METAZOAN PARASITES OF MARINE MAMMALS FROM THE CARIBBEAN AND THE WESTERN COAST OF NORTH AMERICA

By

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ABSTRACT

Studies concerning marine mammal parasites are scarce and some are outdated. I document the metazoan parasites of cetaceans and sirenians from Puerto Rico, the U.S. and British Virgin Islands, and of cetacean and pinnipeds from California using both morphological and genetic identification. Forty cetaceans and manatees were salvaged in the Caribbean between 1992 and 2004 and 28 marine mammals were salvaged in California between 1974 and 2002. Parasitic specimens were collected after necropsy and fixed in 10% formalin or preserved in 70% ethanol. Parasites were mounted in lactophenol for morphological identification. Because of morphological similarities between nematode parasites, genetic identification was performed on 36 helminthes. For California, six species of nematodes, two cestodes, one acanthocephalan and one arthropod were found. For the Caribbean, eight species of nematodes, two cestodes, two acanthocephalans, and three species of trematodes were identified. These constitute two new host records for the west coast of North America. Seven new host records and five new geographic records were found for the Caribbean.

RESUMEN

Los estudios concernientes a parásitos de mamíferos marinos, resultan escasos y en algunos casos anticuados. Documento parásitos de cetáceos y sirenios para Puerto Rico, las islas Vírgenes Estadounidenses y Británicas, así como los parásitos de cetáceos y pinnípedos de California. La metodología utilizada para la identificación se baso en la morfología y la genética. Los parásitos fueron obtenidos durante las necropsias practicadas, 40 cadáveres de cetáceos y manatíes entre los años 1992-2004 y 28 cadáveres de mamíferos marinos en California entre los años 1974-2002. Los parásitos fueron fijados en formalina al 10% o etanol al 70%. La identificación morfológica se realizó usando preparaciones en lactofenol de los ejemplares examinados. Debido a las similitudes entre los nemátodos parasíticos, fue llevado a cabo un análisis en 36 helmíntos. Fueron encontradas seis especies de nemátodos, dos céstodos, un acantocéfalo, y un artrópodo para los mamíferos procedentes de California, ocho especies de nemátodos, dos céstodos, dos acantocéfalos, y tres tremátodos para los mamíferos procedentes del Caribe. Los resultados incluyen dos nuevos reportes de hospedero para la costa oeste de Norte América y siete nuevos reportes geográficos para el área del Caribe.

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INTRODUCTION

Reports of metazoan parasites from marine mammals date back to Carolus Linnaeus and gained thrust in the last 50 years (Aznar et al. 2001) because of the work of Soviet helminthologists (Delyamure 1955, Delyamure and Skrjabin 1985). Parasites have served biologists as indicators of current and historical ecological relationships (Aznar et al. 2001) and they provide useful information on host ecology, biogeography and phylogeny (Gardner and Campbell 1992, Brooks and McLennan 1993, Hoberg 1996, Hoberg 1997). Nevertheless, parasitological studies on marine mammals tend to be opportunistic, a by-product of pathology assessment of these protected species (Raga et al. 1997). When conducted, these studies have documented parasitic biodiversity in different geographic localities that serve as comparisons for variations in the zoogeographic distribution, biology and evolution of their respective host.

Although parasites are common in marine mammals, they are considered relatively unimportant, most of the time causing no observable clinical signs or pathological conditions in their hosts (Dierauf 1990). Unfortunately, the latter statement only considers clinical and pathological aspects. Research on parasite populations has provided important information on host population. For instance, Dailey (1979) recommended using parasites as biological tags or indicators for host's migration and feeding, social structure, general health condition, and as an aid in assessing mortality. Additionally, they play an important role in the aspect of biodiversity that should be evaluated in the future (Windsor 1995, Hoberg 1997, Brooks and Hoberg 2000).

Justification and significance of study

Even though the presence of parasites has been documented in the Caribbean and in the west coast of North America, these reports are either scarce or outdated. Furthermore, no previous records have been found concerning both a genetic and morphological study for marine mammal parasites from these areas. Morphological study together with genetic identification has recently proven to reveal the correct identification and species classification allowing a more clear perspective on how the host and the parasite evolve (Mattiucci 1993).

Parasite diversity documentation is essential in understanding different aspects of the biology, ecology, evolution and distribution of marine mammals representing a valuable tool for conservation and management plans ongoing on endangered marine species.

Objectives of the study

This study aims to identify and document the parasitic fauna from certain marine mammals stranded in the west coast of North America (1974-2002) and the Caribbean (1992-2004), adding to the list of parasite biodiversity. Morphological and molecular protocols are applied for species identification, thus providing valuable information on parasite record and diversity, parasite evolution and recognition of sibling species (i.e., recognition of morphologically similar species but reproductively isolated), and status of parasites controversial taxa (Paggi et al. 1991), hence, corroborating current morphological identification.

REVIEW OF LITERATURE

Metazoan parasites of marine mammals

More than 120 living species of marine mammals have been documented worldwide: 84 cetaceans, 36 pinnipeds, 4 sirenians, the sea otter (*Enhydra lutris* [Linnaeus, 1758]) and the polar bear (*Ursus maritimus* Phipps, 1774) (Hoelzel 2002). Most parasite species infecting cetaceans belong to the families Polymorphidae (Acanthocephala), Cyamidae (Amphipoda), Campulidae (Digenea), Diphyllobothriidae and Tetrabothriidae (Cestoda), Anisakidae, Pseudaliidae and Crassicaudidae (Nematoda) (Aznar et al. 2001). Most of the parasitic families in pinnipeds are similar, i.e., Diphyllobothriidae and Tetrabothiidae (Cestoda), Anisakidae (Nematoda) and Polymorphidae (Acanthocephala), but the Heterophyidae (Digenea), Echinophthiriidae (Hexapoda), and Halarachnidae (Acarina) are not found in cetaceans and sirenians (Aznar et al. 2001). The lack of hair to attach the eggs and a proper surrounding environment are clear reasons for the absence of lice and acari in cetaceans (Aznar et al. 2001). Coccidia of the genera *Eimeria*, *Sarcocystis* and *Toxoplasma* are the most common protozoans that have been reported from pinnipeds and cetaceans (Dailey 1985, Lauckner 1985). *Eimeria phocae*, has been reported to be responsible for causing coccidiosis and death of harbor seals (*Phoca vitulina* Linnaeus, 1758) on the Atlantic coast of North America (Aznar et al. 2001).

Several species of parasites infecting cetaceans, pinnipeds, and the sea otter, are specific to their host and as a result, they are limited in distribution, i.e., Pseudaliidae,

Crassicaudidae and Cyamidae in cetaceans, Echinophthiriidae in pinnipeds, and Campulidae and Diphyllobothriidae in cetaceans, pinnipeds, and the sea otter (Aznar et al. 2001). Fifty-five genera of macroparasites or symbionts have been reported in cetaceans, of which 76% were found to be exclusive, and 11% were shared with pinnipeds and/or other hosts (Aznar et al. 2001). However, 42% of these macroparasites are specific to pinnipeds and the sea otter, 14% are shared with cetaceans, and 44% are shared with cetaceans and/or other hosts, mainly terrestrial carnivores and/or marine birds (Aznar et al. 2001).

Parasitic fauna for sirenians seem to be more distinct, probably because of the host's herbivorous diet. Digenians, of the family Opisthotrematidae are most commonly found in these marine mammals. Cestodes and arthropods are rare and acanthocephalans are not present (Aznar et al. 2001). Even though the presence of these creatures has been documented over time there are still new species of parasites to be identified following the evolution, distribution and biology of marine mammals.

Metazoan parasites of marine mammals collected off the west coast of North America

In the western coast of North America, studies concerning marine mammal parasites are outdated. Prior to the 1990s, a considerable number of comprehensive studies were reported on cetaceans from the area including Dailey (1969; 1971), Schmidt and Dailey (1971), Margolis and Dailey (1972), Dailey and Brownell (1972), Dailey and Perrin (1973), Dailey (1975), Dailey and Ridgway (1976), Dailey and

Walker (1978), Dailey and Nutting (1979), and Dailey (1985). However, subsequent to the 1990s, only Dailey et al. (2000), Dailey (2001), and Dailey et al. (2002) reported finding endoparasites on marine mammals from the area. In addition, no previous reports were found using genetics to identify marine mammal parasites from California.

A list of parasitic fauna reported for marine mammals stranded in California are summarized below.

- **False killer whale (*Pseudorca crassidens* [Owen 1846])**—The trematodes *Nasitrema attenuata*, *N. globicephalae* and *N. gondo* have been found in the air sinuses (Neiland et al. 1970, Dailey and Brownell 1972, Morimitsu et al. 1987). The nematode *Stenurus globicephalus* has been collected from the pterygoid sinus complex and lungs (Hall and Schimpf 1979, Odell et al. 1980). In addition, two nematodes (*Anisakis simplex* and *A. typica*) were collected form the stomach (Zam et al. 1971, Dailey and Brownell 1972, Baird et al. 1988, Baird et al. 1989). Two whale lice, *Syncyamus pseudorcae* and *Isocyamus delphini,* (Bowman 1955, Leung 1967) and one acanthocephalan from the intestine (*Balbosoma capitalum*) were also reported (von Linstow 1880, Dailey and Brownell 1972). An unidentified crassicaudid nematode was found in the pterygoid sinus complex of an individual (Odell et al. 1980). Caldwell et al. (1970) found the pseudostalked barnacle *Xenobalanus globicipitus*.

- **Harbor porpoise (*Phocoena phocoena* [Linnaeus 1758])**—Twenty-two helminthes have been reported as parasites of harbor porpoise. Numerous parasites are classic components of the helminth fauna of this species. For example, the nematodes *Pseudalius* sp., *Stenurus* sp., *Halocercus* sp., and *Tonyurus* sp., were found in the air passages and sinuses (Arnold and Gaskin 1975, Balbuena et al. 1994). The trematode *Campula* sp. has been found in the liver and pancreas (Botero-Anug 1995) and the nematode *Anisakis* sp. occurs frequently in the stomach (Smith, 1989). *Crassicauda* sp. is rarely present in the blubber and mammary gland (Botero-Anug 1995). Most adult harbor porpoises carry heavy loads of parasites, even without disease or health problems. These heavy parasite loads may worsen other health problems, but are unlikely to cause significant risk to robust animals (Read 1994).
- **California sea lion (*Zalophus californianus* [Lesson 1828])—**Mense et al. (1992) reported Apicomplexans like *Sarcocystis* sp. from this species. Flagellates like *Giardia* sp. has also been reported by Deng et al. (2000). Helminths reported include *Contracaecum corderoi* (previously known as *C. ogmorhini*) known to cause severe peritonitis and death in this species (Fletcher et al. 1998). Trematodes found in the gastrointestinal system of pinnipeds consist of 10 genera (*Cryptocotyle*, *Galactosomum*, *Rossicotrema*, *Phagicola*, *Stictodera*, *Phocitrema*, *Pricetrema*, *Microphallus*, *Maritrema*, and *Ogmogaster*), of which *Pricetrema* is reported most commonly (Dailey 2001). Several species of cestodes are also found in pinnipeds, representing the same

two families as in cetaceans (Diphyllobothriidae and Tetrabothriidae) (Dailey 2001). Acanthocephalans of the genus *Corynosoma* have been reported from this species, with *C. obtuscens, C. strumosum* (= *C. semerme*), *C. villosum*, and *C. wegeneri* (= *C. hadweni*) the most commonly encountered in captive animals (Dailey 2001). Nematodes found in the respiratory and circulatory systems include those belonging to the Family Filaroididae, i.e., *Filaroides* sp. (*Parafilaroides*), Crenosomatidae, i.e., *Otostrongylus circumlitus*, and Filariidae, i.e., *Acanthocheilonema* (= *Dipetalonema*, *Skrjabinaria*) *odendhali*, *A. spirocauda*, and *Dirofilaria immitis* (Dailey 2001). Classifications of these lungworms have been reviewed by Measures (2001). Only trematodes infect the liver, pancreas, and biliary system of these animals. They consist of two families (Campulidae, Opistorchiidae) and five genera (*Orthosplanchnus*, *Zalophotrema*, *Opistorchis*, *Metorchis*, and *Pseudamphistomum*). Of these the most commonly reported is *Z. hepaticum*. Additionally, mites in the nares, nasopharynx, airways, and lungs of phocids belong to the genus *Halarachne* (Dailey 2001).

