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Cover Photograph: *Trichechus manatus* (West Indian Manatee) with attached *Chelonibia testudinaria* (Turtle Barnacle) and scars of detached barnacles in Three Sisters Spring, Crystal River, FL, USA. Photograph © Luis Orlando Torres .

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Barnacles Associated with Whales, Dolphins, Manatees, and Sea Turtles from the Puerto Rico Archipelago and Florida

Antonio A. Mignucci-Giannoni[1,2,*], Jamilette Cintrón-de Jesús[3], Carla I. Rivera-Pérez[1,2], Gabriela S. Rivera-Tritsare[1], and John D. Zardus[4]

Abstract - Epizoic barnacles on marine megafauna encompass various species that maintain strict to moderate host specificity. For the megafaunal hosts, knowing what particular suites of epibionts accompany them can help define populations and offer insight into migration patterns for these often elusive and endangered organisms. Herein, we provide an inventory for Florida and the Puerto Rico archipelago of barnacles epizoic with marine mammals and reptiles compiled from ~4 decades of rescuing and salvaging debilitated and stranded cetaceans, manatees, and sea turtles from these regions. From 115 salvage or rescue cases, 11 barnacle species were identified. Two species of barnacles were opportunistic types, found attached to other barnacles epizoic with manatees. The remaining 9 were species that are obligate with 1 or several marine megafauna. One, *Conchoderma auritum*, was found attached only to the underlying shells of other epizoic barnacles, not to the megafaunal host itself. Two notable barnacle species were *Coronula reginae* from a *Megaptera novaeangliae* (Humpback Whale), documented in the northern hemisphere of the North Atlantic Ocean only once before, and the first report of *Cylindrolepas darwiniana* from manatees, otherwise known only from sea turtles. Larger-bodied hosts (whales), carried higher numbers of barnacles encompassing a maximum of 3 species, but barnacle diversity was higher on manatees and sea turtles (5 species each). The only barnacles occurring with a single host species in this data set were the 2 whale barnacles *Coronula diadema* and *C. reginae* from Humpback Whales. Noteworthy was the absence of the barnacle *Xenobalanus globicipitis* which otherwise is cosmopolitan with numerous delphinids. We did not find this barnacle with any of the 94 individuals of 10 dolphin species examined. The epizoic barnacle fauna of marine megafauna from Puerto Rico and Florida indicate a similar pattern of predominantly coastal habitat use for adult sea turtles, freshwater incursions by manatees in Florida but not Puerto Rico, and intermittent oceanic/neritic residence of cetaceans.

Introduction

Barnacles are crustacean arthropods belonging to the subclass Cirripedia and infraclass Thoracica (true barnacles; Chan et al. 2021a). They can be classified by morphological differences into several orders of which 2 are commonly encountered: the acorn barnacles (order Sessilia, “balano”, “ballocas”, “bayocas”, or “caracolillos” in Spanish), and the stalked or “gooseneck” barnacles (order

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Pedunculata, "percebes" in Spanish). All barnacle species are marine, although a few can tolerate freshwater (i.e., *Amphibalanus improvisus* (Darwin) [Bay Barnacle]; Zullo 1979). Some are edible and are commercially managed (López et al. 2012, Molares and Freire 2003). While some barnacles are parasitic on other organisms (i.e., infraclass Rhizocephala), the rest are usually attached to rocky and shelly substrates or partner in commensal, symbiotic relationships by attaching themselves to other aquatic wildlife species, such as fish, cetaceans, sirenians, and sea turtles (Fig. 1; Clarke 1966, Fordyce et al. 1979, Gittings et al. 1986, Ross and Leatherwood 1994, Williams 1978, Williams and Williams 1986).

The epizoic barnacle fauna associated with large marine megafauna of the Caribbean has not been thoroughly investigated. Bigelow (1900) described some cirripeds collected in Puerto Rico, including some epizoic species; however, it was not until the latter part of the 20th century that barnacle distributions in the region were again assessed. Bacon (1976) surveyed barnacles in Trinidad, including species from sea turtles, and Granadillo and Urosa (1984) did the same from nearby Venezuela. Gittings et al. (1986), in their survey of barnacles in the Gulf of Mexico, described epibiotic barnacles from *Trichechus manatus* L. (West Indian Manatee) and *Caretta caretta* L. (Loggerhead Sea Turtle) from western Florida, and Eckert

Figure 1. West Indian Manatee with attached Turtle Barnacles and scars of detached barnacles in Three Sisters Spring, Crystal River, FL, USA. Photograph © Luis Orlando Torres, with permission.

and Eckert (1988) investigated barnacles from *Dermochelys coriacea* (Vandelli) (Leatherback Sea Turtle) in St. Croix. Rodríguez-Fourquet (1992) studied the relationship between recruitment and larval abundance of *Amphibalanus eburneus* A.A. Gould (Ivory Barnacle), and Mignucci-Giannoni (1996), Mignucci-Giannoni et al. (1998, 1999a, 1999b), Rodríguez-López and Mignucci-Giannoni (1999), and Rosario-Delestre et al. (1999) reported these as epibionts of whales, dolphins, and manatees. Frick et al. (2003) reported on the barnacles from *Eretmochelys imbricata* (L.) (Hawksbill Sea Turtle) in Antigua, Torres-Pratts et al. (2009) studied barnacle genetic diversity from the latter turtle species in Mona Island, PR, and Blick et al. (2010) examined barnacle material from archeological sea turtle remains in The Bahamas.

Many of these studies have presumed that the association with whales, manatees, and sea turtles is host-specific for different species of barnacles. Certainly, barnacles must be adapted to the type of substratum they attach; for instance, whale barnacles have unique morphological features allowing them to affix to a somewhat resilient surface that travels at high velocity (Seilacher 2005). Some are known from only 1 species of whale. For example, *Tubicinella major* lives embedded in the callosities of *Eubalaena australis* (Desmoulins) (Southern Right Whale; Best 1999), and *Cryptolepas rachianecti* occurs almost exclusively with *Eschrichtius robustus* (Lilljeborg) (Gray Whale; Dall 1873, but see Ridgway et al. 1997 for an unusual exception). However, Zardus (2021) recently noted a paradox with barnacles that live commensally with sea turtles, primarily in the skin; though specific to turtles, the barnacles mostly do not discriminate strongly among turtle species, and 1 species even occurs also with mammals, reptiles, and crabs (Zardus et al. 2014). Whether tightly species-specific or accepting of a broader taxonomic array of hosts, a crucial enigma for barnacles that specialize in mobile hosts is how they are able locate and recognize their relatively rare and itinerant substratum. The few life-history investigations of barnacles found on whales and turtles confirm that they undergo typical barnacle development with free-swimming larval stages that cannot attach until the terminal molt is reached (Nogata and Matsumura 2006, Zardus and Hadfield 2004). It seems likely that once the larvae have developed sufficiently in the plankton, they seek chemical and tactile cues to identify their settlement destination. Still, their larval attachment organs offer few clues about how site selection is achieved (Dreyer et al. 2020). Distinguishing which barnacles occur with which hosts is preliminary to understanding what mechanisms they are using, what choices they may be making in the recruitment process, and how their presence can inform our understanding of host ecology and behavior.

