OCCURRENCE OF THE BARNACLES *CORONULA DIADEMA, C. REGINAE* AND *CETOPIRUS COMPLANATUS* (CIRRIPEDIA) ON RIGHT WHALES

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ABSTRACT

On 20 March 1982, a right whale (*Eubalaena glacialis*) was observed off Half Moon Bay, California (37°30'N, 122°03'W). Approximately 300 coronuline barnacles were observed on the whale. By analyzing photographs of the whale, we identified the barnacles as probably being *Coronula diadema* and *C. reginae*, although the possible occurrence of *Cetopirus complanatus* can not be eliminated. It is hypothesized that the right whale acquired the barnacles during association with a humpback whale (*Megaptera novaeangliae*), although the barnacles could have been acquired from one of several other whale species. A review of the literature yielded 22 previous reports of coronuline barnacles on right whales, 10 of *Coronula* spp., 4 of *Cetopirus complanatus*, and 8 of unspecified barnacles. Most of these early reports appear to be descriptions of not barnacles but instead the right whale's callosities or whale lice (*Cyamus* spp.). However, two prior records of *Coronula diadema* and two records of *Cetopirus complanatus* are well documented. A summary of known cetacean host — coronuline barnacle associations is included.

This article describes the first well documented observation of coronuline barnacles on a northern right whale (*Eubalaena glacialis* (Muller, 1776)). The barnacles were tentatively identified as *Coronula diadema* (Linnaeus, 1767) and *C. reginae* Darwin (1854), two species usually associated with humpback whales (*Megaptera novaeangliae*) (Borowski, 1781), although they have been reported from other species (see Table 1). With two exceptions (Tomilin, 1957; Watson, 1981), recent literature reviews on whales (Margolis, 1954; Slijper, 1962; Dailey and Brownell, 1972; Nishiwaki, 1972; Reeves and Brownell, 1982) or barnacles (Pilsbry, 1916; Cornwall, 1955; Tarasov and Zevina, 1957; Newman and Ross, 1976) have reported no coronuline barnacle other than *Tubicinella major* Lamarck (1802) as occurring on right whales.

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TABLE 1. WHALE BARNACLES AND THEIR HOSTS

Barnacle species	Host species	Source
Coronula diadema	Humpback whale (*Megaptera novaeangliae*) found in large numbers on nearly all individuals.	
	North Pacific	Scammon (1874); Cornwall (1924, 1927, 1928, 1955); Scheffer (1939); Nishiwaki (1959); Rice (1963)
	North Atlantic and Southern Hemisphere	Kakuwa, Kawakami and Iguchi (1953); Tomilin (1957)
	Blue whale (*Balaenoptera musculus*), Fin whale (*B. physalus*) Sperm whale (*Physeter macrocephalus*) found on approx. 1% of the individuals taken in commercial operations.	Wheeler and Mackintosh (1929); Nilsson-Cantell (1930, 1939); Tomilin (1957); Mizue and Murata (1951); Nishiwaki and Oye (1951); Kakuwa *et al.* (1953)
Coronula reginae	Common on humpback whale, rare on blue, fin, sei, and sperm whales (all oceans)	Nilsson-Cantell (1939); Scheffer (1939); Mizue and Murata (1951); Cornwall (1955); Rice (1963)
Cetopirus complanatus	Right whale (*Eubalaena glacialis*) Southern Hemisphere	Darwin (1854); Gruvel (1903); Pilsbry (1916); Nilsson-Cantell (1931)
Crytolepas rhachianecti	Gray whale (*Eschrichtius robustus*) abundant on nearly all individuals. Not reported from other species.	Rice and Wolman (1971) Newman and Abbott (1980)
Tubicinella major	Right whale Embedded in the callosities	
	Southern Hemisphere North Atlantic?	Darwin (1854); Marloth (1902); Gruvel (1903); Pilsbry (1916); Barnard (1924)
Conchoderma auritum	Common on humpback whale, rare on blue, fin, and sperm whales Usually attached to *C. diadema* or *C. reginae*	Cornwall (1927, 1955); Nilsson-Cantell (1939); Rice (1963); Newman and Ross (1971)
Conchoderma virgatum	facultative hyperepizoite which sometimes grows on the stalks of *Penella* spp., a copepod parasite on cetaceans.	Dailey and Brownell (1972)
Xenobalanus globicipitis	resembles stalked barnacle found infrequently on *Balaenoptera* spp., *Globicephala*, and delphinids. cosmopolitan	Pilsbry (1916); Rice (1963); Nilsson-Cantell (1978); Cornwall (1955)

METHODS AND OBSERVATIONS

At about 1030h on 20 March 1982, during a charter whale-watching cruise, Tom Johnson and I encountered a single right whale about 1.5 km SW of

Fig. 1. Side view of left dorsal side of the right whale showing the blowholes, callosities, barnacles, scars and sloughed epidermis (courtesy of Tom Johnson).