- **Harbor seal (*Phoca vitulina* Linnaeus 1758)**—Peritonitis, bronchitis, and catarrhal pneumonia are associated with the lungworm *Parafilaroides grymnurus*. Infections around the lips and mouth are commonly related with *Pseudomonas* sp. Van Pelt and Dieterich (1973) reported on how a hand-fed new born contracted a staphylococcal infection and toxoplasmosis. In addition, harbor seals are one of the terminal hosts of the larval nematode *Terranova* (=

Porrocaecum) *decipiens,* which infests the musculature of many species of fish, reducing marketability (Bigg 1981).

- **Cuvier's beaked whale (*Ziphius cavirostris* G. Cuvier 1823)—**Ectoparasites have been reported from a few stranded specimens including the barnacles *Xenobalanus* sp. from the flukes and dorsal fin, and *Conchoderma auritum* on the erupted apical teeth (Heyning 1989). The following internal parasites have been reported: *Anisakis* sp., *Crassicauda boopis*, *C. anthonyi* and *C. crassicauda* (nematodes), *Phyllobothrium delphini* (cestodes) and the cyamid *Cyamus monodontis* (Heyning 1989, Mignucci-Giannoni et al. 1998).
- **Shortsnout common dolphin (*Delphinus delphis* Linnaeus 1758)—**Because the longsnout common dolphin (*Delphinus capensis* Gray 1828) was thought to be a synonym of *D. delphis* no parasite species had been reported for this dolphin. *Pennella balaenoptera* and *Larnaeonema* sp. have been reported as external parasites on specimens collected in the Atlantic and Pacific Oceans. Generally, *P. balaenoptera* is mistaken for *Xenobalanus* sp. (Evans 1999). Internal parasites associated with common dolphins include trematodes (six species), cestodes (one species), nematodes (six species), and acanthocephalans in the intestine (three species). Nematodes (*Nasitrema* sp.) are quite common in the middle ear cavities (Evans 1999). Dailey and Stroud (1978) and Dailey and Walker (1978) identified 14 genera of parasites associated with this host and other stranded cetaceans along the California and Oregon coasts. Cholangiohepatitis associated with the trematode *Campulla*

palliate was common in common dolphins examined by Cordes and O'Hara (1979) in New Zealand.

- **Peruvian beaked whale (*Mesoplodon peruvianus* Reyes, Mead and Van Waerebeek 1991)—**Reyes et al. (1991) reported one unidentified nematode from the stomach and trematodes from the genus *Nasitrema* sp. from the pterygoid sinuses. No additional parasite records have been found for this animal.

Metazoan parasites of cetaceans and sirenians from Puerto Rico and the U.S. and British and Virgin Islands

Arnold and Gaskin (1975) reported *Stenurus globicephala* Baylis and Daubney 1925 in a shortfin pilot whale (*Globicephala macrorhynchus* Gray 1846) in St. Lucia in October 1972. Morales-Vela and Olivera-Gómez (1993) reported nematodes (*S. globicephala*, *S. minor*, *Crassicauda* sp., and digenians (*Nasitrema globicephalae* from a shortfin pilot whale from Cozumel, Mexico. Debrot and Barros (1994) reported the collection of five unidentified nematodes from Cuvier's beaked whale (*Ziphius cavirostris*) from Curaçao.

Parasite fauna reported from marine mammals of Puerto Rico was limited as well. Mignucci-Giannoni et al. (1998) conducted the most recent study of the metazoan parasite fauna of cetaceans in the Caribbean reporting helminthes and other parasites for 16 cetaceans from Puerto Rico and the U.S Virgin Islands from 1986-1997 including humpback whale (*Megaptera novaeangliae* [Borowski 1781]), sperm whale

(*Physeter macrocephalus* Linnaeus 1758), pygmy sperm whale (*Kogia breviceps* [de Blainville 1838]), dwarf sperm whale (*Kogia simus* [Owen 1866]), Cuvier's beaked whale, densebeak whale (*Mesoplodon densirostris* [de Blainville 1817]), Antillean beaked whale (*Mesoplodon europaeus* [Gervais 1855]), shortfin pilot whale, pygmy killer whale (*Feresa attenuata* Gray 1874), Risso's dolphin (*Grampus giseus* (G. Cuvier)), melonhead whale (*Peponocephala electra* [Gray 1846]), roughtooth dolphin (*Steno bredanensis*, [Lesson 1828]), Fraser's dolphin (*Lagenodelphis hosei* Fraser 1956), longsnout common dolphin, bottlenose dolphin (*Tursiops truncatus* [Montagu 1821]) and Atlantic spotted dolphin (*Stenella frontalis* [G. Cuvier 1829]). Eighteen species of endoparasitic helminths were found, including eight species of nematodes, two digenians, six cestodes, and two acanthoephalans (Mignucci-Giannoni et al. 1998). Three species of whale lice and two species of barnacles were also collected from this study (Mignucci-Giannoni et al. 1998).

The only representative of the Order Sirenia for the Caribbean is the West Indian manatee (*Trichechus manatus* Linnaeus 1758). Mignucci-Giannoni et al. (1999a) presented an assessment of the endoparasites of the West Indian manatee in Puerto Rico, followed by documentation of these for manatees in the Dominican Republic (Mignucci-Giannoni et al. 1999b), and the manatee's association with barnacles (Cintrón-DeJesus 2000). The parasite fauna reported include *Heterocheilus tunicatus* in the stomach, *Chocleotrema chocleotrema* in the nares and *Chiorchis groshafti* in the small and large intestines. Mora-Pinto (2000) detailed the occurrence of the intestine trematode in manatees from Florida, Puerto Rico, Dominican Republic, and Mexico

and corrected the species identification of Mignucci-Giannoni et al. (1999a, 1999b) from *Chiorchis fabaceus* to *Chiorchis groshafti*.

No previous taxonomic identifications in the Caribbean have been corroborated by genetic studies.

MATERIALS AND METHODS

Parasites and commensals were collected from stranded marine mammals salvaged in Puerto Rico between 1992 and 2004 and in the west coast of North America between 1974 and 2002. Dead marine mammals were examined during necropsy for endo and ectoparasites including the entire gastro intestinal tract, major organ systems, blubber, ear canals and nares. Skin and teeth were also examined for ectoparasites such as crustaceans and commensals. Early collections of specimens were fixed in 10% formalin and stored in glass vials with 70% ethanol. Since 2001, all parasites collected were preserved in 70% ethanol to provide for both morphological and genetic identification. Each vial was labeled with information from the stranding or mortality event, the date of collection, and in most cases, the location in the host.

Helminthes were identified morphologically by observation using a phase-contrast or dissection stereomicroscope and a compound-light microscope. For nematodes, their cephalic and caudal end (i.e., spicules, postanal papillae, preanal papillae), postanal tail with typical mucron (for larvae identification), esophagus, lips, and body at level of intestinal ventricular junction were examined by mounting in lactophenol and compared to descriptions given in keys of Yamaguti (1959-1963). In addition, keys of Yamaguti (1959-1963), Schmidt (1986) for cestodes, and Schell (1985) and Yamaguti (1975) for trematodes were used. For each parasite the following information was detailed:

- Taxonomy of parasite (phylum, class, order, family, genus and species)

- Host (genus and species)
- Parasite location in host. (If available)
- Date of collection
- Host geographic location

Specimens of larval nematodes and some other specimens in poor condition were only morphologically identified to genus as specified and then proceeded with genetic identification in order to achieve species level identifications.

Because of the morphological similarities between nematode parasites and poor morphological condition encountered in the specimens collected, genetic identification was performed in some specimens to assure a correct identification of the parasite. This part of the study was conducted by Dr. Alessio Valentini from the University of Tuscia, Italy. *Anisakis* sp. specimens were genetically analyzed from dwarf sperm whale, spinner dolphin (*Stenella longirostris* [Gray 1828]), roughtooth dolphin, Cuvier's beaked whale, shortfin pilot whale, bottlenose dolphin, harbor porpoise and the longsnout common dolphin.

RESULTS AND DISCUSSION

The results are subdivided in two sections: one for parasites found from marine mammals off the west coast of North America and one for parasites found from marine mammals in the Caribbean.

Metazoan parasites from marine mammals stranded off the west coast of North America

Abstract

Parasites were collected from dead marine mammals salvaged in California between 1974 and 2002. Specimens of each parasite found were initially fixed in 10% formalin and later transferred and stored in glass vials with 70% ethanol. A detailed morphological identification was conducted by mounting specimens in lactophenol. Because of the morphological similarities between nematode parasites, and their poor morphological condition, genetic identification was performed on eight parasitic specimens to corroborate species identification. A total of 10 species of endoparasitic helminthes from 28 carcasses of marine mammals were found and morphologically identified, including six species of nematodes, two species of cestodes, one species of acanthocephalan, and one arthropod. Two new host records were found.

Introduction

Metazoan parasites infecting marine mammals such as whales, dolphins, seals and sea lions include digeneans (flukes), cestodes (tapeworms), nematodes (roundworms), acanthocephalans (spiny headed worms), amphipods, as well as hexapods, and acari. These serve biologist as markers of contemporary and historical ecological relationships. In addition, they have proven to give useful information on host ecology, biogeography and phylogeny (Gardner and Campbell 1992, Brooks and

McLennan 1993, Hoberg 1996, Hoberg 1997). Nevertheless, parasitological studies on marine mammals tend to be opportunistic, a by-product of pathology assessment of these protected species (Raga et al. 1997). When conducted, these studies have documented parasitic biodiversity in different geographical localities that serve as comparisons for variations in the zoogeographic distribution of their respective host.

In California, studies concerning marine mammal parasites are outdated. Prior to the 1990s, a considerable number of comprehensive studies were reported on cetaceans from the area including Dailey (1969, 1971), Schmidt and Dailey (1971), Margolis and Dailey (1972), Dailey and Brownell (1972), Dailey and Perrin (1973), Dailey (1975), Dailey and Ridgway (1976), Dailey and Walker (1978), Dailey and Nutting (1979), and Dailey (1985). However, subsequent to the 1990s' only Dailey et al. (2000), Dailey (2001), and Dailey et al. (2002) reported finding endoparasites on marine mammals from the area. In addition, no previous reports have been found concerning any genetic study of Californian marine mammal parasites, I further document the metazoan parasites of cetaceans and pinnipeds from the area, using both morphological and genetic identification.

Methods

Parasites were collected from dead cetaceans and pinnipeds salvaged in California between 1974 and 2002. Personnel of Moss Landing Marine Laboratories examined dead marine mammals during necropsy for endo- and ectoparasites including the entire gastro intestinal tract, major organ systems, blubber and ear canals. Skin and

teeth were also examined for ectoparasites such as crustaceans and commensals. Sub samples of each parasite were fixed in 10% formalin and later transferred and stored in glass vials with 70% ethanol. Each vial was labeled with information from the stranding or mortality event, the date of collection and, in most cases, the site where found in the host.

Helminthes were identified morphologically by observation using a phase-contrast or dissection stereomicroscope for external features and a compound-light microscope for morphologic landmarks. For nematodes, their cephalic and caudal end (i. e**.,** spicules, postanal papillae, preanal papillae), postanal tail with typical mucron (for larvae identification), esophagus, lips, and body at level of intestinal ventricular junction were mounted in lactophenol for a more detailed morphological identification.

