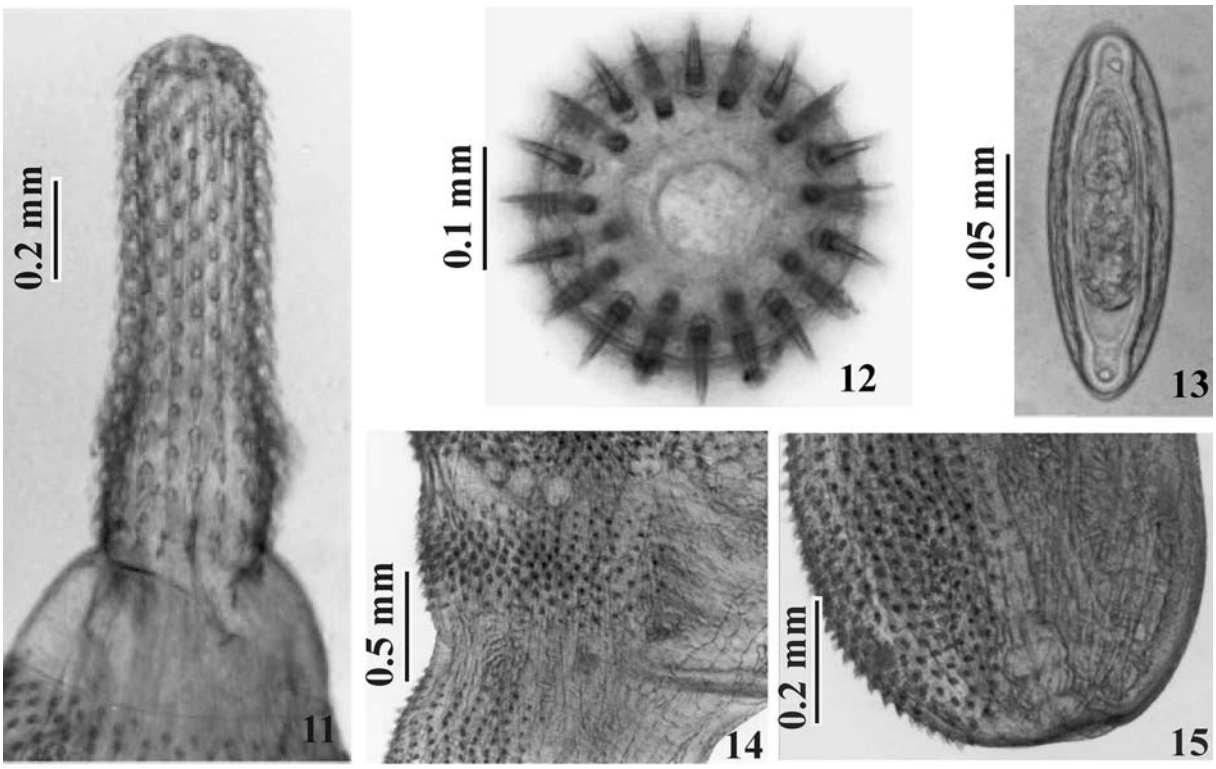
Description (Figures 9–15)

With characteristics of previous descriptions of this species. Hooks arranged in 20–21 rows (usually 20). Each row comprises 13–15 hooks, 11–13 anterior ones (usually 12) with well-developed, anteriorly directed roots and 2–3 (usually 2) small basal hooks with small, posteriorly directed roots. Following combinations of anterior/basal hooks were observed: 11/2, 11/3, 12/2, 12/3 and 13/2 (usually 12/2). Up to 3 different combinations of anterior/basal hooks were recorded in single specimen.

Genital armature absent in both sexes. All specimens from *A. australis* smaller than those from *P. blainvillei* and immature, especially obvious in females, whose embryophores were not observed. Cystacanths from fish hosts with characteristics of adults, but smaller in size, although proboscis is almost of same size, with developing genitalia. Measurements are given in Table 3.

Male (based on 6 adults from *P. blainvillei*, 6 juveniles from *A. australis* and 6 cystacanths from *C. guatucupa*). Somatic armature covers 71.5 (65.8–75.2)% of trunk length ventrally in adults, 69.1 (63.6–74.6)% in juveniles and 71 (57.5–77.1)%. Genital opening devoid of spines.

Female (based on 6 adults from *P. blainvillei*, 6 juveniles from *A. australis* and 6 cystacanths from *C. guatucupa*). Somatic armature covers 95.2 (93.9–96.5)% of trunk length ventrally in adults, 96.8 (96–97.4)% in juveniles and 94.9 (94.3–95.8)% in cystacanths. Ventrally trunk exhibits 2 transverse folds delimiting blunt lobe between fore- and hind-trunks. In most specimens, at level of both transverse folds, ventral somatic armature is interrupted by 2 fields devoid of spines, or less frequently having smaller spines, situated at 43.5 (34.8–48.8)% and 61.6 (52.2–68.3)% of trunk length, respectively, in adults; in juveniles these percentages were 49.1 (47.1–52.6)% and 65 (63.6–



Figures 11–15. *Corynosoma cetaceum* Johnston & Best, 1942. 11. Detail of the proboscis, lateral view.12. Detail of the proboscis showing 20 rows of hooks, apical view. 13. Embryophore. 14. ventral trunk of female showing somatic spines, lateral view. 15. Posterior end of female showing somatic spines near the genital opening, similar in shape and size to the anterior spines, lateral view.