Pillar Point, near Half Moon Bay, California (37°30′N, 122°03′W). For two hours, while our separate boats idled in the water, the right whale repeatedly approached each boat in turn to within 5 m. We both were able to photograph at close range the dorsal part of the whale from near the tip of the rostrum to the flukes. The photographs were taken with 35 mm SLR cameras on color transparency film using either a 200 mm lens and Kodachrome 64 (Fig. 1) or a 400 mm lens and Ektachrome 200 (Figs 2 and 3). No attempt was made to collect barnacle specimens because of the risk of harassment to the whale.

The whale was an adult, approximately 16 m in length of indeterminate sex. It showed no injuries or abnormal behavior. The surface water temperature at the time of the sighting was not measured directly, but was estimated by the boat's crew as about 13°C based on measurements made earlier in the week. Two photographs of this sighting have previously been published elsewhere: Fig. 1 (Patent, 1984: P. 30), Fig. 3 (Johnson, 1982).

IDENTITY OF BARNACLES

The several species of barnacles which occur on whales and their reported hosts are shown in Table 1. Inspection of about 60 photographs of the right whale including Figs 1-3 show the barnacles to be similar to *Coronula diadema*, *C. reginae*, and *Cetopirus complanatus* (Mörch, 1852). All three barnacle species have white, more or less radially symmetrical shells and yellow opercular membranes. All are relatively large, being as much as 50–85 mm in diameter

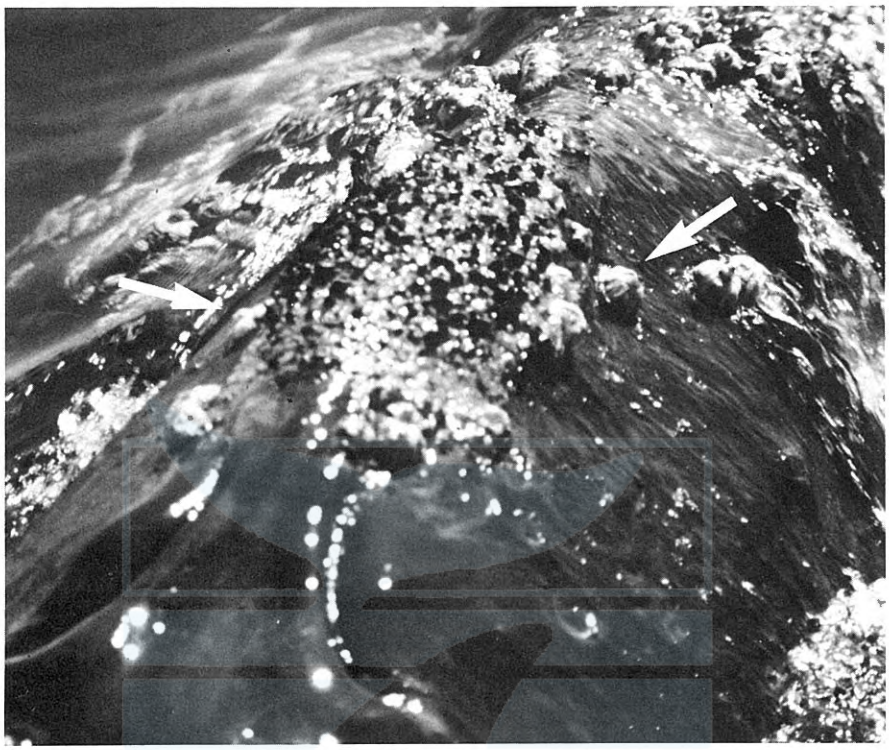

Fig. 2. Dorsal view of right whale looking from the area of the blowholes anteriorly at the callosity, rostrum and left lower lip and showing *Coronula diadema* (right arrow) and *C. reginae* (left arrow).