Specimens of larval nematodes and some other specimens in poor condition where only morphologically identified to genus as specified and then proceeded with genetic identification in order to achieve species level of identification.

Results

I examined parasite sub samples from 28 carcasses of marine mammals stranded in the California coast including false killer whale, (*Pseudorca crassidens*), Peruvian beaked whale (*Mesoplodon peruvianus*), Cuvier's beaked whale (*Ziphius cavirostris*), longsnout common dolphin (*Delphinus capensis*), California sea lion (*Zalophus*

californianus), harbor seal (*Phoca vitulina*), and harbor porpoise (*Phocoena phocoena*).

All specimens of parasites were analyzed morphologically. Genetic identification was performed on eight parasitic specimens of a harbor porpoise and a longsnout common dolphin to assure a correct identification of the parasite specimen.

A total of 10 species of endoparasitic helminthes were found and morphologically identified, including 6 species of nematodes, two species of cestodes, one species of acanthocephalan, and one species of arthropod (Table 1)

Nematodes included: *Anisakis simplex* sensu lato in harbor porpoises and longsnout common dolphin, *Anisakis* sp. (L4) in a harbor porpoise, *Pseudoterranova decipiens* and *Pseudoterranova* sp. (L4) in harbor seals, *Contracaecum ogmorhini* in a California sea lion, *Contracaecum* sp. (L4) in a California sea lion and harbor seals, *Stenurus* cf. *minor* in a harbor porpoise, *Pharurus* cf.*dalli* in a harbor porpoise, and *Otostrongylus circumlitus* in a harbor seal (Table 1). Cestodes found included: *Phyllobothrium delphini* in the blubber of the longsnout common dolphin and the Cuvier's beaked whale, and *Tetrabothrius* sp. in the intestine of a Peruvian beaked whale. One species of acanthocephalan was found, *Bolbosoma capitatum*, in the intestine of a false killer whale and one arthropod, *Halarachne miroungae,* was found in the nasal passages of a harbor seal (Table 1).

Two new host records were found: *Tetrabothrius* sp. in the Peruvian beaked whale, and *Phyllobothrium delphini* in the longsnout common dolphin.

Discussion

Acanthocephala

Two genera of acanthocephalans in the family Polymorphidae (*Corynosoma* and *Bolbosoma*) have been reported in marine mammals. Species of *Bolbosoma* are characteristic parasites in the intestines of odontocetes and mysticete cetaceans (Delyamure 1955). In California, *Bolbosoma* sp. has been reported in the sei whale (*Balaenoptera borealis* Lesson 1828), the blue whale (*Balaenoptera musculus* [Linnaeus 1758]) and the humpback whale (*Megaptera novaeangliae*) (Margolis and Dailey 1972). Specimens of *Bolbosoma capitatum* has been found in shortfin pilot whales (*Globicephala macrorhynchus*) from Puerto Rico (Mignucci-Giannoni et al. 1998), and longfin pilot whales (*Globicephala melas* [Traill 1809]) from Canadian and Mediterranean waters (Baylis 1932, Cowan 1967; Balbuena and Raga 1993). They are also known to infect oceanic cetaceans, such as the sperm whale (*Physeter macrocephalus*) (Baylis 1932; Andrade et al. 1998) the longfin pilot whale, and the false killer whale (Odell et al. 1980).

Nematoda

Ascaridoids and metastronglyoids were found among 24 individuals of four species of marine mammals (three odontocetes, one otarid) (Table 1). Species of *Anisakis* were the most prevalent nematodes. Morphological species identification has been limited to adult male worms, although larvae (L4) and adult females were abundant in some collections (Table 1).

Anisakis simplex is known to infect the Californian sea lion, common dolphin, Pacific white-sided dolphin (*Lagenorynchus obliquidens* Gill 1865), northern right whale dolphin (*Lissodelphis borealis* Peale 1848), Baird's beaked whale (*Berardius bairdi* Stejneger 1883), the killer whale (*Orcinus orca* [Linnaeus 1758]), Dall's porpoise (*Phocoenoides dalli* [True, 1885]), and sperm whale (Dailey 1975, Dailey and Walker 1978, Margolis and Dailey 1972). In addition, Mignucci-Giannoni et al. (1998) reported this parasite in the longsnout common dolphin for the Caribbean.

Genetic studies on the taxonomy of *Anisakis simplex* revealed the existence of three sibling species, hence, becoming the *Anisakis simplex* complex and corresponding to: 1) *Anisakis simplex* sensu stricto, which was previously named *A. simplex* B and is widespread between 30°N and the Antartic polar circle, 2) *A. pegreffi*, which was previously named *A. simplex* A and occurs between 35°S and 55°S as well as in the Mediterranean Sea, and 3) *A. simplex* C which shows marked genetic variation when compared to the two other sibling species and has not yet been described. In addition, its range includes the Pacific Canada and the region south of 35°S (Mattiucci et al. 1997). One specimen of *Anisakis* was collected: *Anisakis simplex* sensu lato (previously named *Anisakis simplex* complex) from the stomach of a longsnout common dolphin, and from the kidney, esophagus and stomach of a harbor porpoise. Mixed infections of these species were not found. Larvae (L4) of *Anisakis* were consistently found in the stomach of respective cetacean hosts. Adults, however, were found in a variety of sites: (1) in the kidney, stomach, forestomach and

esophagus of a Harbor porpoise, and (2) in the stomach of a longsnout common dolphin.

Other ascaridoids included larvae (L4) of *Pseudoterranova* and adults of *Pseudoterranova decipiens* (Table 1) occurring in the stomach and esophagus of a harbor seal. *Pseudoterranova decipiens* occurred in mixed infections with *Contracaecum* larvae (L4) in the harbor seal, this may be due to the lack of host specificity in their intermediate (crustacean and teleost) and definitive host (Dailey 1975). For the western coast of North America, *Pseudoterranova decipiens* had been reported for the Northern fur seal, (*Callorhinus ursinus* [Linnaeus 1758]), sea otter, bearded seal (*Erignathus barbatus* [Erxleben (1777]), Pacific harbor seal (*Phoca vitulina richardii* [Gray 1864]), ringed seal (*Pusa hispida* [Schreber 1775]), California sea lion, and the Northern sea lion *Eumetopias jubatus* [Schreber 1776]) (Delyamure 1955, Dailey 1975).

Contracaecum ogmorhini (Johnston et Mawson 1941) sensu lato (or *Contracaecum ogmorhini* complex) and *Contracaecum* larvae (L4) were consistently found in the stomach of Californian sea lions, although, one *Contracaecum* larvae (L4) was found in the pharynx of a harbor seal. This nematode was first described from the leopard seal (*Hydrurga leptonyx* [Blainville 1820]) but was later found in synonymy with *C. osculatum* by Johnston and Mawson (1945). Subsequently, Fagerholm and Gibson (1987) compared specimens of *C. ogmorhini* from leopard seals and *C. osculatum* from newly obtained parasites of different otariid pinnipeds and concluded that *C. ogmorhini* was a valid taxon. After species validation, genetic

analysis of *C. ogmorhini* collected from boreal regions (i. e., the western coast of North America, and the austral regions of Argentina and South Africa) and two gene pools were distinguished within a *C. ogmorhini* sensu lato: *Contracaecum ogmorhini* sensu stricto and a new sibling species for the boreal region, *Contracaecum margolisi* (Mattiucci et al. 2003). In the western coast of North America, Johnston et al. (1966) reported *Contracaecum* (larva) from a ringed seal and Martin et al. (1970) recorded *Contracaecum* sp. form the brain of a Pacific white-sided dolphin. Dailey (1975) summarized records of *C. osculatum* recorded for a number of pinnipeds from New Zealand, Australia, South America and the west coast of North America including: the Steller's sea lion, Southern sea lion, (*Otaria flavescens* [Shaw 1800]), Australian sea lion (*Neophoca cinerea* [Perón 1817), California sea lion, the South American fur seal (*Arctocephalus australis* [Zimmermann 1783]), Australian fur seal (*Arctocephalus pusillus doriferus* [Wood Jones 1925]), South African fur seal, (*A. pusillus pusillus* [Schreber 1776]), Subantarctic fur seal (*A. tropicalis* [Gray 1872]),the harbor seal, Baikal seal (*Pusa sibirica* [Gmelin 1788]), bearded seal, grey seal (*Halichoerus grypus* [Fabricius 1791]), harp seal *(Pagophilus groenlandicus* [Erxleben 1777]), and the ribbon seal (*Histriophoca fasciata* [Zimmermann 1783]).

Specimens of the metastrongylid nematode *Stenurus* cf. *minor* were collected from the left and right tympanic bulla cavity, left and right lungs, and from connective tissue in the reproductive tract of a harbor porpoise (Table 1). *Stenurus minor* has been reported previously from this cetacean (Bryden et al. 1997, Cannon 1977, Forrester et al. 1980) and from a shortfin pilot whale (Morales-Vela and Olivera-Gómez 1993).

Margolis and Dailey (1972) and Dailey and Walker (1978) reported *S. minor* to occur in the air sinus of Dall's porpoise stranded in southern California. Dougherty (1943) and Johnston and Ridgway (1969) reported this parasite to occur in the lung and head sinuses of a harbor porpoise and the Dall's porpoise for the same area.

Another specimen of metastrongylid nematode collected from the left lung and the left and right tympanic bulla cavity of a harbor porpoise was *Pharurus* cf. *convolutus* (Kuhn 1829). Mignucci-Giannoni et al. (1998) reported lung lesions consistent with infections by either species of *Halocercus* sp., or *Pharurus* sp., during histopathological examination of the tissues from three pygmy killer whales involved in a herd stranding in the British Virgin Islands. Additionally, in the western area of North America Dougherty (1943) and Scheffer and Slipp (1948) reported this parasite from a harbor porpoise stranded in California and Washington, respectively.

The metastrongylid nematode *Otostrongylus circumlitus* was found in the lungs and esophagus of a harbor seal. This parasite is known to inhabit the primary and secondary bronchi of harbor seals and Northern elephant seals (*Mirounga angustirostris* [Gill 1866]) and seems to be unique to pinnipeds, along with *Parafilaroides* and *Skrjabinaria* nematodes (Dailey 1975). It has been reported that this parasite causes prominent bronchiectasis. As with most lungworms, a verminous pneumonia may develop as a result of secondary bacterial infection (Möeller 1997). Dailey (1975) reported this parasite to infect the harbor seal, the ringed seal and the harp seal.

Eucestoda

Strobilate tetrabthriids, diphyllobothrids, and metacestodes of phyllobothriids were collected (Table 1). Only a single species was found in two individuals of odontocetes.

Tetraphyllidean metacestodes were represented by *Phyllobothrium delphini*. Specimens of *P. delphini* were found in the blubber of the longsnout common dolphin and the Cuvier's beaked whale. Although morphological types of *Phyllobothrium* larvae have been described from cetaceans throughout the World's oceans and in some cases may represent discrete species (Delyamure 1955, Skrjabin 1972, Testa and Dailey 1976), these were not characterized for this study due to their poor morphological condition. In the west coast on North America, *P. delphini* has been reported for the fin whale (*Balaenoptera physalus* [Linnaeus 1758]), Baird's beaked whale, shortsnout common dolphin, Pacific white-sided dolphin, and sperm whale (Margolis and Dailey 1972).