66.5)%; in cystacanths were 48.4 (43.2–52)% and 64.4 (55.5–70.9)%. In some specimens these unarmed fields are only ventrolateral and narrow continuous ventral field of spines is observed along entire trunk. Genital opening devoid of spines.

New definitive host: *Arctocephalus australis* (Zimmerman).
New intermediate host: *Cynoscion guatucupa* (Cuvier).
New localities: Mar del Plata (38°08′S, 57°32′W) and San Clemente del Tuyú (36°30′S, 56°20′W), Argentina.

Genetic differentiation between *Corynosoma australe* and *C. cetaceum* and allozyme markers for their identification

The alleles found and their frequencies observed in the populations of *C. australe* and *C. cetaceum* analysed are reported in Table 4. Most of the enzymatic loci examined were found to be monomorphic in both species. Some enzyme loci (i.e. *Lap-1, Pep B, Pep C-1*) were found to be polymorphic in *C. cetaceum* with no statistically significant departure from the H-W equilibrium. Genetic homogeneity was also found within *C. australe*, despite its occurrence in two different definitive hosts, *A. australis* and *M. leonina*. In *C. australe*, the enzyme loci *6-Pgdh* and *Lap-1* were observed to be polymorphic (Table 4) without statistically significant departures from the H-W equilibrium. Alternative alleles at all the 13 enzymatic loci studied were observed between *C. australe*, from the intestine of *A. australis*, and *C. cetaceum*, from the stomach of *P. blainvillei*.

In addition, electrophoretic migration at the locus *Acph* was found to be anodal in *C. cetaceum* but cathodal in *C. australe*. Nei's standard genetic Distance and Identity values between the two species were found to be $D_{Nei}=\infty$ ($I_{Nei}=0.00$), respectively. Indeed, no alleles were shared by *C. australe* and *C. cetaceum* at any of the studied

Table 3. Measurements (mm) of *Corynosoma cetaceum* adults from *Pontoporia blainvillei*, juveniles from *Arctocephalus australis* and cystacanths from *Cynoscion guatucupa.*