Here, we detail the various species of barnacles found associated with stranded and rescued marine mammals and sea turtles from Florida and the Puerto Rico archipelago.

Methods

Acorn and stalked barnacles were collected opportunistically from the skin or teeth of cetaceans, the skin of manatees, and from the skin or carapace of sea turtles

as part of documenting stranding cases in Florida (Bossart et al. 2004, Reynolds and Odell 1991) and the Puerto Rico archipelago (Mignucci-Giannoni et al. 1999b, 2000; Ortiz-Rivera et al. 2002). The Puerto Rico archipelago includes the main and adjacent islands and cays of Puerto Rico and the US and British Virgin Islands. The collection of barnacles from Florida included 13 coastal counties on both the Gulf and North Atlantic coasts of the peninsula. In addition to opportunistic examination of stranded manatees, sea turtles, and cetaceans in Puerto Rico and the Virgin Islands between 1989 and 2021, we examined 94 individuals of 10 delphinid species, including *Steno bredanensis* (Lesson) (Rough-toothed Dolphin, n = 5), *Tursiops truncatus* (Montagu) (Common Bottlenose Dolphin, n = 36), *Stenella frontalis* (G. Cuvier) (Atlantic Spotted Dolphin, n = 12), *Stenella longirostris* (Gray) (Spinner Dolphin, n = 2), *Stenella coeruleoalba* (Meyen) (Striped Dolphin, n = 1), *Lagenodelphis hosei* Fraser (Fraser's Dolphin, n = 6), *Grampus griseus* (G. Cuvier) (Risso's Dolphin, n = 4), *Peponocephala electra* (Gray) (Melon-headed Whale, n = 2), *Feresa attenuata* Gray (Pygmy Killer Whale, n = 6), and *Globicephala macrorhynchus* Gray (Short-finned Pilot Whale, n = 20).

Specimens were collected between the 1980s and 2021 during health assessment, rescue, salvage, and necropsy procedures and preserved in 70% ethanol. We examined large barnacles by cutting the specimen with a geologic saw and dissected smaller barnacles using pliers. We used a small brush to clean the barnacles of inorganic and organic material. We observed each barnacle specimen under a stereoscope and identified them based primarily on their external morphological features using Anderson (1994), Darwin (1854), Gittings et al. (1986), Newman and Ross (1976), Pilsbry (1916), and Zullo (1979) as reference.

Results

Barnacles were collected and identified from 115 whales, dolphins, manatees, and sea turtles (Table 1). Eleven epizoic barnacle species were identified from these marine vertebrates, including 2 stalked barnacles and 9 acorn barnacles (Table 1, Fig. 2). *Megaptera novaeangliae* Borowski (Humpback Whales) harbored the acorn barnacles *Coronula diadema* (L.) (Coronet Barnacle) and *Coronula reginae* Darwin (Queen's Coronet Barnacle), and the stalked barnacle *Conchoderma auritum* (Linnaeus) (Rabbit-ear Barnacle) (Table 2, Fig. 3). Coronet Barnacles were more commonly found on Humpback Whales than the Queen's Coronet Barnacles, but both species occurred on 2 of the whales studied from Puerto Rico. Most commonly, Rabbit-ear Barnacles were found attached to Coronet Barnacles. Rabbit-ear Barnacles were also collected from the teeth of *Physeter macrocephalus* L. (Sperm Whale), *Ziphius cavirostris* Cuvier (Cuvier's Beaked Whale), *Mesoplodon densirostris* Blainville (Blainville's Beaked Whale), *Mesoplodon europaeus* (Gervais) (Gervais' Beaked Whale), and the delphinid Pygmy Killer Whale (Table 2). *Xenobalanus globicipitis* Steenstrup (Tassel Barnacle), a common associate of delphinids, was not encountered on any of 94 individuals of the 10 dolphin species examined in the Puerto Rico archipelago between 1989 and 2021. However,

a single *Stenella attenuata* (Gray) (Pantropical Spotted Dolphin) calf rescued on 5 January 2019 from the nearby island of Antigua in the Lesser Antilles, and examined by us, harbored 4 Tassel Barnacles in the posterior margin of its caudal fin.

West Indian Manatees in Florida and Puerto Rico had 5 species of barnacles associated with them, including *Amphibalanus amphitrite* Darwin (Striped Barnacle), Ivory Barnacle, *Chelonibia testudinaria* (L.) (Turtle Barnacle), *Platylepas hexastylos* (O. Fabricius) (Layered Clasping Barnacle), and a barnacle that compares favorably with what Frick and Zardus (2010) identified as *Cylindrolepas darwiniana* Pilsbry (Coarse Cylindrical Barnacle) (Table 3). The most commonly found barnacle in Florida and Puerto Rico was the Turtle Barnacle (Fig. 1), followed by the Ivory Barnacle. Both *Amphibalanus* barnacles were found attached to the Turtle Barnacle and not to the skin of the manatee itself. Manatees also had scars of detached barnacles on their skin, particularly in estuarine or freshwater environments (Fig. 1).

Both *Chelonia mydas* (L.) (Green Sea Turtle) and Hawksbill Sea Turtles in Puerto Rico were infested with the Turtle Barnacle, Layered Clasping Barnacle, and

Table 1. Host identification and count by region for barnacle species found on marine mammal and sea turtle hosts from the Puerto Rico archipelago (PR) and Florida, USA.

	Hosts examined		
Host	PR	Florida	Barnacle species
Megaptera novaeangliae (Humpback Whale)	4	1	*Conchoderma auritum**
			Coronula diadema
			Coronula reginae
Physeter macrocephalus (Sperm Whale)	1	-	*Conchoderma auritum***
Ziphius cavirostris (Cuvier's Beaked Whale)	3	-	*Conchoderma auritum***
Mesoplodon densirostris (Blainville's Beaked Whale)	1	-	*Conchoderma auritum***
Mesoplodon europaeus (Gervais' Beaked Whale)	1	-	*Conchoderma auritum***
Feresa attenuata (Pygmy killer whale)	1	-	*Conchoderma auritum***
Trichechus manatus (West Indian Manatee)	39	52	*Amphibalanus amphitrite**
			*Amphibalanus eburneus**
			Chelonibia testudinaria
			Cylindrolepas darwiniana
			Platylepas hexastylos
Eretmochelys imbricata (Hawksbill Sea Turtle)	5	-	*Chelonibia caretta*
			Platylepas hexastylos
			Stomatolepas elegans
Chelonia mydas (Green Sea Turtle)	5	-	*Chelonibia caretta*
			Chelonibia testudinaria
			Lepas anatifera
			Platylepas hexastylos
			Stomatolepas elegans
Lepidochelys olivacea (Olive Ridley Sea Turtle)	1	-	*Lepas anatifera*
Caretta caretta (Loggerhead Sea Turtle)	1	-	*Lepas anatifera*
Total	62	53	