Because *Delphinus capensis* was thought to be a synonym of *D. delphis* (Wilson and Reeder 1993) and now is considered a separate valid species (Heyning and Perrin 1994, Heyning 1999) no parasite species had been reported for this odontocete. Hence, no reports of *P. delphini* could be found for the longsnout common dolphin. Our report constitutes a new host record, although Margolis and Pike (1955), Rice (1963), Rigdway and Johnston (1965), and Johnston and Ridgway (1969) have reported this parasite for the common dolphin without specifying it to be longsnout or shortsnout. Previous reports of *P. delphini* have been documented for Cuvier's beaked whales (Tomilin 1957), sperm whales (Sokolov 1955, Testa and Dailey 1976, Rice 1989,

McAlpine et al. 1997), Risso's dolphin (*Grampus griseus*) (Baylis 1932), and Fraser's dolphin (*Lagenodelphis hosei*) (McColl and Obendorf 1982). Dailey and Walker (1978) reported *P. delphini* to occur in the blubber of the common dolphin, the Pacific whiteside dolphin, the Northern right whale dolphin and the striped dolphin (*Stenella coeruleoalba* ([Meyen 1833]) stranded in southern California. The typical sites of infection reported for these cestodes are the skin and blubber.

Tetrabothrius sp. was found in the intestine of a Peruvian beaked whale. Reyes et al. (1991) reported trematodes of the genus *Nasitrema*, and one single unidentified anisakid nematode for the Peruvian beaked whale. Our record constitutes a new host record.

Arthropoda: Mites

Lung mites are common parasites of the nasal passages, trachea, bronchi, and bronchioles in marine mammals (Möeller 1997). The most common mites observed in seals and sea lions are *Orthohalarachne diminuata* and *Orthohalarachne attenuata* (Dailey 2001). *Halarachne* cf. *miroungae* was found in the nasal passages of a harbor seal. This mite has been observed in sea otters (Möeller 1997) and in California, this parasite has been reported for the sea otter, the Northern elephant seal, and the Pacific harbor seal (Margolis and Dailey 1972)

This study provides an updated report of the parasite fauna encountered in marine mammals stranded along the central Californian coast in the years 1974-2002. I provide the first genetic and morphological study of parasites in Californian marine

mammals, thus providing valuable information on parasite records and diversity, parasite evolution and recognition of sibling species and status of parasites with controversial taxa. Morphological species-level identification was limited to adult male worms, although larvae (L4) and adult females where usually more abundant in some collections in which genetic species-level identification was effective.

The discovery of an *Anisakis simplex* complex (sensu lato) in the longsnout common dolphin, and the harbor porpoise could represents marked differentiation in the parasite genetic variation possibly because of different geographical distributions or possible population barriers leading to genetic differentiation within their host. More data on parasite diversity for this host throughout the North Atlantic as well as a host population genetic study would be needed in order to give a more detailed analysis.

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Additional records of metazoan parasites of marine mammals from the Caribbean

Abstract

In the Caribbean, studies of marine mammal parasites are scarce. An assessment was conducted for marine mammal endo and ecto parasites form Puerto Rico and the U.S Virgin Island, but extending to other areas of the Caribbean between 1989-1994. The present study expands on the latter. Parasites were collected from 40 carcasses of stranded cetaceans and manatees. Specimens of each parasite were fixed in 10% formalin or in 70% ethanol and stored in glass vials. A total of 14 species of endoparasitic helminthes were morphologically identified, including seven species of nematodes, two species of cestodes, two species of acanthocephalans, and three species of trematodes. Because of morphological similarities between nematode parasites, genetic identification was performed on four species of helminthes to assure a correct identification of parasite specimen. Seven new host records and five new geographic records were found.

Introduction

Marine mammals (whales, dolphins, manatees and seals) are parasitized by a variety of helminthes, including tapeworms, roundworms, and flukes, and lice (Dierauf 1990). Some cause disease on their host, but rarely to an extent causing death to the animal. In the Caribbean, studies concerning marine mammal parasites are

scarce. Prior to the early1990s, only Arnold and Gaskin (1975), Morales-Vela and Olivera-Gómez (1993) and Debrot and Barros (1994) reported finding endoparasites on cetaceans from the area. Mignucci-Giannoni et al. (1998) conducted the most comprehensive and recent study of the metazoan parasitic fauna of cetaceans in the Caribbean. Mignucci-Giannoni et al. (1999a) also presented an assessment of the endoparasites of the West Indian manatee (*Trichechus manatus*) in Puerto Rico, followed by documentation of these for manatees in the Dominican Republic (Mignucci-Giannoni et al. 1999b), and the manatee's association with barnacles (Cintrón De Jesus 2000).

No previous records have been found of using genetic tools for corroborating taxonomic identification for parasites in the Caribbean.

Methods

Parasites were collected from 40 carcasses of stranded cetaceans and manatees salvaged in Puerto Rico between 1992 and 2004. I examined dead marine mammals during necropsy for endo and ectoparasites including the entire gastro intestinal tract, major organ systems, blubber, ear canals and nares. Skin and teeth were also examined for ectoparasites such as crustaceans and commensals. Sub samples of parasites were fixed in 10% formalin and stored in glass vials with 70% ethanol. Since 2001, all parasites collected were only preserved in 70% ethanol to provide for both morphologic and genetic identification. Each vial was labeled with information from

the stranding or mortality event, the date of collection and, in most cases, the location in the host.

Helminthes were identified morphologically with a phase-contrast or dissection stereomicroscope for external features and with a compound-light microscope for morphologic landmarks. For nematodes, their cephalic and caudal end (i. e., spicules, postanal papillae, preanal papillae), postanal tail with typical mucron (for larvae identification), esophagus, lips, and body at level of intestinal ventricular junction were examined by mounting them in lactophenol and comparing them to descriptions given in keys of Yamaguti (1959-1963). In addition, keys of Schmidt (1986) for cestodes, plus Schell (1985) and Yamaguti (1971) for trematodes were used.

Results

I examined 40 carcasses of marine mammals from Puerto Rico and the U. S. British and Virgin Island, including roughtooth dolphin (*Steno bredanensis*, spinner dolphins (*Stenella longirostris*), melonhead whales (*Peponocephala electra* [Gray 1846], pygmy sperm whale (*Kogia breviceps*), densebeak whales (*Mesoplodon densirostris*), bottlenose dolphins (*Tursiops truncatus*) Fraser's dolphins (*Lagenodelphis hosei*), dwarf sperm whales (*Kogia simus*), shortfin pilot whales (*Globicephala macrorhynchus*), West Indian manatees (*Trichechus manatus*) and Cuvier's beaked whales (*Ziphius cavirostris*) (Table 2),

For these, a total of 14 species of endoparasitic helminthes were found and morphologically identified, including seven species of nematodes, two species of

cestodes, two species of acanthocephalans, and three species of trematodes (Table 2). Specimens of larval nematodes and some other specimens in poor condition where only morphologically identified to genus as specified and then proceeded with genetic identification for species identification.

Because of the morphological similarity between parasitic nematodes encountered in this study, genetic identification was performed. Twenty-eight specimens of nematodes from dwarf sperm whales, roughtooth dolphins, bottlenose dolphins, spinner dolphins, Cuvier's beaked whale, and Shortfin pilot whales were used for genetic identification in order to compare both morphological and genetic methods. In these, I found four species of nematodes: *Anisakis brevispiculata*, *Anisakis typica*, *Anisakis ziphidarum*, and *Anisakis simplex* sensu lato. A total of five geographic records and seven new host records were found (Table 3).

Discussion

Digenea

The three species of trematodes found in the West Indian manatee *Chiorchis groschafti*, *Chlocheotrema chlocheotrema* and *Moniligerum blairi* are characteristic parasites of sirenians and are constantly found in the intestine and nares respectively (Beck and Forrester 1988, Dailey et al. 1988, Upton et al. 1989, Mignucci-Giannoni et al. 1999a, Mora-Pinto 2000).

Moniligerum blairi was collected from the Puerto Rico for the first time from the intestine of the West Indian manatee. This trematode was also found to parasitize

Florida manatees (Beck and Forrester 1988, Dailey et al. 1988, Upton et al. 1989) and is commonly found in these hosts although it has never been reported for the Caribbean, hence, our report is a new geographic record.

An unidentified trematode was found in the liver of the bottlenose dolphin but could not be identified because of its poor internal and external conditions.

Eucestoda

Tetraphyllidean metacestodes were represented by *Phyllobothrium delphini* and *Monorygma grimaldi*. Specimens of *P. delphini* occurred in the blubber of six species including dwarf sperm whales, pygmy sperm whales, roughtooth dolphins, Cuvier's beaked whale, Fraser's dolphin, and bottlenose dolphins. Morphological types of *Phyllobothrium* larvae have been described from cetaceans throughout the world's oceans and in some cases may represent discrete species (Delyamure 1955, Skrjabin 1972, Testa and Dailey 1976). Previous reports of these larvae have been reported as *P. delphini* in Cuvier's beaked whale (Tomilin 1957), sperm whales (Sokolov 1955, Testa and Dailey 1976, Rice 1989, McAlpine et al. 1997), Risso's dolphin, and Fraser's dolphin (McColl and Obendorf 1982). In the Caribbean, Mignucci-Giannoni et al. (1998) reported them for Risso's dolphins, pygmy sperm whales, Fraser's dolphins, melonhead whale, Cuvier's beaked whale, and Atlantic spotted dolphins.

Specimens of *M. grimaldi* were found in the blubber of a shortfin pilot whale, in the urinary bladder of Fraser's dolphin, in the abdominal cavity of Cuvier's beaked

whale, and in the gonads of a spinner dolphin. The typical site of infection of these cestodes is the abdominal cavity. Forrester (1992) reported from the striped dolphin (*Stenella coeruleoalba* [Meyen, 1833]) in the Atlantic Ocean. Previously Mignucci-Giannoni et al. (1998) reported them for pygmy killer whales, shortfin pilot whales, and Fraser's dolphin in the Caribbean Sea. Sharks are probably the definitive host of these cestodes (Testa and Dailey 1976), hence, supporting the idea that marine mammals could act as intermediate host of these tetraphyllideans. Previously, *M. grimaldi* had also been reported in both the shortfin pilot whale (Dailey and Brownell 1972) and Fraser's dolphin (McColl and Obendorf 1982).

Nematoda

Species of *Anisakis* were the most prevalent nematode. Morphological species-level identification was limited to adult male worms, although larvae 4, larvae 2 (i. e., undeveloped individuals of anisakid adults) and adult females where abundant in some collections. Genetic species-level identification was successful in all specimens.

Although *A. simplex* is particularly prevalent in pilot whales only, *Anisakis* sp. has been reported for the shortfin pilot whale (Kagel et al. 1967, Dailey and Brownell 1972, Mignucci-Giannoni et al. 1998). No reference was found for *A. simplex* in this toothed whale. Genetic studies on the taxonomy of *A. simplex* revealed the existence of three sibling species, hence, becoming the *Anisakis simplex* sensu lato (previously named *Anisakis simplex* complex) and corresponding to:

1) *Anisakis simplex* sensu stricto, previously named *A. simplex* B and widespread between 30°N and the Antartic polar circle,
2) *A. simplex* A, occurring between 35°S and 55°S as well as in the Mediterranean sea, and
3) *A. simplex* C, showing marked genetic variation when compared to the latter two and not yet described. It has a discontinuous range including Pacific Canada and the region south of 35°S (Mattiucci et al. 1997).

Anisakis simplex sensu lato was found consistently in the stomach of the shortfin pilot whale, therefore, representing a new host and geographic record. This discovery represents a marked differentiation in the parasite genetic variation possibly because of different cetacean geographical distributions or possible marine mammal groupings leading to genetic differentiation within their host.

All cetaceans recorded (Table 2) are documented hosts for species of *Anisakis*. *Anisakis brevispiculata* (Figure 1, Figure 2) was differentiated genetically from *A. physeteris*, and found to have as definite host the pygmy sperm whale (Mattiucci et al. 2001). No previous records exist of *A. brevispiculata* in the dwarf sperm whale, thus constituting a new host record. Mignucci-Giannoni's et al. (1998) records of *A. physeteris* in a pygmy sperm whale and *Anisakis* sp. in a dwarf sperm whale should be reviewed, as they are most probable misidentifications of *A. brevispiculata*.