Host	*P. blainvillei*		*A. australis*		*C. guatucupa*	
	male (n = 6)	female (n = 6)	male (n = 6)	female (n = 6)	male (n = 6)	female (n = 6)
Total length	7.47 (7.10–8.00)	5.09 (4.50–5.40)	5.92 (5.08–6.58)	4.75 (4.42–4.98)	5.26 (5.04–5.64)	4.61 (4.30–4.80)
Maximum width	2.46 (2.28–2.60)	2.33 (1.86–2.70)	1.77 (1.64–2.04)	1.79 (1.60–1.92)	1.53 (1.40–1.64)	1.62 (1.44–1.76)
Proboscis length	1.14 (1.00–1.20)	1.11 (1.06–1.16)	1.03 (0.94–1.10)	1.04 (0.94–1.10)	0.95 (0.90–1.04)	1.10 (1.04–1.20)
Proboscis width	0.33 (0.32–0.36)	0.32 (0.28–0.34)	0.33 (0.29–0.34)	0.34 (0.32–0.37)	0.30 (0.26–0.34)	0.33 (0.32–0.36)
Neck length	0.28 (0.26–0.32)	0.27 (0.24–0.29)	0.28 (0.22–0.32)	0.28 (0.25–0.32)	0.32 (0.22–0.38)	0.34 (0.30–0.40)
Neck maximum width	0.63 (0.58–0.66)	0.66 (0.56–0.74)	0.59 (0.48–0.70)	0.54 (0.48–0.58)	0.53 (0.44–0.60)	0.54 (0.40–0.60)
Trunk length	6.14 (5.80–6.54)	3.66 (3.14–4.10)	4.67 (4.08–5.20)	3.38 (3.04–3.58)	4.11 (3.86–4.36)	3.09 (2.82–3.30)
Fore-trunk ventral length	2.48 (2.00–3.16)	2.25 (2.00–2.80)	2.13 (1.70–2.30)	2.20 (2.02–2.30)	2.00 (1.80–2.20)	1.99 (1.72–2.24)
Fore-trunk dorsal length	3.22 (2.90–3.60)	2.95 (2.36–3.80)	2.50 (2.20–2.96)	2.20 (1.40–2.58)	2.38 (2.20–2.56)	2.30 (2.20–2.40)
Hind-trunk ventral length	3.54 (3.20–3.90)	1.19 (1.00–1.30)	2.42 (2.00–2.86)	1.13 (1.10–1.20)	1.96 (1.84–2.10)	0.91 (0.84–1.04)
Hind-trunk dorsal length	3.24 (3.00–3.60)	1.29 (1.06–1.40)	2.15 (1.86–2.60)	1.13 (0.96–1.20)	1.65 (1.44–1.84)	1.02 (0.92–1.12)
Hind-trunk width at midlength	0.97 (0.84–1.10)	1.16 (0.96–1.40)	0.69 (0.62–0.76)	0.79 (0.68–0.88)	0.52 (0.40–0.70)	0.73 (0.66–00.84)
Somatic spine length*	55 (52–59)	60 (54–53)	58 (52–65)	49 (44–52)	52 (46–57)	47 (42–52)
Somatic spine width*	22 (21–27)	20 (19–21)	15 (15–17)	23 (21–25)	16 (15–19)	24 (23–25)
Proboscis receptacle length	1.51 (1.44–1.56)	1.50 (1.40–1.60)	1.22 (1.24–1.26)	1.33 (1.26–1.44)	1.36 (1.20–1.46)	1.43 (1.30–1.50)
Proboscis receptacle width	0.40 (0.36–0.44)	0.38 (0.30–0.44)	0.24 (0.20–0.26)	0.22 (0.20–0.24)	0.31 (0.26–0.36)	0.37 (0.32–0.40)
Lemnisc length	0.73 (0.60–0.90)	0.74 (0.60–0.84)	0.74 (0.60–0.88)	0.72 (0.60–0.84)	0.73 (0.54–0.83)	0.62 (0.50–0.70)
Lemnisc width	0.58 (0.50–0.68)	0.55 (0.36–0.70)	0.42 (0.46–0.76)	0.48 (0.42–0.56)	0.41 (0.36–0.46)	0.41 (0.36–0.46)
Right testis length	0.68 (0.44–0.80)	–	0.39 (0.24–0.50)	–	0.18 (0.12–0.24)	–
Right testis width	0.44 (0.30–0.52)	–	0.27 (0.14–0.44)	–	0.15 (0.08–0.26)	–
Left testis length	0.65 (0.40–0.78)	–	0.41 (0.26–052)	–	0.18 (0.14–0.26)	–
Left testis width	0.44 (0.34–0.56)	–	0.26 (0.16–0.34)	–	0.15 (0.10–0.24)	–
Everted bursa length	1.17 (1.04–1.30)	–	–	–	–	–
Everted bursa width	0.96 (0.90–1.06)	–	–	–	–	–
Embryophore length*	–	158 (147–178)	–	–	–	–
Embryophore width*	–	50 (44–58)	–	–	–	–

*In micrometres.

Table 4. Characteristic alleles, with their frequencies (in parenthesis), at 13 enzymatic loci studied in *Corynosoma australe* in relation to *C. cetaceum*.

Locus	*C. australe*	*C. cetaceum*
Mdh-1	*100* (1.00)	*90* (1.00)
Me	*100* (1.00)	*110* (1.00)
6Pgdh	*100* (0.82), *93* (0.13), *105* (0.05)	*80* (1.00)
Gapdh	*100* (1.00)	*115* (1.00)
Sod-1	*100* (1.00)	*80* (1.00)
Aat-2	*100* (1.00)	*107* (1.00)
Adk-1	*100* (1.00)	*110* (1.00)
Lap-1	*100* (0.96), *93* (0.04)	*85* (0.97), *80* (0.03)
Lap-2	*100* (1.00)	*95* (1.00)
Acph	*100* (1.00)	*115* (1.00)
Pep B	*100* (1.00)	*90* (0.90), *85* (0.10)
Pep C-1	*100* (1.00)	*95* (0.96), *85* (0.03), *105* (0.01)
Gpi	*100* (1.00)	*105* (1.00)
He	0.029 (±0.08)	0.024 (±0.05)

The sign "–" indicates cathodal migration.
He, Expected mean heterozygosity per locus.

loci. On the other hand, a low value of genetic distance was found between populations of *C. australe* from the two definitive hosts ($D_{Nei} = 0.01$). The corresponding interpopulational genetic diversity in this taxon was $Fst = 0.03$.

A similar level of genetic variability, based on the 13 enzyme loci, for the parameter *He* was found in both species (Table 4). The percentage of polymorphic loci, according to the 0.99 criterion, resulted $P_{99} = 0.15$ in *C. australe* and $P_{99} = 0.23$ in *C. cetaceum*.

All of the specimens collected from the intestine of both *A. australis* and *M. leonina* were found to correspond to *C. australe*. While, the 28 acanthocephalan specimens recovered from the stomach of *P. blainvillei* were identified genetically as *C. cetaceum*. Moreover, the few individuals collected from the stomach of one specimen of *A. australis* were also found to correspond to *C. cetaceum*. Furthermore, cystacanths recovered from the fish *C. guatucupa* were identified genetically; of the 34 cystacanths tested, 17 corresponded to *C. australe* and 17 to *C. cetaceum*.