* Species attached to another barnacle's shell, not directly attached to the host
** Species attached to tooth of host

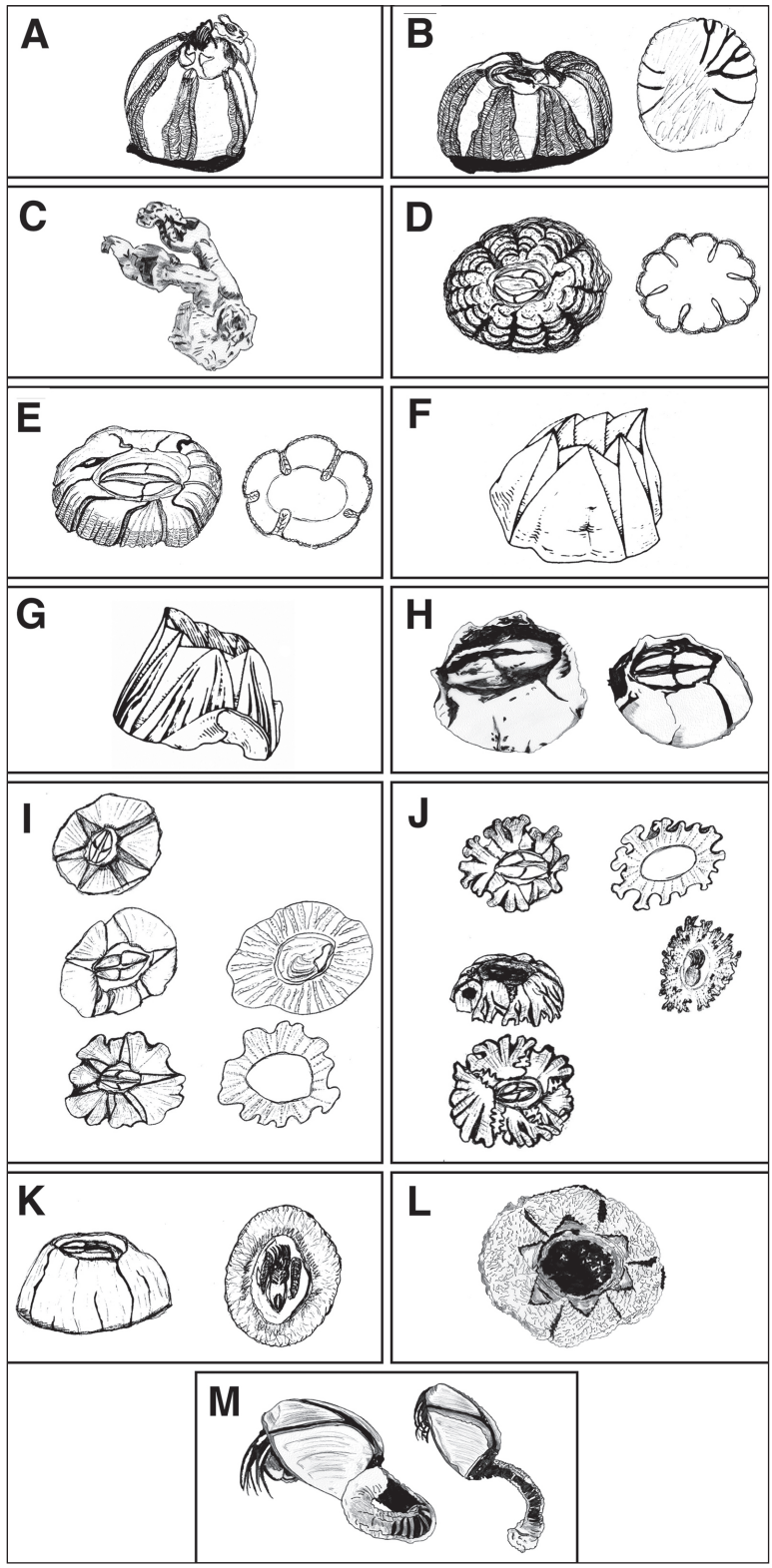

Figure 2. Illustration of the 11 species of barnacles found from marine mammal and sea turtles hosts in the Puerto Rico archipelago and Florida: (A) *Coronula diadema* [Coronet Barnacle], (B) *Corunula reginae* [Queen's Coronet Barnacle], (C) *Conchoderma auritum* [Rabbit-ear Barnacle], (D) *Platylepas hexastylos* [Layered Clasping Barnacle], (E) *Cylindrolepas darwiniana* [Coarse Cylindrical Barnacle], (F) *Amphibalanus eburneus* [Ivory Barnacle], (G) *Amphibalanus amphitrite* [Striped Barnacle], (H, I, J) *Chelonibia testudinaria* [Turtle Barnacle], (K) *Chelonibia caretta* [Hawksbill-turtle Barnacle], (L) *Stomatolepas elegans* [Elegant Cup Barnacle], and (M) *Lepas anatifera* [Duck Barnacle].

Stomatolepas elegans (Costa) (Elegant Cup Barnacle), with the latter sea turtle also harboring the barnacle *Chelonibia caretta* (Spengler) (Hawksbill-turtle Barnacle) (Table 4). In addition, the oceanic stalked barnacle *Lepas anatifera* L. (Duck Barnacle) was found on the carapace of a Green Sea Turtle, a *Lepidochelys olivacea* (Eschscholtz) (Olive Ridley Sea Turtle), and a Loggerhead Sea Turtle (Table 4,

Table 2. Barnacle species identified on cetacean hosts from the Puerto Rico archipelago and Florida with host identification and locality.

Field no.	Date	Host	Locality	Body of water
Conchoderma auritum (Rabbit-ear Barnacle)				
-	1980s	*M. novaeangliae*	Brevard, FL	North Atlantic Ocean
NEPST145	5 Feb 1991	*Z. cavirostris*	St. Croix, USVI	Caribbean Sea
NEPST179	28 Dec 1991	*P. macrocephalus*	Aguadilla, PR	North Atlantic Ocean
NEPST233	12 Sep 1993	*M. europaues*	St. Croix, USVI	Caribbean Sea
NEPST526	25 Feb 1997	*F. attenuata*	Aguada, PR	North Atlantic Ocean
NEPST509	22 Feb 1998	*M. novaeangliae*	Naguabo, PR	Caribbean Sea
NEPST385	29 Jul 1998	*Z. cavirostris*	Aguadilla, PR	North Atlantic Ocean
NEPST505	25 Nov 1998	*Z. cavirostris*	Aguada, PR	North Atlantic Ocean
NEPST881	31 Jan 2004	*M. densirostris*	Ceiba, PR	Caribbean Sea
Coronula diadema (Coronet Barnacle)				
-	1980s	*M. novaeangliae*	Brevard, FL	North Atlantic Ocean
NEPST026	7 Apr 1986	*M. novaeangliae*	Mayagüez, PR	Caribbean Sea
NEPST497	4 Feb 1996	*M. novaeangliae*	Rincón, PR	North Atlantic Ocean
NEPST509	22 Feb 1998	*M. novaeangliae*	Naguabo, PR	Caribbean Sea
NEPST900	17 Mar 2005	*M. novaeangliae*	Arecibo, PR	North Atlantic Ocean
Coronula reginae (Queen's Coronet Barnacle)				
NEPST497	4 Feb 1996	*M. novaeangliae*	Rincón, PR	North Atlantic Ocean
NEPST509	22 Nov 1998	*M. novaeangliae*	Naguabo, PR	Caribbean Sea

Figure 3. Coronet Barnacles with attached Rabbit-ear Barnacles from a Humpback Whale from Puerto Rico.