Mignucci-Giannoni et al. (1998) reported *Anisakis typica* from the Atlantic spotted dolphin and shortfin pilot whale, providing the first records of *A. typica* in toothed

whales. Specimens of *A. typica* (Figure 3) were found in the stomach and intestine of a roughtooth dolphin.

Anisakis ziphidarum (Figure 4) was recently differentiated genetically and morphologically from other species of *Anisakis* (Paggi et al. 1998) and found in a Cuvier's beaked whale from the Mediterranean and a Layard's beaked whale (*Mesoplodon layardi* [Gray 1865]) and a Cuvier's beaked whale from South Africa. The records of *A. ziphidarum* from Cuvier's beaked whales from Puerto Rico and the Virgin Islands constitute new geographical records.

Pseudoterranova ceticola (Figure 5) was found in the stomach of a dwarf sperm whale. Gunter and Overstreet (1974) and Deardorff and Overstreet (1981) reported *P. ceticola* from a dwarf sperm whale from Mississippi.

The nematode *Heterocheilus tunicatus* are found to be characteristic parasites in the stomach and very rarely in the intestines of sirenians (Dailey et al. *19*88, Upton et al. 1989, Beck and Forrester 1998, Mignucci-Giannoni et al. 1999a). They were commonly found in all manatees salvaged.

Spirurids were represented by species of *Crassicauda*. Previous records of *Crassicauda* spp. from Cuvier's beaked whales include *Crassicauda anthonyi, Crassicauda boopis*, and *Crassicauda crassicauda* (see Baylis 1932, Deliamure 1955, Heyning 1989, Raga 1994). However, Dollfus (1966) and Raga and Balbuena (1990) questioned some of these records. *Crassicauda sp*. was reported from a shortfin pilot whale by Morales-Vela and Olivera-Gómez (1993). Mignucci-Giannoni et al. 1998

reported *Crassicauda anthonyi* for Cuvier's beaked whale, and *Crassicauda duguyi* for pygmy sperm whales.

Acanthocephala

Species of *Bolbosoma* Porta 1908 are characteristic parasites in the intestines of odontocetes and mysticete cetaceans (Delyamure 1955). Mignucci-Giannoni et al. (1998) reported two species for the Caribbean: *Bolbosoma capitatum* from the intestine of a shortfin pilot whale and *Bolbosoma vasculosum* from the intestine of a pigmy killer whale and an Atlantic spotted dolphin. *B. capitatum* has been reported among large odontocetes (reviewed by Hoberg et al. 1993) and has been found in longfin pilot whales (*Globicephala melas* [Traill 1809]) in Canadian waters (Cowan 1967). *Bolbosoma vasculosum* is known from the shortsnout common dolphin (*Delphinus delphis* Linnaeus 1758), pygmy sperm whale, Sowersby's beaked whale (*Mesoplodon bidens* Sowerby 1804), Atlantic spotted dolphin, pygmy sperm whale, and pygmy killer whale.

Specimens of *Bolbosoma capitatum* from a shortfin pilot whale and a melonhead whale are reported herein.

This study contributes to additional records of metazoan parasites for Caribbean marine mammals between the years 1992-2004. Morphological species identification was limited to adult male worms, although larvae (L4) and adult females where usually more abundant in some collections, in which genetic species identification proved to have no or little limitations and was thoroughly achieved. The discovery of

Anisakis simplex sensu lato in shortfin pilot whale represents a marked differentiation in the parasite genetic variation possibly because of different geographical distributions or possible groupings in cetacean populations leading to parasite genetic differentiation within their host. Additional sampling and genetic identification of both the host and its parasite fauna would be needed in order to give a more detailed analysis. Also, it should be examined on a broader geographic scale to determine its distribution and possible significance.

This second report of the taxonomic composition of helminth in Caribbean marine mammals adds new information about the diversity of its parasite fauna. A detailed knowledge of both the parasite fauna and their interactions with these hosts is necessary for proper management and conservation.

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CONCLUSIONS AND RECOMMENDATIONS

Morphological species-level identification was limited to adult male worms, although larvae (L4) and adult females were usually more abundant in some collections. Genetic species-level identification was successful in all specimens. A morphological study together with a genetic assay of a specimen revealed the correct species classification.

I provide the second assessment of helminth diversity from marine mammals in the Caribbean. Twenty-eight parasite specimens were analyzed genetically. A total of seven new host record and five new geographic records were found for the Caribbean. *Phyllobothrium delphini* and *Anisakis typica* for the roughtooth dolphin, *Bolbosoma capitatum* for the melonhead whale, and *Monorygma grimaldi* for the Cuvier's beaked whale constitute new host records. New geographical records include: *Bolbosoma vasculosum* for Puerto Rico, *Anisakis brevispiculata*, *Pseudoterranova ceticola* and *Moniligerium blairi* for the Caribbean and Puerto Rico, and *Anisakis ziphidarum* for the Caribbean, Puerto Rico and the Virgin Islands.

An updated report for helmith diversity for the west coast of North America was completed. Genetic identification was performed on eight parasitic specimens of a harbor porpoise and a longsnout common dolphin including: *Anisakis simplex* sensu lato, *Anisakis* (L4); *Pseudoterranova decipiens*; *Pseudoterranova* (L4); *Contracaecum ogmorhini* sensu lato; *Contracaecum* (L4) to successfully identify correctly the species of the parasite specimens.

Two new host records were reported: *Tetrabothrius* sp. constitutes a new host record for the Peruvian beaked whale while, and *Phyllobothrium delphini* represent a new host record for the longsnout common dolphin. Ten nematodes were found including: *Anisakis simplex* sensu lato, *Anisakis* (L4); *Pseudoterranova decipiens*; *Pseudoterranova* (L4); *Contracaecum ogmorhini* sensu lato; *Contracaecum* (L4); *Stenurus minor*; *Pharurus* cf. *convlutus*; *Otostrongylus circumlitus*. In addition, a morphological identification study was carried out on two cestodes (*Phyllobothrium delphini* in the blubber of the longsnout common dolphin and the Cuvier's beaked whale, and *Tetrabothrius* sp. in the intestine of a Peruvian beaked whale), one acanthocephalan (*Bolbosoma capitatum* in the intestine of a false killer whale), and one arthropod (*Halarchane miroungae* in the nasal passages of a harbor seal).

Research on parasite diversity helps us understand marine mammal populations and serves as a tool for the conservation and management assessments of some of these endangered marine species. Future work should include:

- Continue parasite collection and identification through the established carcass salvage program.
- Preserve parasite specimens in 70% ethanol and some frozen in –80°C to provide for genetic identification and alloenzyme electrophoresis. The use of 10% formalin should be discontinued until newer genetic techniques are developed to handle formalized specimens.

- Compare and review old morphological identification from the Caribbean parasite collection to corroborate species identification using genetic methods.
- Elaborate a reference catalogue of known Caribbean marine mammal parasites, including illustrations of their diagnostic morphological characteristics to serve for identification in future studies or salvage procedures.
- Elaborate a world-wide summary table of marine mammal and parasite fauna, with host/parasite association and geographical records.
- Evaluate genetic and morphological results of parasite fauna of marine mammals for its relationship in terms of host ecology, biology, zoogeography, behavior and evolution.

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TABLES

Table 1. Parasite identification from marine mammals examined for endo and ectoparasites in California.

Host Field number	Collection date	Sex	Length (cm)	Locality	Parasite species	Location in host
Harbor porpoise (*Phocoena phocoena* [Linnaeus 1758])						
MLMLMM030	22 Aug 1990	M	129. 8	Monterey, California	*Anisakis simplex* sensu lato	Kidney
MLMLMM342	31 Oct 1996	M	-	Marina State Beach, California	*Stenurus* cf. *minor*	Left and right tympanic bulla cavity
MLMLMM398	13 Aug 1996	F	129	Salinas River Mouth, California	*Pharurus* cf. *dalli*	Left and right tympanic bulla cavity, lung
MLMLMM425	-	F	142	Monterey, California	*Stenurus* cf. *minor*	Lung
MLMLMM435	1 Apr 1997	F	173	Monterey, California	*Anisakis*L4	Stomach
MLMLMM439	1 Apr 1997	F	155	Monterey, California	*Anisakis*L4	Stomach/forestomach
MLMLMM446	12 Apr 1997	M	145	Monterey, California	*Stenurus* cf. *minor*	Connective tissue in reproductive tract
					Stenurus cf. *minor*	Left lung
					*Anisakis*L4	Stomach
MLMLMM492	7 Oct 1998	F	168	Monterey, California	*Anisakis*L4	Stomach
MLMLMM524	6 Nov 1998	F	164. 5	Monterey, California	*Stenurus* cf. *minor*	Left lung
MLMLMM606	30 Sep 1998	M	117. 5	California	*Anisakis*L4	Forestomach
MLMLMM624	30 Oct 1998	M	142. 5	Monterey, California	*Pharurus* cf. *dalli*	Left lung
MLMLMM7 19	27 Apr 2000	F	161	Monterey, California	*Anisakis simplex* sensu lato	Esophagus
MLMLMMC-183	28 May 1975	M	-		*Anisakis simplex* sensu lato	Stomach
MLMLMMTRK-109	-	M	-	California	*Anisakis*L4	Stomach
Longsnout common dolphin (*Delphinus capensis* Gray 1828)						
MLMLMM582	16 Jan 1998	M	207	Moss Landing Beach, California	*Anisakis simplex* sensu lato	Stomach
MLMLMM786	3 Mar 1999	M	239	Monterey, Pacific Grove, California	*Anisakis simplex* sensu lato	Stomach
					Phyllobothrium delphini	Blubber

Table 1. (Continued).

Host Field number	Collection date	Sex	Length (cm)	Locality	Parasite species	Location in host
False killer whale (*Pseudorca crassidens* [Owen 1846])						
MLMLMMC-178	1 Sep 1974	F	-	California	*Bolbosoma capitatum*	Intestine
Cuvier's beaked whale (*Ziphius cavirostris* G. Cuvier 1823)						
MLMLMM499	11 Feb 1998	F	600	Monterey, California	*Phyllobothrium delphini*	Blubber
Peruvian beaked whale (*Mesoplodon peruvianus* Reyes, Mead and Van Waerebeek 1991)						
MLMLMM858	31 Jan 2001	F	-	Monterey, California	*Tetrabothrius* sp.	Intestine
Californian sea lion (*Zalophus californianus* [Lesson 1828])						
MLMLMM061	31 Aug 1990	M	196. 5	Santa Cruz Harbor, California	*Contracaecum ogmorhini* sensu lato	Stomach
MLMLMM360	2 Feb 1999	F	106	Monterey, California	*Contracaecum* L4	Stomach
MLMLMM451	5 May 1997	M	162	Monterey, California	*Contracaecum ogmorhini* sensu lato	Stomach
Harbor seal (*Phoca vitulina* Linnaeus 1758)						
MLMLMM001	17 Oct 1989	M	114	Davenport,California	*Pseudoterranova* cf. *decipiens*	Stomach
MLMLMM399	18 Aug 1996	F	80	Monterey, California	*Pseudoterranova* L4	Stomach
MLMLMM691	4 Mar 2000	F	122	Marina State Beach, California	*Pseudoterranova* cf. *decipiens*	Stomach
MLMLMM729	12 May 2000	M	87	Monterey, California	*Halarachne* cf. *miroungae*	Nose
MLMLMM785	2 Sep 2000	F	103	Santa Cruz, California	*Otostrogylus* cf. *circumlitus*	Lung
					Otostrogylus cf. *circumlitus*	Esophagus
					Pseudoterranova cf. *decipiens*	Esophagus
MLMLMM P-35	9 Feb 2002	M	-	California	*Contracaecum* L4	Pharynx

Table 2. Parasite identification from marine mammals examined for endo and ectoparasites in Puerto Rico and the U. S and British Virgin Islands.