Discussion

The specific status of Corynosoma australe *and* C. cetaceum *in the Southwestern Atlantic Ocean*

The original description of *C. australe* by Johnston (1937) was brief and a number of external and internal features were not included. According Smales (1986), the type-specimens were incompletely extended and the internal features blackened. Therefore, for comparative purposes, measurements for the Australian material were taken from redescription given by Smales (1986). Comparisons of the specimens studied herein with previous descriptions of adult specimens of *C. australe* from Australia (Smales, 1986), the Antarctic (Zdzitowiecki, 1984a) and Uruguay (Morini & Boero, 1960), as well as of cystacanths from Brazil (Pereira & Neves, 1993; Knoff et al., 2001), showed that most morphometric characteristics are relatively uniform; nevertheless, Argentinian and Uruguayan adult specimens have a larger embryophore and body size, and 18 to 20 hook rows on the proboscis. Embryophores from the present study were markedly larger (almost outside the reported ranges) than those given in other papers, including those parasites from the same host species given by Morini & Boero (1960).

George-Nascimento & Marín (1992) found adult specimens of *Corynosoma* sp. in *Otaria byronia* (= *O. flavescens*) and in *A. australis* from Uruguay. These authors observed morphometric differences between parasites from both host species, although they considered that they belong to the same species and that the size variability is a consequence of host-induced effects, suggesting that *A. australis* is the most suitable host species.

They also postulated that parasites partly agreed with either *C. australe* or *C. pseudohammani* Zdzitowiecki, 1984. However, some of the morphometric (i.e. lemnisci larger than the proboscis receptacle, proboscis width) and meristic (number of hooks per row on the proboscis) characteristics given by George-Nascimento & Marín (1992) do not coincide with either *C. australe* or *C. pseudohammani* (see Zdzitowiecki, 1984b; present study). Taking into account the fact that *C. australe* is found in the same host species and in the proximity of the study areas (Argentina and Uruguay) (Aznar et al., 2004; present study), George-Nascimento & Marín's parasites probably belonged to *C. australe*.

Specimens of *C. cetaceum* examined in the present paper agree in general terms with the characteristics that define the species; however, some differences in the number of proboscis hook rows (20–21 versus 18–9) and in the number of hooks per row (13–15 versus 12–13 or 14–16) were observed. The ventrally transverse folds delimiting a blunt lobe between the fore- and hind-trunks in the female, described by Aznar et al. (1999b, 2002b), were also observed in cystacanths in the present study.

Comparisons of samples of *C. cetaceum* on a large geographical scale showed a high level of variability between Southwestern Atlantic and South Australian populations, which were grouped into two well-defined clusters by Principal Component Analysis (Aznar et al., 1999a). In particular, these authors observed a smaller number of hooks per row, a different pattern of somatic spines in females and a tendency for the genital pore to be subterminal in some South American specimens.

C. cetaceum was also found in *A. australis*, but all specimens were smaller than those from *P. blainvillei* and all were juveniles without eggs. This species typically inhabits the stomach of its definitive cetacean hosts (Aznar et al., 2001), but in *A. australis* it was also found parasitising the intestine. *A. australis* appears to be an unsuitable or accidental host for *C. cetaceum* in the study area. Similarly, this parasite has been found in juvenile form in *A. pusillus doriferus* from Australia (Smales, 1986; Aznar et al., 1999a).

Regarding the life-cycle of *C. cetaceum*, and as pointed out by Aznar et al. (1999a), fish are a likely necessary component of their life-cycle, given the feeding habits of their mammalian hosts. In the present paper, the presence of cystacanths of this species in fish is confirmed by both morphological and allozyme evidence, and their first description is provided.

Genetic comparisons with further populations from different geographical areas will enable an assessment of whether the genetic homogeneity observed within samples of *C. australe* and *C. cetaceum* from Argentina is constant over a large geographical range.

The generic status of Corynosoma cetaceum

Corynosoma cetaceum was first described from the common dolphin *Delphinus delphis* and from the bottlenose dolphin *Tursiops truncatus* in Australian waters (Johnston & Best, 1942). These authors included it in *Polymorphus* due to the absence of genital spines in both sexes, which is the only criterion separating *Corynosoma* Lühe, 1904 from *Polymorphus* Lühe, 1911 (see Schmidt & Dailey, 1971). However, the presence of six cement-glands (instead of four) is an additional criterion for separating *C. cetaceum* from typical species of *Polymorphus*. This feature was discussed by Smales (1986), who found that, due to the number of cement-glands, *C. cetaceum* (as *P. cetaceum*) falls within *Hexaglandula* Petrochenko, 1950, rather than in *Polymorphus* (according to the key proposed by Schmidt, 1973). *Hexaglandula* was later synonymised with *Polymorphus* by Amin (1992), but this has not been accepted by other authors (see Nickol et al., 2002b).