(Pilsbry, 1916). All can be distinguished from the barnacle *Cryptolepas rhachianecti* Dall (1872) (Fig. 4) commonly found on gray whales, *Eschrichtius robustus* (Lilljeborg, 1861), because *Cryptolepas* is more flattened and the spaces between the ridges radiating from the opercular membrane are not covered over (Newman and Abbott, 1980). In *Cryptolepas*, these ridges often have a darker coloring than surrounding parts of the shell giving the barnacle a striped appearance in contrast to the more uniform coloration of *Coronula* spp.

A fully grown *C. diadema* (Fig. 5) can be distinguished from *C. reginae* (Fig. 6) and *Cetopirus complanatus* (Fig. 7) because of *C. diadema*'s greater height (30–59 mm in the North Pacific), its barrel shape, and its position on the whale with most of its shell emergent from the epidermis (Darwin, 1854; Pilsbry, 1916). Individuals of *C. reginae* are noticeably shorter (13–19 mm) (Fig. 6). This relative shortness is exaggerated *in situ* by the habit of the barnacle to be imbedded in the skin of the whale, reducing the exposed shell (Darwin, 1854; Pilsbry, 1916; Cornwall, 1928; 1955).

Fig. 2 shows several barnacles on the rostrum of the right whale. This photograph also appears in Patent (1984:30). Two barnacles on the right side

Fig. 3. View of left dorsal surface of tailflukes and peduncle of the right whale with *Coronula reginae* and depressions where barnacles had been attached.

of the rostrum have the high, barrel-like shape characteristic of *C. diadema*. In contrast, at least one barnacle on the left side of the rostrum has the greatly flattened shell characteristic of *C. reginae*. Fig. 3 shows several barnacles on the flukes of the whale. These are all flat and appear to have a ridge of skin over the distal edges of the barnacle, characteristic of *C. reginae*.

Cetopirus complanatus (Fig. 7) has rarely been described in the literature. Detailed descriptions with drawings or photographs can be found in Darwin (1854) (as *Coronula balaenaris*) and in Pilsbry (1916) (as *Coronula complanata*). Externally, *Cetopirus complanatus* closely resembles *C. reginae*, sharing the same flattened shape and habit of being deeply embedded in the epidermis (Darwin, 1854; Gruvel, 1905). Pilsbry (1916) reports that two adult *Cetopirus complanatus* in the U.S. National Museum are 53 and 74 mm in diameter and only 12 and 28 mm in height respectively. All but two reports of *Cetopirus complanatus* are from the Southern Hemisphere; the two other reports from the North Atlantic are questionable.

Because of the lack of prior records of *Cetopirus* in the North Pacific and the unlikelihood of a right whale from the Southern Hemisphere migrating to the Northern Hemisphere, I conclude that the barnacles on the right whale were all *Coronula* spp. However, it is impossible to state conclusively that some