Host Field number	Collection date	Sex	Length (cm)	Locality	Parasite	Location on host
Roughtooth dolphin (*Steno bredanensis* [Lesson 1828])						
NEPST859	30 Mar 2003	F	236	Arroyo, Puerto Rico	*Anisakis typica*	Stomach
					Anisakis typica	Intestine
					Phyllobothrium delphini	Skin
Bottlenose dolphin (*Tursiops truncatus* [Montagu 1821])						
NEPST381	29 Jul 1998	U	251	Manatí, Puerto Rico	*Phyllobothrium delphini*	Blubber
NEPST550	5 Jul 1999	F	273	San Juan, Puerto Rico	*Digenea*	Liver
NEPST558	23 Aug 1999	M	193	Vega Baja, Puerto Rico	*Anisakis typica*	Stomach
Atlantic spotted dolphin (*Stenella frontalis* [G. Cuvier 1829])						
NEPST877	8 Jan 2004	F	182	Luquillo, Puerto Rico	*Nematode*	-
Spinner dolphin (*Stenella longirostris* [Gray 1828])						
NEPST850	23 Sep 2002	F	186	Ponce, Puerto Rico	*Monorygma grimaldii*	Gonads
					Anisakis L4	Liver
					Anisakis L4	Stomach
Fraser's dolphin (*Lagenodelphis hosei* Fraser 1956)						
NEPST319	22 May 1994	M	227	Guánica, Puerto Rico	*Anisakis* L4	Stomach
NEPST842	9 Jun 2002	M	236	Humacao, Puerto Rico	*Anisakis* L4	Stomach
					Monorygma grimaldii	Urinary bladder
					Phyllobothrium delphini	Blubber
Melonhead whale (*Peponocephala electra* [Gray 1846])						
NEPST848	21 Jul 2002	M	214	San Juan, Puerto Rico	*Bolbosoma capitatum*	-

Table 2. (Continued).

Host Field number	Collection date	Sex	Length (cm)	Locality	Parasite	Location on host
Shortfin pilot whale (*Globicephala macrorhynchus* Gray 1846)						
NEPST481	1 Sep 1998	M	236	Cabo Rojo, Puerto Rico	*Bolbosoma capitatum*	Intestine
NEPST481	1 Sep 1998	M	236	Cabo Rojo, Puerto Rico	*Monorygma grimaldi*	Blubber
NEPST560	28 Aug 1999	F	250	Anegada, British Virgin Islands	*Anisakis simplex sensu lato*	Stomach
NEPST562	28 Aug 1999	M	340	Anegada, British Virgin Islands	*Anisakis simplex sensu lato*	Stomach
NEPST563	30 Aug 1999	F	300	Anegada, British Virgin Islands	*Anisakis simplex sensu lato*	Stomach
Cuvier's beaked whale (*Ziphius cavirostris* G. Cuvier 1823)						
NEPST195	9 Jul 1992	F	545	Vieques Island, Puerto Rico	*Crassicauda anthonyi*	Kidney
NEPST382	29 Jul 1998	M	452	Aguadilla, Puerto Rico	*Phyllobothrium delphini*	Blubber
					Phyllobothrium delphini	Blubber
NEPST385	29 Jul 1998	M	530	Aguadilla, Puerto Rico	*Monorygma grimaldii*	Abdominal cavity
					Anisakis larvae Type 2	Intestine
					Crassicauda anthonyi	Kidney
NEPST392	30 Jul 1998	M	505	Aguadilla, Puerto Rico	*Anisakis ziphidarum*	Stomach
					Crassicauda anthonyi	Kidney
NEPST401	30 Jul 1998	M	474	Aguada, Puerto Rico	*Anisakis ziphidarum*	Stomach
NEPST505	25 Nov 1998	M	528	Aguada, Puerto Rico	*Crassicauda anthonyi*	Kidney
					Phyllobothrium delphini	Blubber
NEPST506	25 Nov 1998	F	498	Hatillo, Puerto Rico	*Phyllobothrium delphini*	Skin
					Crassicauda anthonyi	Kidney
NEPST421	12 Apr 1999	U	452	Aguadilla, Puerto Rico	*Phyllobothrium delphini*	Blubber
					Crassicauda anthonyi	Kidney
NEPST575	4 Oct 1999	F	494	St. Thomas, U. S. Virgin Islands	*Crassicauda anthonyi*	Kidney
					Phyllbothrium delphini	Blubber
NEPST576	3 Oct 1999	F	520	St. John, U. S. Virgin Islands	*Anisakis ziphidarum*	Stomach
NEPST601	3 May 2000	M	453	Vieques Island, Puerto Rico	*Anisakis ziphidarum*	Stomach
					Phyllobothrium delphini	Blubber
					Crassicauda anthonyi	Kidney
Densebeak whale (*Mesoplodon densirostris* [de Blainville 1817])						
NEPST838	9 April 2002	M	335	Dorado, Puerto Rico	*Anisakis* L4	Stomach
NEPST881	11 Feb 2004	M	410	Ceiba, Puerto Rico	*Bolbosoma vasculosum*	Stomach

Table 2. (Continued).

Host Field number	Collection date	Sex	Length (cm)	Locality	Parasite	Location on host
Pygmy sperm whale (*Kogia breviceps* [de Blainville 1838])						
NEPST617	10 Apr 2001	M	295	Culebra, Puerto Rico	*Phyllobothrium delphini*	Blubber
Dwarf sperm whale (*Kogia simus* [Owen 1866])						
NEPST393	17 Jul 1998	M	223	Mayaguez, Puerto Rico	*Anisakis brevispiculata*	Stomach
					Phyllobothrium delphini	Blubber
NEPST846	2 Jul 2002	F	214	Luquillo, Puerto Rico	*Pseudoterranova ceticola*	Stomach
NEPST845	4 Jul 2002	F	135	Rio Grande, Puerto Rico	*Anisakis brevispiculata*	Stomach
West Indian manatee (*Trichechus manatus* Linnaeus 1758)						
NEPST559	26 Aug 1999	F	330	Guayanilla, Puerto Rico	*Heterocheilus tunicatus*	Stomach
NEPST640	28 Nov 2001	M	206	Peñuelas, Puerto Rico	*Chiorchis groschafti*	Intestine
NEPST852	11 Nov 2002	F	238	Ponce, Puerto Rico	*Chiorchis groschafti*	Intestine
NEPST854	12 Dec 2002	M	284	Guayama, Puerto Rico	*Cochleotrema cochleotrema*	Nares
					Cochleotrema cochleotrema	Trachea
NEPST860	9 Apr 2003	M	221	Patillas, Puerto Rico	*Moniligerum blairi*	Intestine
					Heterocheilus tunicatus	Stomach
NEPST865	19 Jul 2003	F	279	Guayanilla, Puerto Rico	*Chiorchis groschafti*	Intestine
					Heterocheilus tunicatus	Stomach
NEPST866	21 Jul 2003	F	245	Guayanilla, Puerto Rico	*Chiorchis groschafti*	Intestine
					Cochleotrema cochleotrema	Nares
					Heterocheilus tunicatus	Stomach
NEPST873	9 Nov 2003	F	290	Guayanilla, Puerto Rico	*Cochleotrema cochleotrema*	Nares
					Chiorchis groschafti	Intestine
NEPST875	23 Nov 2003	F	273	Naguabo, Puerto Rico	*Chiorchis groschafti*	Intestine
					Heterocheilus tunicatus	Stomach

Table 3. Revised annotated list of parasites from marine mammals from the Caribbean.

Taxonomic group Helminth Host	Collection locality	Location on host	New record	References
Phylum Acanthocephala				
Family Polymorphidae				
Bolbosoma capitatum				
shortfin pilot whale	PUR	Intestine	Host, CAR, PUR	4, 5
melonhead whale	PUR	Intestine	Host	This paper
Bolbosoma vasculosum				
Atlantic spotted dolphin	VIR	Intestine	Host, CAR, VIR	5
pygmy killer whale	VGB	Intestine	Host, VGB	5
dense beaked whale	PUR	Intestine	Host, PUR	This paper
Bolbosoma sp.				
pygmy sperm whale	PUR	Intestine		5
Phylum Nemathelminthes				
Family Anisakidae				
Anisakis brevispiculata				
dwarf sperm whale	PUR	Stomach	Host, CAR, PUR	This paper
Anisakis ziphidarum				
Cuvier's beaked whale	PUR, VIR	Stomach	CAR, PUR, VIR	This paper
Anisakis typica				
shortfin pilot whale	PUR, JAM	Stomach	Host, CAR, PUR, JAM	5
Atlantic spotted dolphin	PUR/VIR	Stomach	Host, VIR	5
roughtooth dolphin	PUR	Stomach	Host	This paper
bottlenose dolphin	PUR	Stomach		This paper
Anisakis physeteris				
pygmy sperm whale	PUR, VIR	Stomach	CAR, PUR, VIR	5
Anisakis simplex				
longsnout common dolphin	VEN	Stomach	CAR, VEN	5
shortfin pilot whale	VGB	Stomach	VGB	This paper
Anisakis sp.				
Cuvier's beaked whale	PUR, VIR	GI tract	CAR, PUR, VIR	5
pygmy killer whale	PUR, VGB	Stomach	Host, VBG	5
shortfin pilot whale	PUR, JAM	Stomach		5
dwarf sperm whale	PUR	Stomach		5
pygmy sperm whale	PUR, VIR	Stomach		5
Atlantic spotted dolphin	PUR, VIR	Stomach		5
Fraser's dolphin	PUR	Stomach		This paper
dense beaked whale	PUR	Stomach		This paper
Terranova ceticola				
pygmy sperm whale	PUR, VIR	Stomach	CAR, PUR, VIR	5
Terranova sp				
dwarf sperm whale	PUR	Stomach	CAR, PUR	5
pygmy killer whale	PUR, VGB	Stomach	Host, VGB	5
pygmy sperm whale	PUR, VIR	Stomach	VIR	5
Pseudoterranova ceticola				
dwarf sperm whale	PUR	Stomach	Host, CAR, PUR	This paper
Family Heterocheilidae				
Heterocheilus tunicatus				
West Indian manatee	PUR, DOM	Stomach	CAR, PUR, DOM	6, 7

Table 3. (Continued).

Taxonomic group Helminth Host	Collection locality	Location on host	New record	References
Family Tetrameridae				
Crassicauda anthonyi				
Cuvier's beaked whale	PUR	Kidney	CAR, PUR	5
Crassicauda duguyi				
pygmy sperm whale	PUR, VIR	Neck muscle	CAR, PUR, VIR	5
Crassicauda sp.				
shortfin pilot whale	MEX	Pelvic girdle	CAR, MEX	3, 5
Family Pseudaliidae				
Stenurus globicephalae				
shortfin pilot whale	LCA, PUR JAM, MEX	Cranial sinus	CAR, LCA, MEX, PUR, JAM	1, 3, 5
pygmy killer whale	VGB	Stomach	VGB	5
melonhead whale	PUR	Ear		5
Stenurus minor				
shortfin pilot whale	MEX	Cranial sinus	CAR, MEX	3
Halocercus sp. */Pharurus* sp.				
pygmy killer whale	VGB	Bronchi	Host, CAR, VGB	5
Phylum Platyhelminthes				
Family Campulidae				
Synthesium tursionis				
bottlenose dolphin	PUR	Intestine	CAR, PUR	5
Family Nasitrematidae				
Nasitrema globicephalae				
shortfin pilot whale	MEX	-	MEX	3
Family Diphyllobotrhiidae				
Diphyllobothrium sp.				
melonhead whale	PUR	Intestine	Host, CAR, PUR	5
Family Tetrabothriidae				
Tetrabothrius forsteri				
Fraser's dolphin	PUR	Intestine	CAR, PUR	5
Trigonocotyle sexitesticulae				
pygmy killer whale	PUR, VGB	Intestine	CAR, PUR, VGB	5
Trigonocotyle sp.				
pygmy killer whale	PUR, VGB	Intestine		5
Family Phyllobotrhiidae				
Monorygma grimaldii				
shortfin pilot whale	PUR	Abdomen	CAR, PUR	5
pygmy killer whale	PUR, VGB	Blubber	Host, VGB	5
Fraser's dolphin	PUR	Abdomen		5
spinner dolphin	PUR	Gonads		This paper
Cuvier's beaked whale		Abdomen	Host	This paper
Phyllobothrium delphini				
Cuvier's beaked whale	VIR, PUR	Blubber	CAR, VIR	5
sperm whale	PUR	Blubber	PUR	5
Risso's dolphin	PUR	Blubber		5
Atlantic spotted dolphin	VIR	Blubber	Host	5
dwarf sperm whale	PUR	Blubber		This paper
Fraser's dolphin	PUR	Blubber		5
roughtooth dolphin	PUR	Blubber	Host	This paper
pygmy sperm whale	PUR	Blubber		5

Table 3. (Continued).