As stated by Aznar et al. (1999a), the concept of genital spines is problematical, due to its ambiguous definition with respect to somatic spines. Therefore, using a less restricted definition of a genital spine, *P. cetaceum* was retained as *C. cetaceum* by Aznar et al. (1999a) and sustained by Aznar et al. (2002a). This problem appears to arise from the definition of a genital spine based only on its position relative to the genital opening (see Aznar et al., 1999a) and without consideration of genital and somatic spine morphology. Females of *C. cetaceum* bear spines in the vicinity of the genital pore, which are identical to the somatic spines, whereas in *C. australe* genital spines are stout, triangular and clearly discernable in both sexes. Therefore, *C. cetaceum* lacks genital spines (*sensu stricto*). In a recent paper, Aznar et al.

(2002a) found one of 80 males of *C. cetaceum* from two specimens of *D. delphis* off Patagonia as having two small spines adjacent to the genital pore and isolated from the somatic spines; they stated that this finding confirmed the reassignment of *C. cetaceum* to *Corynosoma* (see Aznar et al., 1999a). However, the presence of only one male having genital spines in over 3,000 males examined from different host in several regions (Aznar et al., 2002a) suggests that it cannot be taken as a reliable diagnostic feature at the generic level. This, however, does not preclude *C. cetaceum* from *Corynosoma*, because some species from marine mammals, which lack genital spines in both sexes, are included within *Corynosoma*, e.g. *C. falcatum* Van Cleave, 1953, *C. sudsuche* Belopolskaja, 1959 and *C. septentrionalis* Treshtchev, 1966 (see Aznar et al., 1999a).

Despite the evidence relating to both the genital spine definition and the number of cement-glands, the discrimination between *Corynosoma* and *Polymorphus* remains controversial and further revision is required, specifically for *C. cetaceum*. In fact, Smales (1986) stated that the combination of characters found in *C. cetaceum* does not agree with any of the generic diagnoses proposed by Schmidt (1973, 1975). Furthermore, and despite of the morphological similarity that this species shares with most species of *Corynosoma* that use marine mammals and fish as definitive and paratenic hosts, respectively, most species of *Corynosoma* mature in pinnipeds, whereas *C. cetaceum* parasitises cetaceans. On the other hand, typical species of *Polymorphus* exhibit a freshwater cycle with crustaceans as intermediate hosts and waterfowl as the normal definitive hosts, but do not use fish as paratenic hosts (Aznar et al., 1999a).

Nickol et al. (1999) concluded that, for polymorphid genera, the occurrence in different groups of crustacean intermediate hosts implies substantial life-history differences and justifies differentiation at the generic level. Perhaps this criterion can also be applied to the use of definitive hosts (pinnipeds for most *Corynosoma* spp. maturing in mammals and cetaceans for *C. cetaceum*). In this sense, *Hexaglandula*, which has six cement-glands as *C. cetaceum*, parasitises decapod crustaceans, fish and birds as intermediate, paratenic and definitive hosts, respectively, and, according Nickol et al. (2002b), must be retained as a valid genus; therefore, *C. cetaceum* is excluded from *Hexaglandula*.

Allozyme studies have indicated a high genetic divergence between *C. australe* and *C. cetaceum*, suggesting a generic distinction between them. Similarly, García-Varela et al. (2005) inferred the phylogenetic relationships between 10 nominal species of *Corynosoma* (including *C. australe* and *C. cetaceum*) based on the analysis of the internal transcribed spacer and 5.8S ribosomal RNA sequences. These authors found that *C. cetaceum* appeared to be the sister taxon of all other species of *Corynosoma*. However, they could not resolved the generic status of this species because of the relatively limited taxa sampled. They also suggested that the genital spines could be a homoplastic character (Aznar, *pers. comm.*). The high genetic differentiation here inferred from other nuclear markers (allozymes), of *C. cetaceum* with respect to a species from pinnipeds, *C. australe*, appears to confirm this finding, and that the presence of genital spines could only be an adaptative character of limited phylogenetic value.

Indeed, the high genetic heterogeneity found within *Corynosoma* and the high genetic differentiation observed between *C. australe* and *C. cetaceum* in the present study are at the same level as that found, using the same genetic markers, between two congeneric acanthocephalans, the marine *Echinorhynchus gadi* Zoega in Müller, 1776 and the brackish-water *E. salmonis* Müller, 1784, ($I = 0.00$) (Väinöla et al., 1994). Similarly, a very high genetic divergence was also reported between species of anisakid nematodes of the genus *Contracaecum* Railliet & Henry, 1913, whose definitive hosts are pinnipeds, with respect to species of the same genus that use fish-eating birds as definitive hosts (Nascetti et al., 1990) and which exhibit the same morphological characters at the generic level.