Table 3. Barnacle species identified on West Indian Manatee hosts from Puerto Rico and Florida with host identification and locality. [Table continued on following 2 pages.]

Field no.	Date	Locality	Body of Water
Amphibalanus amphitrite (Striped Barnacle)			
M8111	29 Jan 1981	Monroe, FL	Gulf of Mexico
NEPST077	13 Aug 1984	Peñuelas, PR	Caribbean Sea
Amphibalanus eburneus (Ivory Barnacle)			
M8111	29 Jan 1981	Monroe, FL	Gulf of Mexico
M8128	15 Feb 1981	Collier, FL	Gulf of Mexico
M8126	16 Feb 1981	Collier, FL	Gulf of Mexico
M8129	22 Feb 1981	Lee, FL	Gulf of Mexico
M8167	31 Dec 1981	Martin, FL	North Atlantic Ocean
M8202	14 Jan 1982	Monroe, FL	Gulf of Mexico
M8218	23 Feb 1982	Lee, FL	Gulf of Mexico
M8226	4 Mar 1982	Lee, FL	Gulf of Mexico
M8228	22 Mar 1982	Lee, FL	Gulf of Mexico
M8229	24 Mar 1982	Lee, FL	Gulf of Mexico
M8415	20 Feb 1984	Martin, FL	North Atlantic Ocean
NEPST077	13 Aug 1984	Peñuelas, PR	Caribbean Sea
NEPST532	21 Jan 1998	Juana Díaz, PR	Caribbean Sea
NEPST873	9 Nov 2003	Guayanilla, PR	Caribbean Sea
MNE0907	31 Jan 2009	Volusia, FL	North Atlantic Ocean
MNE0909	13 Feb 2009	Duval, FL	North Atlantic Ocean
MEC0928	19 Feb 2009	Brevard, FL	North Atlantic Ocean
Chelonibia testudinaria (Turtle Barnacle)			
M7926	21 Dec 1979	Martin, FL	North Atlantic Ocean
M8021	21 Aug 1980	Collier, FL	Gulf of Mexico
M8027	23 Dec 1980	Collier, FL	Gulf of Mexico
M8108	26 Jan 1981	Collier, FL	Gulf of Mexico
M8111	29 Jan 1981	Monroe, FL	Gulf of Mexico
M8112	29 Jan 1981	Lee, FL	Gulf of Mexico
M8114	31 Jan 1981	Collier, FL	Gulf of Mexico
M8115	2 Feb 1981	Lee, FL	Gulf of Mexico
M8123	12 Feb 1981	Collier, FL	Gulf of Mexico
M8128	15 Feb 1981	Collier, FL	Gulf of Mexico
M8126	16 Feb 1981	Collier, FL	Gulf of Mexico
M8129	22 Feb 1981	Lee, FL	Gulf of Mexico
M8150	16 May 1981	Lee, FL	Gulf of Mexico
M8158	18 Aug 1981	Lee, FL	Gulf of Mexico
M8165	16 Dec 1981	Collier, FL	Gulf of Mexico
M8167	31 Dec 1981	Martin, FL	North Atlantic Ocean
M8169	31 Dec 1981	Lee, FL	Gulf of Mexico
M8202	14 Jan 1982	Monroe, FL	Gulf of Mexico
M8203	15 Jan 1982	Palm Beach, FL	North Atlantic Ocean
M8206	3 Feb 1982	Charlotte, FL	Gulf of Mexico
M8211	12 Feb 1982	St. Lucie, FL	North Atlantic Ocean
M8212	13 Feb 1982	Lee, FL	Gulf of Mexico
M8216	16 Feb 1982	Lee, FL	Gulf of Mexico
M8217	20 Feb 1982	Lee, FL	Gulf of Mexico
M8218	23 Feb 1982	Lee, FL	Gulf of Mexico
M8219	25 Feb 1982	Lee, FL	Gulf of Mexico

Table 3, continued

Field no.	Date	Locality	Body of Water
M8222	25 Feb 1982	Lee, FL	Gulf of Mexico
M8224	28 Feb 1982	Charlotte, FL	Gulf of Mexico
M8225	3 Mar 1982	Lee, FL	Gulf of Mexico
M8226	4 Mar 1982	Lee, FL	Gulf of Mexico
M8228	22 Mar 1982	Lee, FL	Gulf of Mexico
M8229	24 Mar 1982	Lee, FL	Gulf of Mexico
M8230	30 Mar 1982	Broward, FL	North Atlantic Ocean
M8232	1 Apr 1982	Lee, FL	Gulf of Mexico
M8401	2 Jan 1984	Palm Beach, FL	North Atlantic Ocean
M8404	16 Jan 1984	Martin, FL	North Atlantic Ocean
M8415	20 Feb 1984	Martin, FL	North Atlantic Ocean
NEPST077	13 Aug 1984	Peñuelas, PR	Caribbean Sea
M8428	29 Sep 1984	Sarasota, FL	Gulf of Mexico
M8608	29 Jan 1986	Lee, FL	Gulf of Mexico
M8609	29 Jan 1986	St. Lucie, FL	North Atlantic Ocean
M8612	10 Mar 1986	Brevard, FL	North Atlantic Ocean
NEPST164	31 May 1991	Cabo Rojo, PR	Caribbean Sea
TPR11	9 Aug 1997	Mayagüez, PR	Caribbean Sea
NEPST532	21 Jan 1998	Juana Díaz, PR	Caribbean Sea
TPR12	4 Apr 1998	Mayagüez, PR	Caribbean Sea
NEPST612	26 Oct 2000	Guánica, PR	Caribbean Sea
TPR14	18 Jul 2003	Cabo Rojo, PR	Caribbean Sea
CPR0301	20 Jul 2003	Guayanilla, PR	Caribbean Sea
CPR0302	21 Jul 2003	Guayanilla, PR	Caribbean Sea
TPR16	4 Nov 2003	Cabo Rojo, PR	Caribbean Sea
TPR17	5 Nov 2003	Guayanilla, PR	Caribbean Sea
TPR18	5 Nov 2003	Guayanilla, PR	Caribbean Sea
TPR19	6 Nov 2003	Guayanilla, PR	Caribbean Sea
CPR0303	7 Nov 2003	Guayanilla, PR	Caribbean Sea
NEPST873	9 Nov 2003	Guayanilla, PR	Caribbean Sea
MEC0887	10 Dec 2003	Brevard, FL	North Atlantic Ocean
NEPST175	19 Jan 2004	Naguabo, PR	Caribbean Sea
TPR20	7 Jun 2004	Guayanilla, PR	Caribbean Sea
TPR21	7 Jun 2004	Guayanilla, PR	Caribbean Sea
TPR22	8 Jun 2004	Guayanilla, PR	Caribbean Sea
NEPST913	12 Nov 2005	Cabo Rojo, PR	Caribbean Sea
NEPST932	9 Dec 2006	Ponce, PR	Caribbean Sea
MSE0830	9 Dec 2008	Palm Beach, FL	North Atlantic Ocean
MEC0887	10 Dec 2008	Brevard, FL	North Atlantic Ocean
MSE0834	23 Dec 2008	Palm Beach, FL	North Atlantic Ocean
MSE0906	25 Jan 2009	Monroe, FL	Gulf of Mexico
MNW0901	26 Jan 2009	Pinellas, FL	Gulf of Mexico
MNE0907	31 Jan 2009	Volusia, FL	North Atlantic Ocean
MNE0909	13 Feb 2009	Duval, FL	North Atlantic Ocean
MSE0924	20 Feb 2009	Palm Beach, FL	North Atlantic Ocean
DRN0038	13 Aug 2010	Ponce, PR	Caribbean Sea
NEPST939	24 Aug 2010	Carolina, PR	North Atlantic Ocean
DRN0060	6 Aug 2011	Cabo Rojo, PR	Caribbean Sea
DRN0063	17 Aug 2011	Loiza, PR	North Atlantic Ocean
DRN0076	11 Nov 2012	Cabo Rojo, PR	Caribbean Sea