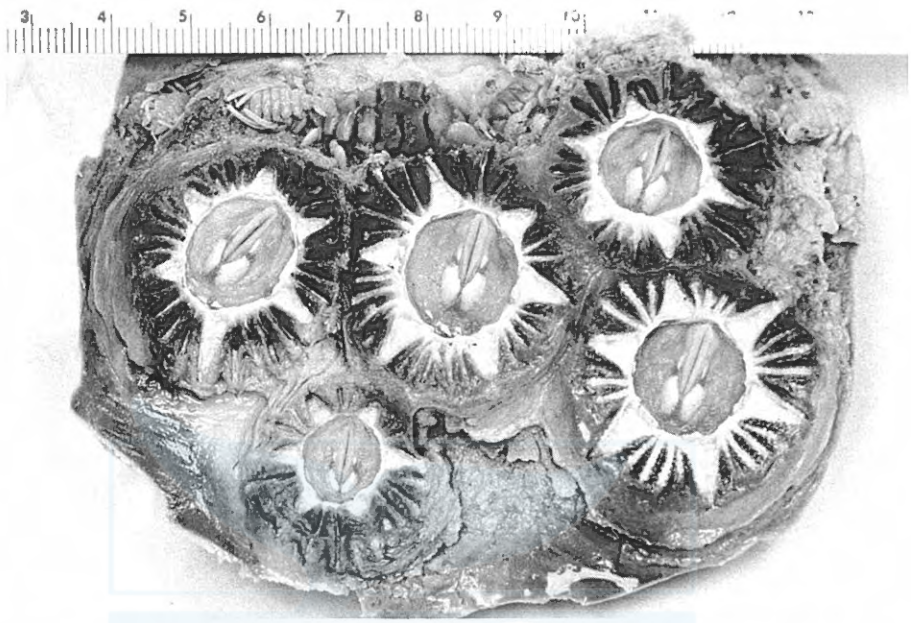

Fig. 4. *Cryptolepas rhachianecti*, species endemic to the gray whale. Ruler in cm. (from the collection of the California Academy of Sciences).

of the barnacles on the whale were not *Cetopirus complanatus* because the subtle external field marks of this species cannot be discerned given the resolution of the photographs.

DISTRIBUTION OF THE BARNACLES ON THE WHALE

There appeared to be a general segregation of the two species into different areas of the whale. The *C. diadema* appeared to be restricted to the areas anterior to the blowholes, whereas *C. reginae* appeared primarily in the area around the flukes, although some also occurred on the head.

C. diadema barnacles were common on the dorsal surface of the whale from the area of the nares to the anterior tip of the rostrum, although they did not appear to grow on the callosities themselves. The barnacles were particularly abundant along the edge of the lower lip (see Fig. 1) and densely distributed laterally as far as could be seen to the area near the eye and the lower margin of the cheek. Barnacles were also observed on the pectoral fins. There were at least 150 barnacles on the right side of the whale and at least 80 on the left side. Of note because of their proximity to the blowholes was a group of five barnacles anterior to the right nares approximately 2 cm from the edge of the blowhole (see Fig. 2).

The above distribution of attached *C. diadema* is somewhat similar to, but

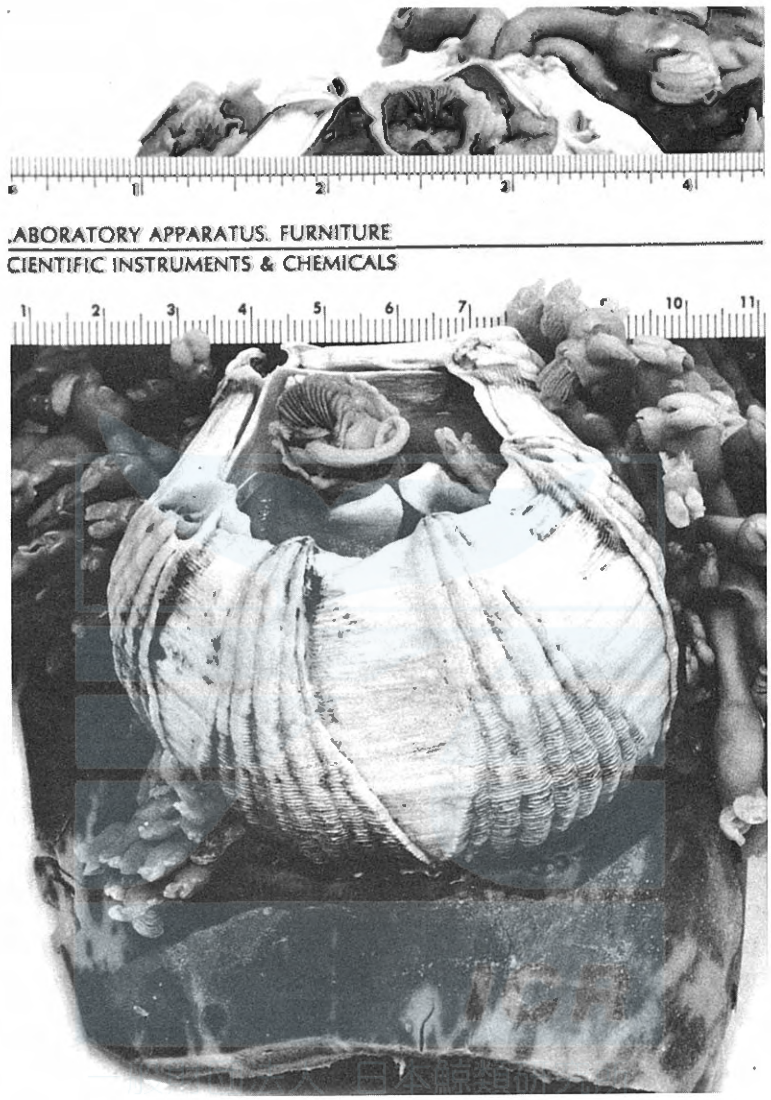

Fig. 5. *Coronula diadema* attached to a piece of skin from a humpback whale with numerous *Conchoderma auritum* attached. Ruler in inches (top) and cm. (bottom) (from the collection of the California Academy of Sciences).