Further extensive studies, including other species of *Corynosoma* from other hosts and geographical areas are needed to determine whether *C. cetaceum* should be retained as a member of *Corynosoma*.

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References

Aho J.M., Mulvei M., Jacobson K.C. & Esch G.W. (1992) Genetic differentiation among congeneric acanthocephalans in the yellow-bellied slider turtle. *Journal of Parasitology*, **78**, 974–981.

Amin O.M. (1985) Classification. *In*: Crompton, D.W.T. & Nickol, B.B. (Eds) *Biology of the Acanthocephala*. Cambridge: Cambridge University Press, pp. 27–72.

Amin O.M. (1992) Review of the genus *Polymorphus* Lühe, 1911 (Acanthocephala: Polymorphidae), with the synonymization of *Hexaglandula* Petrochenko, 1950, and *Subcorynosoma* Hoklova, 1967, and a key to the species. *Qatar University Science Journal*, **12**, 115–123.

Andrews R.H. & Chilton N.B. (1999) Multilocus allozyme electrophoresis: a valuable technique for providing answers to problems in parasite systematics. *International Journal for Parasitology*, **29**, 213–253.

Aznar F.J., Raga J.A., Corcuera J. & Monzón F. (1994a) Helminths as biological tags for franciscana (*Pontoporia blainvillei*) (Cetacea, Pontoporidae) in Argentinian and Uruguayan waters. *Mammalia*, **59**, 427–435.

Aznar F.J., Balbuena J.A. & Raga J.A. (1994b) Helminth communities of *Pontoporia blainvillei* (Cetacea, Pontoporidae) in Argentinian waters. *Canadian Journal of Zoology*, **72**, 702–706.

Aznar F.J., Bush A.O. & Raga J.A. (1999a) *Polymorphus arctocephali* Smales, 1986, a synonym of *Corynosoma cetaceum* Johnston, Best, 1942 (Acanthocephala: Polymorphidae). *Systematic Parasitology*, **44**, 61–72.

Aznar F.J., Bush A.O., Fernández M. & Raga J.A. (1999b) Constructional morphology and mode of attachment of the trunk of *Corynosoma cetaceum* (Acanthocephala: Polymorphidae). *Journal of Morphology*, **241**, 237–249.

Aznar F.J., Bush A.O, Balbuena J.A. & Raga J.A. (2001) *Corynosoma cetaceum* in the stomach of franciscanas, *Pontoporia blainvillei* (Cetacea): an exceptional case of habitat selection by an acanthocephalan. *Journal of Parasitology*, **87**, 536–541.

Aznar F.J., Berón-Vera B., Crespo E. & Raga J.A. (2002a) Presence of genital spines in a male *Corynosoma cetaceum* Johnston, Best, 1942 (Acanthocephala). *Journal of Parasitology*, **88**, 403–404.

Aznar F.J., Bush A.O. & Raga J.A. (2002b) Reduction and variability of trunk spines in the acanthocephalan *Corynosoma cetaceum*: the role of physical constraints on attachment. *Invertebrate Biology*, **121**, 104–114.

Aznar F.J., Cappozzo H.L., Taddeo D., Montero F.E. & Raga J.A. (2004) Recruitment, populations structure, and habitat selection of *Corynosoma australe* (Acanthocephala) in South American fur seals, *Arctocephalus australis*, from Uruguay. *Canadian Journal of Zoology*, **82**, 741–748.

Cremonte F. & Sardella N.H. (1997) The parasitofauna of *Scomber japonicus* Houttuyn, 1782 (Pisces: Scombridae) in two zones of the Argentine Sea. *Fisheries Research*, **31**, 1–9.

Dailey M.D. & Brownell R.L. Jr (1972) A checklist of marine mammal parasites. *In*: Ridgway, S.H. (Ed), *Mammals of the sea. Biology and medicine*. Springfield, Illinois: Charles C. Thomas, pp. 528–589.

Dans S.L., Reyes L.M., Pedraza S.M, Raga J.A. & Crespo E.A. (1999) Gastrointestinal helminths of the dusky dolphin, *Lagenorhynchus obscurus* (Gray, 1828), off Patagonia, in the Southwest Atlantic. *Marine Mammal Science*, **15**, 649–660.

De Buron I., Renaud F. & Euzet L. (1986) Speciation and specificity of acanthocephalans. Genetic and morphological studies of *Acanthocephaloides geneticus* sp.nov. parasitizing *Arnoglossus laterna* (Bothidae) from the Mediterranean littoral (Sète – France). *Parasitology*, **92**, 165–171.

Delyamure, S.L. (1968) *Helminthofauna of marine mammals (ecology and phylogeny)*. Jerusalem: Israel Program for Scientific Translation, 522 pp. (English translation of Russian original (1955) [*The helminthofauna of marine mammals of the world their ecology and phylogeny*.] Moscow: Nauka, 517 pp.).