Fig. 4). Overall, the Layered Clasping Barnacle was the most numerically abundant barnacle found on sea turtles.

Infestation of barnacles varied within-hosts and between species. The number of acorn barnacles per Humpback Whale averaged 29.0 ± 36.5 (min–max =1–70), whereas the number on manatees averaged 15.8 ± 15.9 (min–max =1–70). The

Table 3, continued

Field no.	Date	Locality	Body of Water
DRN0090	16 Jul 2013	Ponce, PR	Caribbean Sea
DRN0094	29 Jul 2013	Ponce, PR	Caribbean Sea
CCMPR160513Tm01	13 May 2016	Salinas, PR	Caribbean Sea
CCMPR161020Tm01	20 Oct 2016	Ponce, PR	Caribbean Sea
CCMPR180205Tm01	5 Feb 2018	Juana Díaz, PR	Caribbean Sea
DRN0167	27 Mar 2018	Guayama, PR	Caribbean Sea
CCMPR180427Tm01	27 Apr 2018	Naguabo, PR	Caribbean Sea
CCM180817Tm01	17 Aug 2018	Ponce, PR	Caribbean Sea
DRN0182	6 Oct 2019	Salinas, PR	Caribbean Sea
CCM200921Tm01	21 Sep 2020	Guánica, PR	Caribbean Sea
CCM211015Tm01	15 Oct 2021	San Juan, PR	North Atlantic Ocean
Cylindrolepas darwiniana (Coarse Cylindrical Barnacle)			
M8150	16 May 1981	Lee, FL	Gulf of Mexico
NEPST077	13 Aug 1984	Peñuelas, PR	Caribbean Sea
CPR9801	5 Apr 1998	Mayagüez, PR	Caribbean Sea
DRN0060	6 Aug 2011	Cabo Rojo, PR	Caribbean Sea
Platylepas hexastylos (Layered Clasping Barnacle)			
M8111	29 Jan 1981	Monroe, FL	Gulf of Mexico
M8150	16 May 1981	Lee, FL	Gulf of Mexico
CPR9702	8 Aug 1997	Mayagüez, PR	Caribbean Sea
NEPST532	21 Jan 1998	Juana Díaz, PR	Caribbean Sea
TPR12	4 Apr 1998	Mayagüez, PR	Caribbean Sea
CPR9801	5 Apr 1998	Mayagüez, PR	Caribbean Sea
MSW1159	19 May 2011	Sarasota, FL	Gulf of Mexico
DRN0094	29 Jul 2013	Ponce, PR	Caribbean Sea

Figure 4. Duck Barnacles on an (A) Olive Ridley Sea Turtle, (B) Loggerhead Sea Turtle, and (C) Green Sea Turtle from Puerto Rico.

number of acorn barnacles per sea turtle was considerably lower, with an average of 5.0 ± 3.6 (min–max =1–8) per Hawksbill Sea Turtle and 9.0 ± 7.5 (min–max =1–16) per Green Sea Turtle. The numbers of Rabbit-ear Barnacles were small compared to acorn barnacles, in most cases not exceeding 4 specimens on each cetacean host. Simultaneous infestation of multiple acorn barnacle species per the same host individual was common in manatees (up to 4 different species) but less common in Humpback Whales and Hawksbill Sea Turtles (up to 2 different species). In 1 instance, Rabbit-ear Barnacles, found on 1 of the Humpback Whales, were attached to Coronet Barnacles and not directly to the host. Similarly, the Ivory Barnacles and Striped Barnacles in manatees were found attached to *Chelonibia* barnacles and not directly to the manatee's skin.

Discussion

Barnacles specializing as epizoites of living hosts, particularly mobile megafauna, is an intriguing and well documented, but not well understood, phenomenon. Intuitively, these crustaceans are variously adapted to their particular substrates, such as the yielding skin of a whale or the rigid shell of a sea turtle, and tuned to the locomotory patterns of their hosts. However, the full extent of biomechanical, biochemical, and behavioral adaptations displayed by barnacles remains largely

Table 4. Barnacle species identified on sea turtle hosts from Puerto Rico with host identification and, if included in the record, the locality within Puerto Rico where collected.

Field no.	Date	Host	Locality	Body of water
Chelonibia caretta (Hawksbill-turtle Barnacle)				
NEPCH230	24 Feb 1996	*E. imbricata*	Rincón	North Atlantic Ocean
NEPCH233	27 May 1996	*E. imbricata*	Ponce	Caribbean Sea
CCMPR160821Cm01	21 Aug 2016	*C. mydas*	Toa Baja	Caribbean Sea
Chelonibia testudinaria (Turtle Barnacle)				
CCMPR160915Ei01	15 Sep 2016	*E. imbricata*	Isla de Vieques	Caribbean Sea
CCM210111Cm01	11 Jan 2021	*C. mydas*	Humacao	Caribbean Sea
CCM210823Cm01	23 Aug 2021	*C. mydas*	Lajas	Caribbean Sea
Lepas anatifera (Duck Barnacle)				
CCM180903Lo01	3 Sep 2018	*L. olivacea*	Lajas	Caribbean Sea
CCM210131Cc01	31 Jan 2021	*C. caretta*	San Juan	North Atlantic Ocean
CCM210823Cm01	23 Aug 2021	*C. mydas*	Lajas	Caribbean Sea
Platylepas hexastylos (Layered Clasping Barnacle)				
NPCH210	1 Jan 1995	*E. imbricata*	Puerto Rico	Caribbean Sea
NEPCH098	17 Jul 1995	*E. imbricata*	Carolina	Caribbean Sea
NEPCH228	14 Jan 1996	*C. mydas*	Isla de Culebra	Caribbean Sea
NEPCH231	6 Jan 1996	*C. mydas*	Puerto Rico	Caribbean Sea
NEPCH230	24 Feb 1996	*E. imbricata*	Rincón	North Atlantic Ocean
NEPCH233	27 May 1996	*E. imbricata*	Ponce	Caribbean Sea
Stomatolepas elegans (Elegant Cup Barnacle)				
NEPCH210	1 Jan 1995	*E. imbricata*	Puerto Rico	Caribbean Sea
NEPCH228	14 Jan 1996	*C. mydas*	Isla de Culebra	Caribbean Sea