Taxonomic group Helminth Host	Collection locality	Location on host	New record	References
Family Paramphistomatidae				
Chiorchis groschafti				
West Indian manatee	PUR, MEX CUB, DOM	Intestine	Host, ATL, CAR, CUB, PUR MEX, DOM	2, 6, 7, 8
Family Opisthotrematidae				
Cochleotrema chocleotrema				
West Indian manatee	PUR, DOM	Nares	CAR, PUR, DOM	6, 7
Moniligerum blairi				
West Indian manatee	PUR	Intestines	CAR, PUR	This paper

Host scientific names—Atlantic spotted dolphin (*Stenella frontalis* [G. Cuvier 1829]), bottlenose dolphin (*Tursiops truncatus* [Montagu 1821]), Cuvier's beaked whale (*Ziphius cavirostris* G. Cuvier 1823), dense beaked whale (*Mesoplodon densirostris* [de Blainville 1817]), dwarf sperm whale (*Kogia simus* [Owen 1866]), Fraser's dolphin (*Lagenodelphis hosei* Fraser 1956), longsnout common dolphin (*Delphinus capensis* Gray 1828), melonhead whale (*Peponocephala electra* [Gray 1846]), pygmy killer whale (*Feresa attenuata* Gray 1874), pygmy sperm whale (*Kogia breviceps* [de Blainville 1838]), Risso's dolphin (*Grampus griseus* [G. Cuvier 1812]), roughtooth dolphin (*Steno bredanensis* [Lesson 1828]), shortfin pilot whale (*Globicephala macrorhynchus* Gray 1846), sperm whale (*Physeter macrocephalus* Linnaeus 1758), spinner dolphin (*Stenella longirostris* [Gray 1828]), West Indian manatee (*Trichechus manatus* Linnaeus 1758).

Country abbreviations—CUB = Cuba, DOM = Dominican Republic, JAM = Jamaica, LCA = St. Lucia, MEX = Mexico, PUR = Puerto Rico, VEN = Venezuela, VIR = US Virgin Islands, VGB = British Virgin Islands.

References—1 = Arnold and Gaskin 1975, 2 = Coy-Otero 1989, 3 = Morales-Vela and Olivera-Gómez 1993, 4 = Williams and Bunkley-Williams 1996, 5 = Mignucci-Giannoni et al. 1998, 6 = Mignucci-Giannoni et al. 1999a, 7 = Mignucci-Giannoni et al. 1999b, 8 = Mora-Pinto 2000.

FIGURES

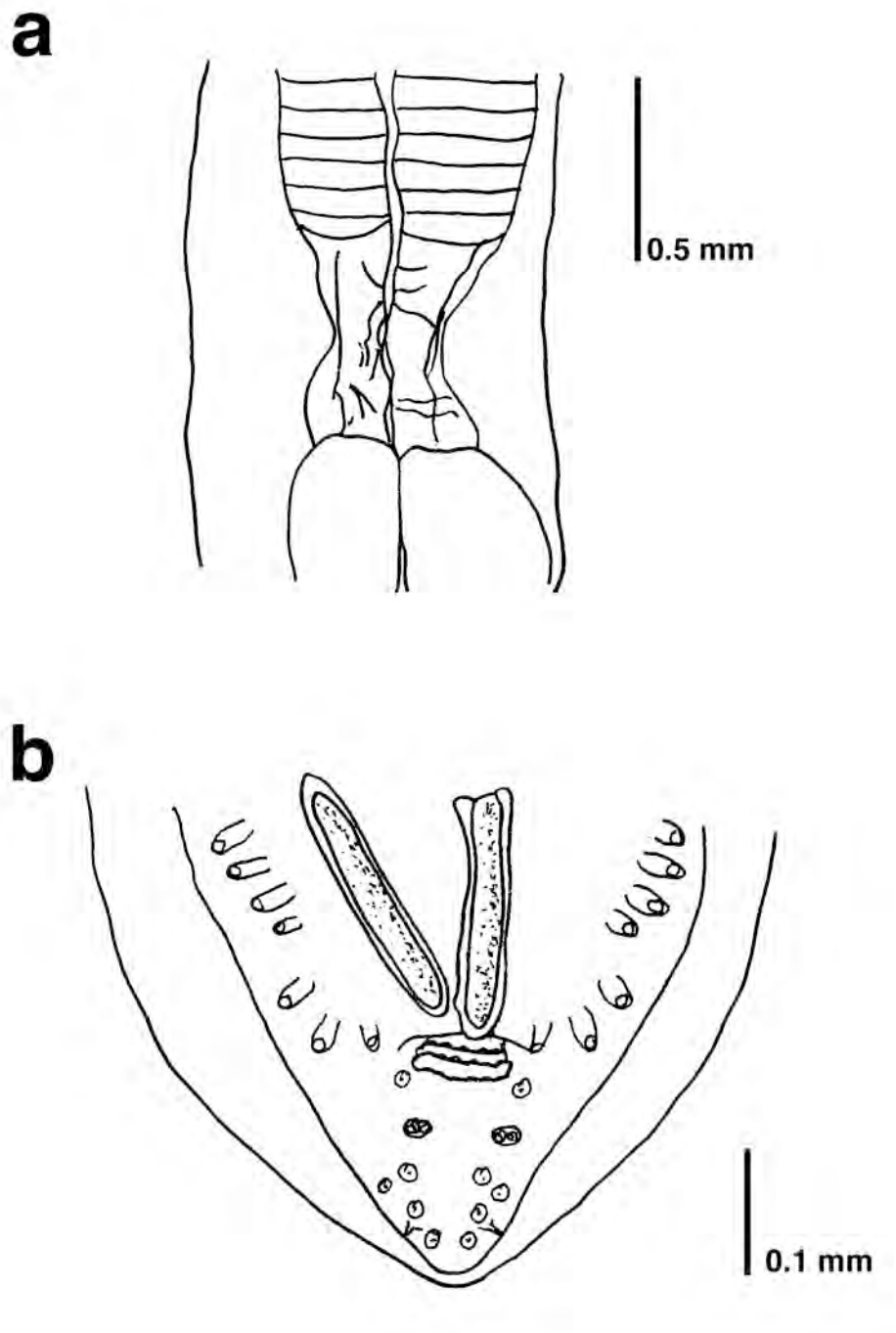

Figure 1. *Anisakis brevispiculata*, showing its (a) ventriculus, and (b) male caudal end.

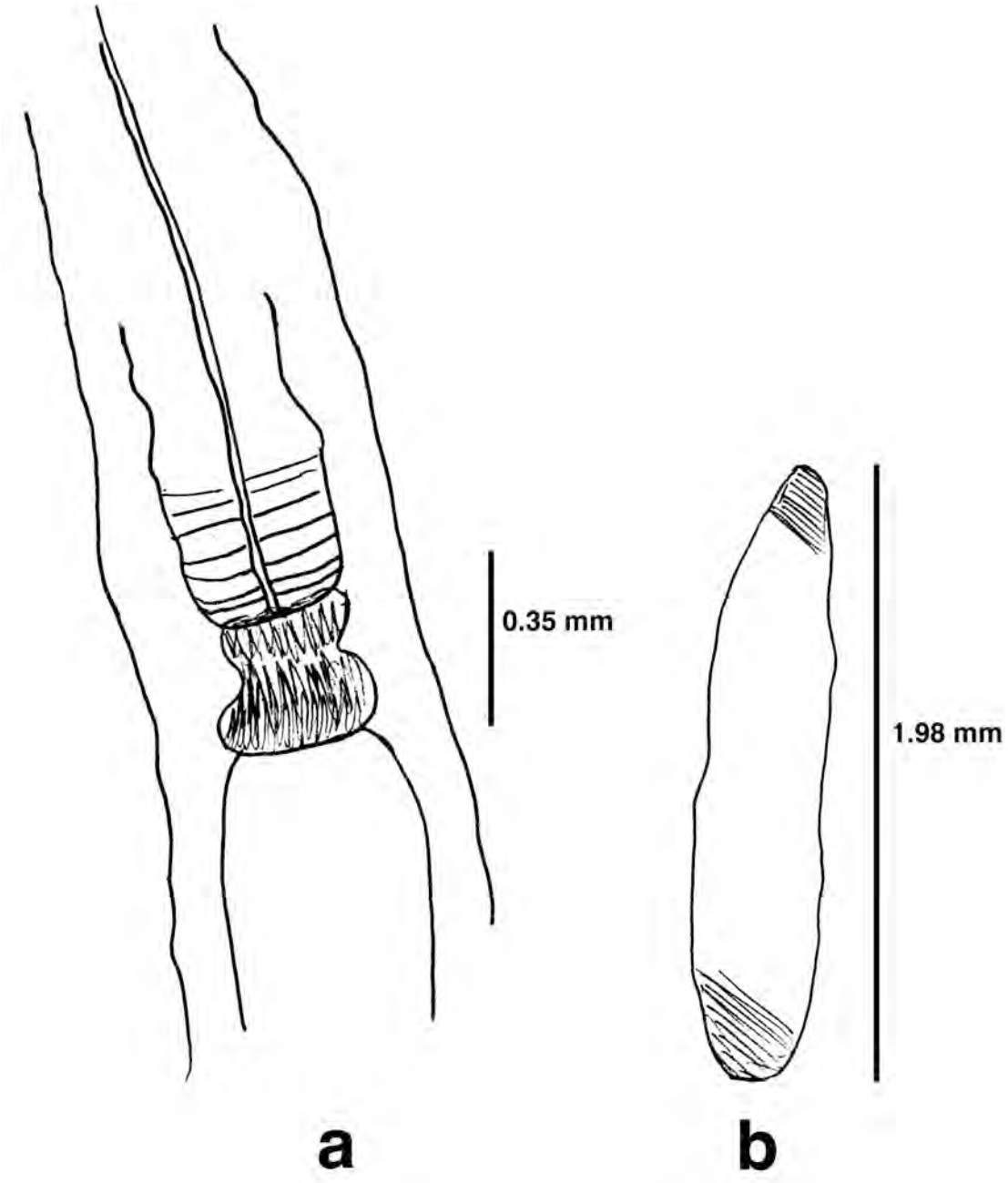

Figure 2. *Anisakis brevispiculata*, showing its (a) ventriculus and (b) a male spicule.