García-Varela, M., Aznar, F.J., Pérez-Ponce de León, G., Piñero, D. & Laclette, J.P. (2005) Molecular phylogeny of *Corynosoma* Lühe, 1904 (Acanthocephala) based on 5.8S and internal transcribed spacer sequences. *Journal of Parasitology*, in press.

George-Nascimento M.F. & Marín S.L. (1992) Efecto de dos especies hospedadoras, el lobo fino austral *Arctocephalus australis* (Zimmerman) y el lobo marino común *Otaria byronia* (Blainville) (Carnivora; Otariidae), sobre la morfología y la fecundidad de *Corynosoma* sp. (Acanthocephala; Polymorphidae) en Uruguay. *Revista Chilena de Historia Natural*, **65**, 183–193.

Ivanov V.A. (1996) *Ecología de los helmintos parásitos de peces marinos*. Tesis Doctoral. Universidad Nacional de La Plata, Facultad de Ciencias Naturales y Museo, 176 pp.

Johnston T.H. (1937) Entozoa from the Australian hair seal. *Proceedings of the Linnean Society of New South Wales*, **62**, 9–16.

Johnston T.H. & Best E.W. (1942) Australian Acanthocephala. No. 3. *Transactions of the Royal Society of South Australia*, **66**, 250–254.

Kagei N., Tobayama T. & Nagasaki Y. (1976) On the helminthum of franciscana, *Pontoporia blainvillei*. *Scientific Report of the Whales Research Institute*, **28**, 161–166.

Knoff M., São Clemente S.C., Pinto R.M. & Gomes D.C. (2001) Digenea and acanthocephala of elasmobranch fished from the Southern coast of Brazil. *Memórias do Instituto Oswaldo Cruz*, **96**, 1095–1101.

Mattiucci S., Nascetti G., Cianchi R., Paggi L., Arduino P., Margolis L., Brattey J., Webb S., D'Amelio S., Orecchia P. & Bullini L. (1997) Genetic and ecological data on the *Anisakis simplex* complex, with evidence for a new species (Nematoda, Ascaridoidea, Anisakidae). *Journal of Parasitology*, **83**, 401–416.

Mattiucci S., Paggi L., Nascetti G., Abollo E., Webb S., Pascual S., Cianchi R. & Bullini L. (2001) Genetic

divergence and reproductive isolation between *Anisakis brevispiculata* and *Anisakis physeteris* (Nematoda: Anisakidae). *International Journal for Parasitology*, **31**, 9–14.

Mattiucci S., Cianchi R., Nascetti G., Paggi L., Sardella N., Timi J., Webb S., Bastida R., Rodriguez D. & Bullini L. (2003) Genetic evidence for two sibling species within *Contracaecum ogmorhini* Johnston et Mawson, 1941 (Nematoda: Anisakidae) from otariid seals of boreal and austral regions. *Systematic Parasitology*, **54**, 13–23.

Morini, E.G., & Boero, J.J. (1960) *Corynosoma otariae* n. sp. (Acanthocephala; Polymorphidae) parásito de un lobo marino (*Otaria flavescens*). *Actas y Trabajos 1° Congreso Sudamericano de Zoología*, La Plata, 1959, pp. 229–234.

Nascetti G., Paggi L., Orecchia P., Smith J., Mattiucci S. & Bullini L. (1986) Electrophoretic studies on the *Anisakis simplex* complex (Ascaridida: Anisakidae) from Mediterranean and North-East Atlantic. *International Journal for Parasitology*, **16**, 633–640.

Nascetti G., Bullini L., Cianchi R., Paggi L., Orecchia P., Mattiucci S. & Berland B. (1990) Genetic relationships among anisakid species belonging to the genera *Contracaecum* and *Phocascaris*. *Bulletin de la Société Française de Parasitologie*, **8**, 261.

Nascetti G., Cianchi R., Matiucci S., D'Amelio S., Orecchia P., Paggi L., Brattey J., Berland B., Smith J.W. & Bullini L. (1993) Three sibling species within *Contracaecum osculatum* (Nematoda, Ascaridida, Ascaridoidea) from the Atlantic Arctic-Boreal region: reproductive isolation and host preferences. *International Journal for Parasitology*, **23**, 105–120.

Nei M. (1972) Genetic distance between populations. *The American Naturalist*, **106**, 283–292.

Nickol B.B., Crompton D.W.T. & Searle D.W. (1999) Reintroduction of *Profilicollis* Meyer, 1931, as a genus in Acanthocephala: significance of the intermediate host. *Journal of Parasitology*, **85**, 716–718.

Nickol B.B., Helle E. & Valtonen E.T. (2002a) *Corynosoma magdaleni* in gray seals from the Gulf of Bothnia, with emended descriptions of *Corynosoma strumosum* and *Corynosoma magdaleni*. *Journal of Parasitology*, ***88***, 1222–1229.