unknown. We contribute to the topic herein by addressing the preliminary task of identifying which barnacle species occur with which marine mammal and reptile megafauna in Puerto Rico and Florida, allowing for comparison with different regions of the world.

Amphibalanus amphitrite (Striped Barnacle). Not typically epizoic, this opportunistic species has a worldwide distribution (Fofonoff et al. 2003). Much like the Ivory Barnacle, it is generally accepted that the global dispersal of this barnacle species is due to anthropogenic transport, leading to Striped Barnacle colonization of numerous non-native sites (Utinomi 1960). Morphologically, this species is characterized by its toothed conical shell adorned with vertical purple striations on its shell walls. Previous studies have explored the possibility of Striped Barnacle attachment on mussel and oyster shells negatively impacting the growth and survival of mollusks (Mathis et al. 2015). We collected Striped Barnacles on only 2 West Indian Manatees in Puerto Rico and Florida, in both instances not attached directly to the manatee but to Turtle Barnacles.

Amphibalanus eburneus (Ivory Barnacle). This rather large, opportunistic barnacle species is considered endemic to the Western North Atlantic waters bordering the eastern coast of the United States and the Caribbean Sea, as well as the Gulf of Mexico (Torres et al. 2013). However, the worldwide spread of Ivory Barnacles is believed to have been caused by anthropogenic means, such as shipping and shellfish culture (Osca and Crocetta 2020). The uniformly pale shell of the Ivory Barnacle, characterized by its cylindrical and conic shape, divides into 6 plates that lead to an irregular pentagonal orifice (Osca and Crocetta 2020). We found Ivory Barnacles commonly on West Indian Manatees from Florida but rarely in Puerto Rico, with other barnacles (i.e., Turtle Barnacles) on the manatees serving as its substratum.

Chelonibia caretta (Hawksbill-turtle Barnacle). This epibiont is globally distributed and commonly identified on marine turtles in the Mediterranean Sea, Caribbean Sea, North Atlantic Ocean, and North Pacific Ocean (Karaa et al. 2012). The Hawksbill-turtle Barnacle has been documented living attached to Hawksbill Sea Turtles, Green Sea Turtles, and Loggerhead Sea Turtles (Gittings et al. 1986, Hayashi 2012, Jones 2010). They are somewhat morphologically similar to the Turtle Barnacle in that the Hawksbill-turtle Barnacle also possesses a robust shell; however, its shell wall is less thick and lacks the starlike radii present in the Turtle Barnacle (Zardus et al. 2014). Hawksbill-turtle Barnacles can be found entrenched into the carapace of marine turtles, particularly along the vertebral scutes (Karaa et al. 2012). Evidence suggests it is predominantly specialized for the Hawksbill Sea Turtle as hosts (Boyd et al. 2021). In our collections, Hawksbill-turtle Barnacle samples were recovered from 2 Hawksbill Sea Turtles and 1 Green Sea Turtle in Puerto Rico.

Chelonibia testudinaria (Turtle Barnacle). This species was previously separated into several species and subspecies on morphological grounds as *Chelonibia manati* Gruvel, *C. manati crenatibasis* Pilsbry, *C. manati lobatobasis* Pilsbry, and *C. patula* Ranzani (Crab Barnacle). These forms are now unified in a single variable species (Zardus et al. 2014) that was thought to be originally native to

the North Atlantic Ocean, Caribbean Sea, Gulf of Mexico, and the Mediterranean Sea. However, the Turtle Barnacle is now known throughout the world's oceans living on sea turtles, manatees, and, occasionally, other reptilian megafauna (Zardus 2021). Previous surveys have documented Turtle Barnacles on the Loggerhead Sea Turtle, Green Sea Turtle, Hawksbill Sea Turtle, Olive Ridley Sea Turtle, Leatherback Sea Turtle, *Lepidochelys kempii* (Garman) (Kemp's Ridley Sea Turtle), *Natator depressus* (Garman) (Flatback Sea Turtle), *Malaclemys terrapin* (Schoepff) (Diamondback Terrapin), *Crocodylus porosus* Schneider (Saltwater Crocodile), *Crocodylus acutus* Cuvier (American Crocodile), and *Alligator mississippiensis* (Daudin) (American Alligator) (Cupul-Magaña et al. 2011, Hayashi 2012, Hiro 1939, Jones 2010, Monroe and Garrett 1979, Newman and Ross 1976, Nifong and Frick 2011, Nilsson-Cantell 1932, Pilsbry 1916, Rees and Walker 1993, Seigel 1983, Walker 1978). Characterized by a large domed shell with unique starlike radii, this species is understood to be an obligate epibiont that engages in commensal relationships (Lazo-Wasem et al. 2011, Ramos-Rivera et al. 2021) and, because of its highly passive behavior, is likely reliant entirely on mobile hosts to feed (Lane et al. 2021). Turtle Barnacles are often found in high abundance amongst marine turtles, as this species can attach throughout the body of its host. This attachment process is facilitated by continuous cement secretion, allowing the barnacle to become anchored to both keratinous and chitinous substrates (Ramos-Rivera et al. 2021, Zardus 2021). Unique among barnacles, this species can also migrate significant distances across its sea turtle substratum to reposition itself for better feeding (Chan et al. 2021b). Notably, it is not uncommon for Turtle Barnacles to serve as an adhering base for other barnacle species seeking a substratum (Lazo-Wasem et al. 2011). We were able to document and identify Turtle Barnacles from various West Indian Manatees in Puerto Rico and, more commonly, Florida. We also observed Turtle Barnacles from a rescued West Indian Manatee from Santa Marta, Colombia, on 12 June 2021.