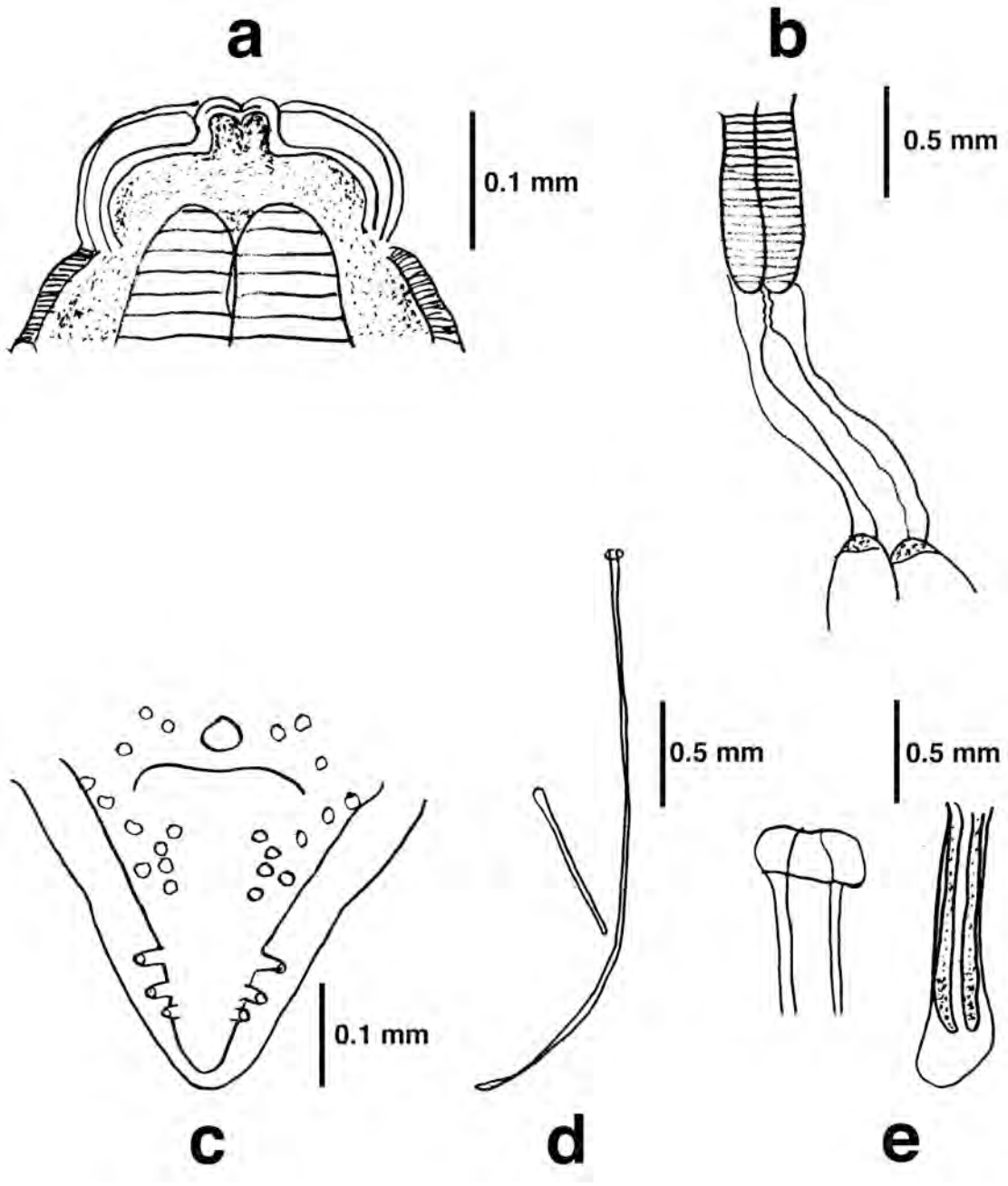

Figure 3. *Anisakis typica*, showing its (a) cephalic end, (b) ventriculus, (c) male caudal end, (d) male spicules, and (e) extremity of male spicules. Adapted with permission from an illustration by S. Mattiucci, Universitá di Roma La Sapienza.

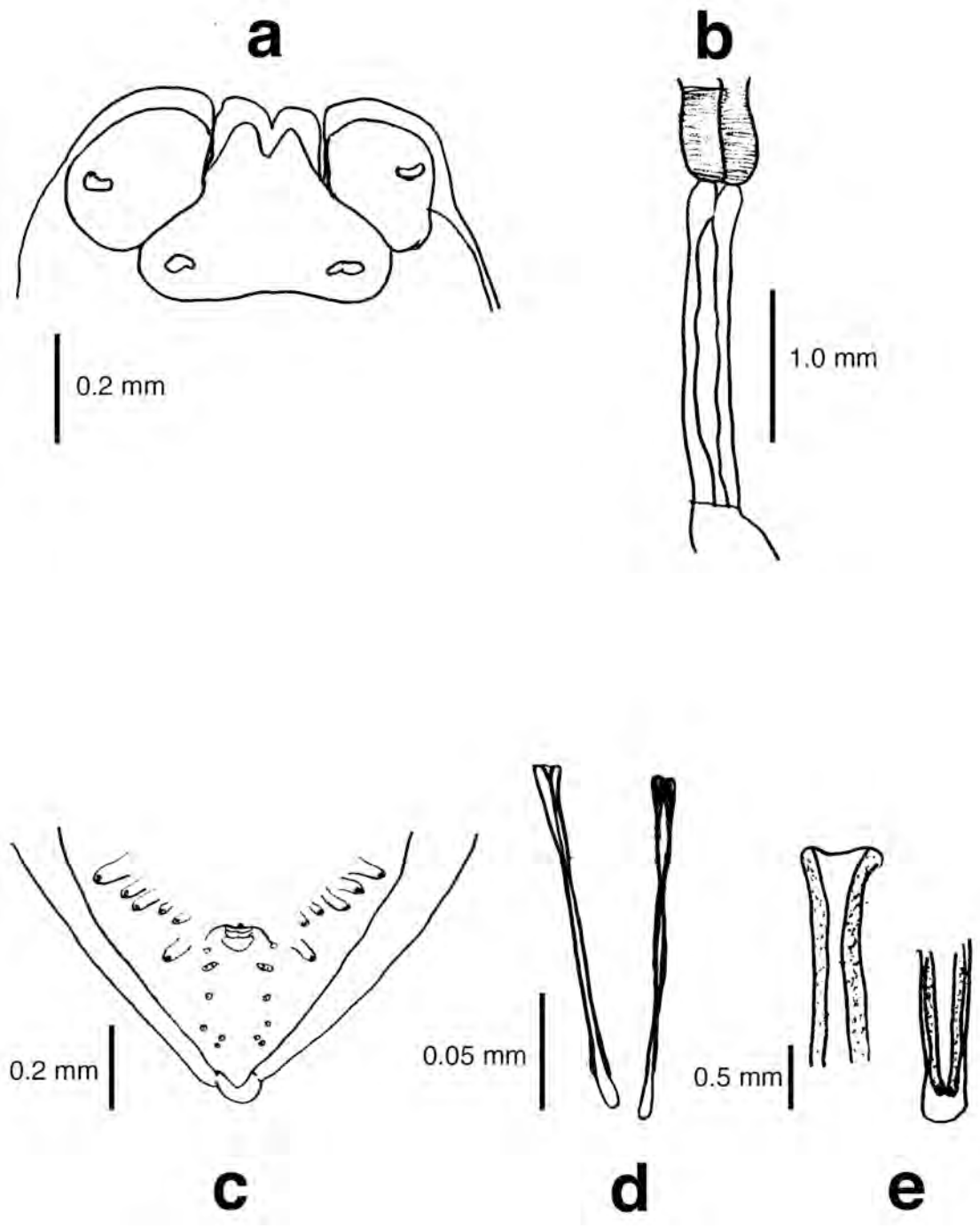

Figure 4. *Anisakis zhiphidarum*, showing (a) cephalic end, (b) ventriculus, (c) male caudal end, (d) male spicules, and (e) extremity of spicules. Adapted with permission from an illustration by S. Mattiucci, Universitá di Roma La Sapienza.

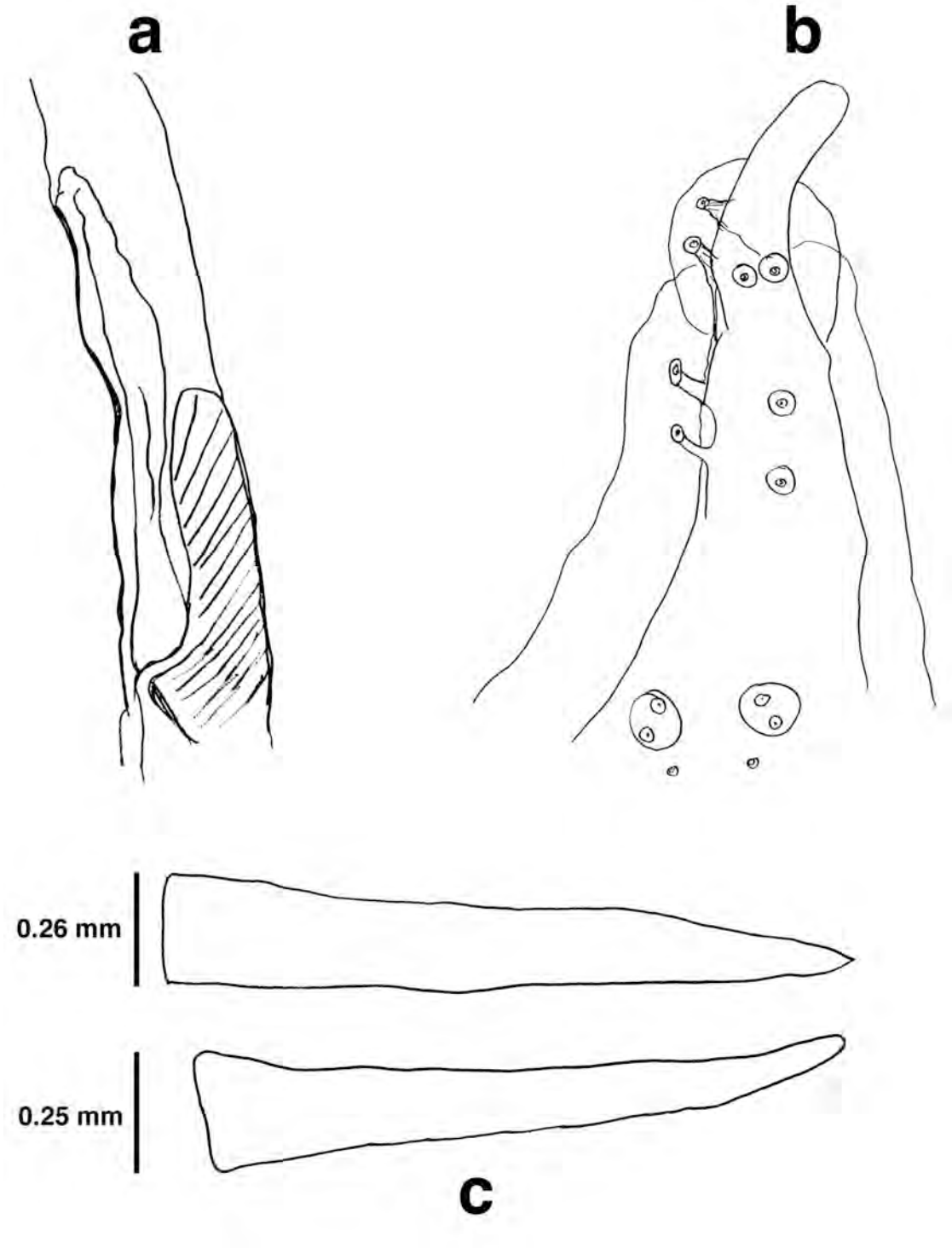

Figure 5. *Pseudoterranova ceticola*, showing (a) ventriculus, (b) male caudal end, and (c) male spicules.