Nickol B.B., Heard R.W. & Smith N.F. (2002b) Acanthocephalans from crabs in the southeastern U.S., with the first intermediate hosts known for *Arhythmorhynchus frassoni* and *Hexaglandula corynosoma*. *Journal of Parasitology*, **88**, 79–83.

Pereira J. Jr & Neves L.F.M. (1993) *Corynosoma australe* Johnston, 1937 (Acanthocephala, Polymorphidae) em *Micropogonias furnieri* (Desmarest, 1823) (Perciformes, Sciaenidae) de litoral do Rio Grande do Sul. *Comunicações do Museu de Ciências e Tecnologia da PUCRS, Série Zoologia*, **6**, 51–61.

Sardella N.H. & Timi J.T. (1996) Parasite communities of *Merluccius hubbsi* from the Argentinean-Uruguayan Common Fishing Zone. *Fisheries Research*, **27**, 81–88.

Sardella N.H., Etchegoin J.A. & Martorelli S.R. (1995) Las comunidades parasitarias de *Micropogonias furnieri* (corvina) en Argentina. *Boletín del Instituto Oceanográfico* (Univ. de Oriente - Venezuela), **34**, 41–47.

Sardella N.H., Avendaño M.F. & Timi J.T. (1998) Parasites communities of *Genypterus blacodes* and *G. brasiliensis* (Pisces: Ophidiidae) from Argentina. *Helminthologia*, **35**, 209–218.

Schmidt G.D. (1973) Resurrection of *Southwellina* Witenberg, 1932, with a description of *Southwellina dimorpha* sp. n., and a key to genera in Polymorphidae (Acanthocephala). *Journal of Parasitology*, **59**, 299–305.

Schmidt G.D. (1975) *Andracantha*, a new genus of Acanthocephala (Polymorphidae) from fish-eating birds, with descriptions of three species. *Journal of Parasitology*, **61**, 615–620.

Schmidt G.D. & Dailey M.D. (1971) Zoogeography and the generic status of *Polymorphus* (*Polymorphus*) *cetaceum* (Johnston, Best, 1942) comb. n. (Acanthocephala). *Proceedings of the Helminthological Society of Washington*, **38**, 137.

Smales L.R. (1986) Polymorphidae (Acanthocephala) from Australian mammals with description of two new species. *Systematic Parasitology*, **8**, 91–100.

Suriano D.M. (1966) Estudio de la fauna de "*Micropogon opercularis*" en relación con problemas zoogeográficos del Atlántico Sur. *Comunicaciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Parasitología*, **1**, 31–47.

Swofford D.L., Selander R.B. (1989) *BYOSYS-1, a computer program for the analysis of allelic variation in population genetics and biochemical systematics*, version 1.7. Champaign: Illinois, Natural History Survey, 31 pp.

Szidat L. (1949) Los parásitos del róbalo (*Eleginops maclovinus* Cuv. & Val.). 1° *Congreso Nacional de Pesquerías Marítimas e Industrias Derivadas, Mar del Plata*, pp. 235–269.

Szidat L. (1969) Los parásitos de la "palometa" *Parona signata* (Jenyns, 1842) Berg, 1895, y su aplicación a problemas zoogeográficos del Atlántico Sur. *Neotrópica*, **15**, 125–131.

Tanzola R.D. & Guagliardo S.E. (2000) Helminth fauna of the Argentine conger, *Conger orbignyanus* (Pisces: Anguilliformes). *Helminthologia*, **37**, 229–232.

Tanzola R.D., Guagliardo S.E., Brizzola S.M. & Arias M.B. (1997) Helminth fauna of *Porichthys porosissimus* (Pisces: Batrachoidiformes) in the estuary of Bahía Blanca Argentina. *Helminthologia*, **34**, 221–227.

Timi J.T. (2003) Parasites of Argentine anchovy, *Engraulis anchoita*, in the Southwest Atlantic, latitudinal patterns and their use for discrimination of host populations. *Journal of Fish Biology*, **63**, 90–107.

Väinöla R., Valtonen E.T. & Gibson D.I. (1994) Molecular systematics in the acanthocephalan genus *Echinorhynchus* (*sensu lato*) in northern Europe. *Parasitology*, **108**, 105–114.

Zdzitowiecki K. (1984a) Some antarctic acanthocephalans of the genus *Corynosoma* parasitizing Pinnipedia, with descriptions of three new species. *Acta Parasitologica Polonica*, **29**, 359–377.

Zdzitowiecki K. (1984b) Redescription of *Corynosoma hamanni* (Linstow, 1892) and description of *C. pseudohamanni* sp. n. (Acanthocephala) from the environs of the South Shetlands (Antarctic). *Acta Parasitologica Polonica*, **29**, 379–393.

Zdzitowiecki K. (1989) New data on the morphology and distribution of two acanthocephalans, *Andracantha baylisi* (Zdzitowiecki, 1986) comb. n. and *Corynosoma australe* Johnston, 1937. *Acta Parasitologica Polonica*, **34**, 167–172.