Conchoderma auritum (Rabbit-ear Barnacle). This lepadomorph goose barnacle is commonly found on oceanic cetaceans of the North Atlantic Ocean or those that undertake long oceanic migrations, such as the Humpback Whale, Sperm Whale, *Balaenoptera musculus* (L.) (Blue Whale), *B. physalus* (L.) (Fin Whale), and *B. acutorostrata* Lacépède (Minke Whale) (Ólafsdóttir and Shinn 2013, Scarff 1986). It evolved as an ectosymbiont of cetaceans in an ecological phoretic association (Ross 1963). Here we report it on Humpback Whales, Cuvier's Beaked Whales, a Sperm Whale, a Blainville's Beaked Whale, a Gervais' Beaked Whale, and the delphinid Pygmy Killer Whale. In addition, it has been previously reported from other dolphins, such as the Atlantic Spotted Dolphin (van Bree 1970). It is often found attached to the teeth of male beaked whales (Ziphiidae) or attached to the plates of the acorn barnacles on whales (Fig. 3; Fertl and Newman 2008).

Coronula diadema (Coronet Barnacle). This cosmopolitan barnacle, named "diadema" due to its tall crown-like shell, is commonly found on Humpback Whales and less often on other cetaceans including Blue Whales, Fin Whales, Sperm Whales, Southern Right Whales, and *Hyperoodon ampullatus* (Flower) (Northern

Bottlenose Whale) (Avila Jiménez et al. 2011, Barnard 1924, Hiro 1935, Newman and Ross 1976, Nilsson-Cantell 1978, Wirtz et al. 2006). *Coronula* is the most generalized of the sessile cetacean barnacles (Scarff 1986), with both the Coronet Barnacle and the Queen's Coronet Barnacle being common epizooites of Humpback Whales (Fertl and Newman 2008). Differentiating between these 2 *Coronula* can be difficult and requires paying attention to their comparative morphology (Fig. 5). In Humpback Whales from Puerto Rico, Coronet Barnacles had an average diameter of 40.3 ± 5.4 mm, an average opercular opening of 23.4 ± 3.4 mm, and an average height of 28.8 ± 6.0 mm, while Queen's Coronet Barnacles had an average diameter of 35.5 ± 4.8 mm, an average opercular opening of 17.3 ± 2.1 mm, and an average height of 14.7 ± 1.9 mm. Although the Coronet Barnacle can be found sporadically on the body of oceanic cetaceans, most of the specimens are found to be primarily located near the jaw, mouth, and flippers of the host (Scarff 1986). Typically, the Coronet Barnacle does not fully embed in the epidermis of its host, leaving most of its barrel-shaped shell exposed. This attachment behavior results in an increased shell surface area, which facilitates and encourages the attachment of stalked barnacles (Félix et al. 2006, Scarff 1986).

Coronula reginae (Queen's Coronet Barnacle). This wide-ranging common barnacle species, which is often confused with and misidentified as the Coronet Barnacle because of their morphological similarities, is differentiated from the former by a rounder and lower-profile (flattened) shell (Fig. 5). It is habitually found living on the epidermis of oceanic cetaceans (Scarff 1986), but is not often reported, especially in the North Atlantic Ocean. Whether they are common but overlooked as Coronet Barnacles or truly scarce in numbers remains unknown. Apart from our present observation, the next most recent positive report, is from a Humpback Whale off the coast of the Netherlands in the North Sea in 2003 (Holthuis and Fransen 2004). Previous studies have identified the Queen's Coronet Barnacle from Humpback Whales, and more rarely from Blue Whales, Fin Whales, Minke Whales, Sperm Whales, *Balaenoptera borealis* Lesson (Sei Whale), and *Eubalaena glacialis* (Muller) (Northern Right Whale). Caldwell (1963) reported this barnacle from a Loggerhead Sea Turtle, likely a misidentification of the Turtle Barnacle. In contrast to the Coronet Barnacle, the attachment mode of the Queen's Coronet Barnacle involves the barnacle beginning its growth from within the

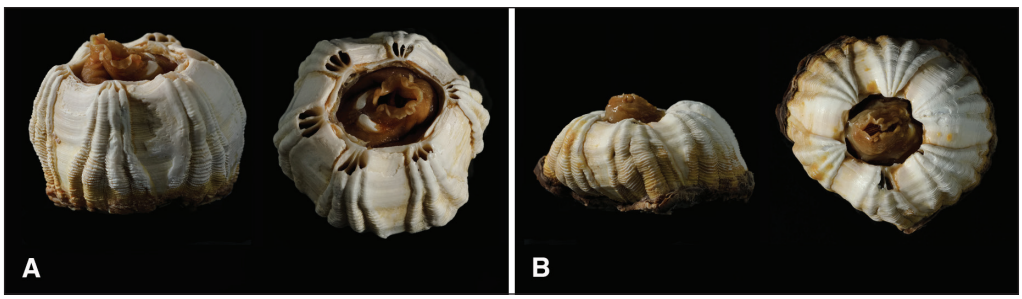

Figure 5. Comparative morphology between the Coronet Barnacle (A) and the Queen's Coronet Barnacle (B) from the same Humpback Whale from Puerto Rico.

epidermis of the host, essentially embedding itself and burrowing in and emerging from underneath the skin, reducing the amount of shell surface area exposed (Felix et al. 2006, Nilsson-Cantell 1930, Scarff 1986). Similar to the Coronet Barnacle, Queen's Coronet Barnacle specimens are known to have the ability to attach to different regions of a cetacean's epidermis; however, they are found in more significant numbers on the flukes, jaw, and flippers of their hosts (Scarff 1986). Only 5 specimens of this *Coronula* species were retrieved in the present study from 2 Humpback Whales sampled in Puerto Rico. It is worth noting that the whale barnacle *Cetopirus complanatus* Mörch (Right Whale Barnacle), an epibiont of critically endangered Northern Right Whales and Southern Right Whales that may occur alongside the Coronet and Queen's Coronet barnacles, can be easily mistaken for the latter. Possibly last reported by Best (1991), there has been no positive, first-hand account of this barnacle species for many years despite the recent observation of another Southern Right Whale barnacle, *Tubicinella major* Lamarck (Burrowing Barnacle; Reeb et al. 2007).

Cylindrolepas darwiniana (Coarse Cylindrical Barnacle). This epizoic species is not commonly found but previously has been known in the Caribbean region to attach only to marine turtles (Frick and Zardus 2010). The shell is roughly as high as it is wide, flat-topped, and has an irregular, rough exterior devoid of ridges or patterns with a covering of wrinkled organic material (Fig. 6a). Its naming history has become complicated since its description by Pilsbry in 1916 (see Frick and Zardus 2010), likely being misattributed to specimens that are seemingly a species of *Platylepas* taken from various locations in the Pacific Ocean (Green 1998, Hubbs 1977, Monroe 1981). In our collection, 4 West Indian Manatees served as hosts to this barnacle, a new host record for this species: 3 in Puerto Rico and 1 in Florida.

Lepas anatifera (Duck Barnacle). Duck Barnacles, a pelagic species, were found alive attached to 3 sea turtles (Loggerhead, Green, and Olive Ridley) in the study area. Duck Barnacles are common in Loggerhead Sea Turtles (Caine 1986, Monroe and Limpus 1979, Relini 1980) but are rarely reported on Olive Ridley Sea Turtles (Sosa-Cornejo et al. 2012) or Green Sea Turtles (Bugoni et al. 2001).

Platylepas hexastylos (Layered Clasping Barnacle). This is a common epibiont of sea turtles and marine mammals (Lazo-Wasem et al. 2011, Ross 1983). It has previously been documented on Loggerhead Sea Turtles, Green Sea Turtles, Hawksbill Sea Turtles, Flatback Sea Turtles, Leatherback Sea Turtles, Olive Ridley Sea Turtles, *Chelonia mydas agassizii* Bocourt (Black Sea Turtle), *Dugong dugong* (Müller) (Dugong), and *Trichechus senegalensis* Link (African Manatee) (Alexander et al. 2004; Hayashi 2012; Hayashi et al. 2011; Jones 2004, 2010; Robinson et al. 2019; Stubbings 1965). Morphologically, this barnacle species is distinguished by its flattened shell and concentric horizontal striations or layers, hence its common name, along with 6 supporting pillars found on the underside of the base (Lazo-Wasem et al. 2011). The Layered Clasping Barnacle can be found throughout the body of sirenians and marine turtles; however, this flattened and layered barnacle (Fig. 6b) has been found in greater abundance in areas surrounding the

beak, neck, and flippers of marine turtles (Ramos-Rivera et al. 2021, Ross 1983). Notably, this epibiont employs a grooved membranous base to facilitate its attachment to sea turtle carapaces (Ramos-Rivera et al. 2021). We collected the Layered Clasping Barnacle from Puerto Rico from 2 Green Sea Turtles, 4 Hawksbill Sea Turtles, and 6 West Indian Manatees. Only 1 manatee from Florida served as host to the Layered Clasping Barnacle.

Stomatolepas elegans (Elegant Cup Barnacle). This commensal species has a global distribution, having been documented in most of the world's oceans attached to sea turtles (Karaa et al. 2012, Ramos-Rivera et al. 2021). In addition, the Elegant Cup Barnacle has previously been identified on Loggerhead Sea Turtles, Green Sea Turtles, Leatherback Sea Turtles, and Olive Ridley Sea Turtles (Hiro 1937, Lazo-Wasem et al. 2011, Utinomi 1970). Reports of it occurring with Leatherback Sea Turtles (Utimoni 1970) are likely misidentifications of *Stomatolepas dermochelys* Monroe & Limpus (Leatherback-turtle Barnacle), which are specific to that host. Morphologically, the Elegant Cup Barnacle presents a rounded bowl-like shell whose plates are separated by sutures, creating sections that are ornamented with a series of scale-like projections adorning its exterior (Frick et al. 2010). Typically, this epibiont embeds superficially in marine turtle epidermis; when sampled, it is most often found attached to the carapace, flippers, and soft skin around the host's neck (Karaa et al. 2012, Ramos-Rivera et al. 2021, Zardus 2021, Zardus and Balazs 2007). We collected 3 specimens of *S. elegans* from 1 Hawksbill Sea Turtle and 1 Green Sea Turtle in Puerto Rico.

Ecological significance

The most familiar barnacles are located in the intertidal zone, usually observed on non-living, coastal rock formations, piers, seawalls, marinas, and boats. Thus, many studies on barnacles focus on adhesion and biofouling by cirripeds in hopes of finding ways to eradicate them. By contrast, barnacles attached and growing on a living organism form a non-parasitic relationship termed epizoic. If the live animal that serves as host is in movement, the symbiotic relationship also becomes one of phoresis. However, the contribution of epizoic and phoretic species to understanding host ecology and natural history has been understudied. Barnacles could potentially benefit some hosts by offering disruptive camouflage or enhanced

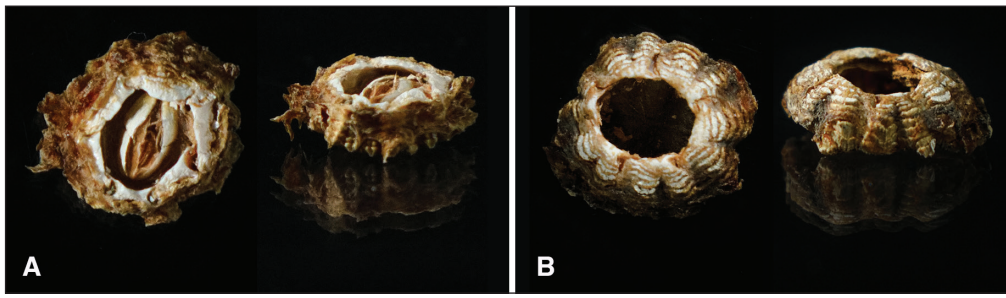

Figure 6. Coarse Cylindrical Barnacle (A) and Layered Clasping Barnacle (B) from a manatee from Puerto Rico, showing morphological differences between the 2 acorn species.

reflectance (Kobayashi 2000, Wahl and Mark 1999). For large marine vertebrates, the phoretic nature of epizoic barnacles could help determine migration routes or specific habitat distribution of both the epibiont and host species. For example, Coronet Barnacles, Queen's Coronet Barnacles, and Rabbit-ear Barnacles are found on oceanic cetaceans, a clear sign of their epipelagic offshore distribution. Similarly, the Duck Barnacle is also an offshore oceanic species, and the fact that they were found from 3 sea turtles in Puerto Rico attests to the fact that these specific turtles were inhabiting or had come from offshore waters.

The other barnacles found in this study are from coastal seagrass bed-inhabiting manatees and sea turtles or reef-inhabiting sea turtles. Turtle Barnacles and Layered Clasping Barnacles are harbored by both manatees and sea turtles in Florida and the Puerto Rico archipelago. However, in this area of study, Striped Barnacles, Ivory Barnacles, and Coarse Cylindrical Barnacles are only found on manatees, and Hawksbill-turtle Barnacles and Elegant Cup Barnacles are only found on sea turtles. As manatees enter freshwater ecosystems in Florida and estuarine habitats in Puerto Rico, the barnacles attached during their ocean venture fall off a few days after entering these lower salinity habitats. Manatees in Puerto Rico are more marine, thus, barnacle attachment is longer-term. Isotopic analysis of fossil and recent barnacle shells may also provide insight into migration patterns of hosts (Detjen et al. 2015, Killingly 1980, Pearson et al. 2020, Taylor et al. 2019). Barnacles may concentrate contaminants in their shell (Royo-Gelabert 1994). Therefore, they may provide crucial information on which contaminants marine mammals and sea turtles may have been exposed to, perhaps affecting their survival. For example, analyzing the presence of heavy metals in the shells or tissues of the barnacles (Killingley and Lutcavage 1983) may indicate if their host was exposed to pollution and other chemical indicators of their health. Future studies of Caribbean barnacles should also focus on documenting the molecular, genetics, and phylogeography of the different species of cirripeds on marine mammals and sea turtles to gain insight on population connectivity in both hosts and symbionts and potentially illuminate unrecognized cryptic species.

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