more widespread, than that reported on humpback whales (Cornwall, 1927, 1955; Scheffer, 1939). However, Cornwall (1955:52), states that on the humpback the barnacle "occurs in scattered numbers over the sides, rarely on the dorsal surface."

The *C. reginae* on the right whale were primarily located on, or near, the tail flukes. From the photographs about 70 barnacles were counted on the

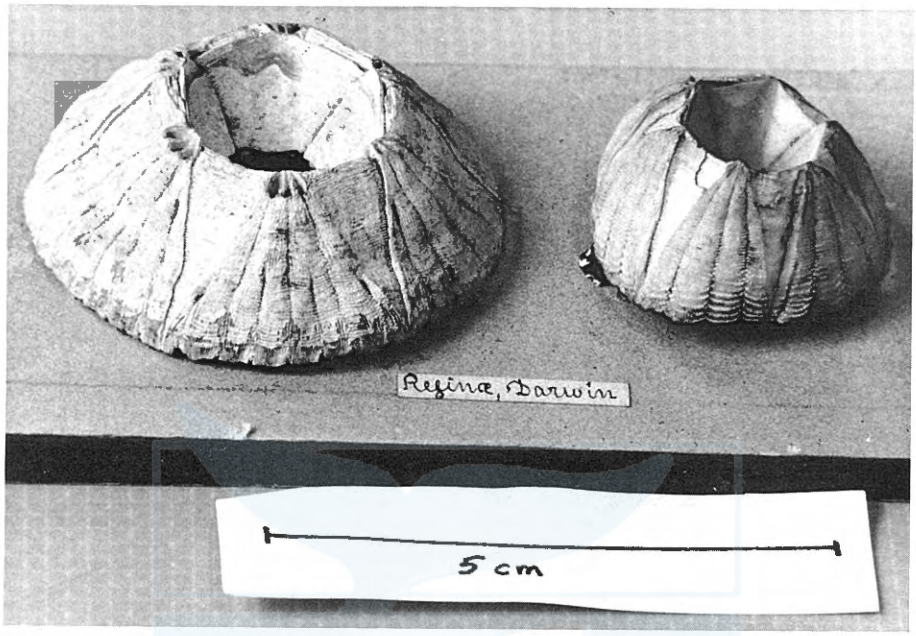

Fig. 6. *Coronula reginae* (from the collection of the British Museum, Natural History).

dorsal surface of the flukes (see Fig. 3) and about 20 on the right ventral surface. On the head of the whale, *C. reginae* appeared to be much less common than *C. diadema*. Although both Cornwall (1955) and Tomilin (1957) state that the occurrence of coronuline barnacles on the flukes of humpback whales is rare, more recent observations suggest that it is not rare, although only a minority of humpbacks with barnacles will have them on their flukes (V. Rowntree, pers. comm.).

There were no attached barnacles in the area between the callosities and the peduncle. However, there were dozens of circular depressions on the dorsal surface from the blowholes posteriorly for at least 8 m. The depressions extended laterally out of view underwater. These circular depressions are visible in Fig. 1. Similar depressions were found on the rostrum adjacent to attached barnacles.

Circular scars on many cetaceans have been described as the result of attacks by lamprey (*Entosphenus tridentatus* and other species) (Nemoto, 1955; van Utrecht, 1959; Slijper, 1962; Rice, 1963; Greenwood *et al.*, 1974) and squaloid shark (*Isistius brasiliensis*) (Jones, 1971). However, because the depressions on the right whale all appear to show healthy dark epidermis in the center, it is unlikely that they were caused by lamprey or shark which typically gouge a large central hole through the epidermis (Nemoto, 1955).

The occurrence of the depressions on the back of the right whale does not argue against barnacles as the cause, for although *Coronula* spp. are

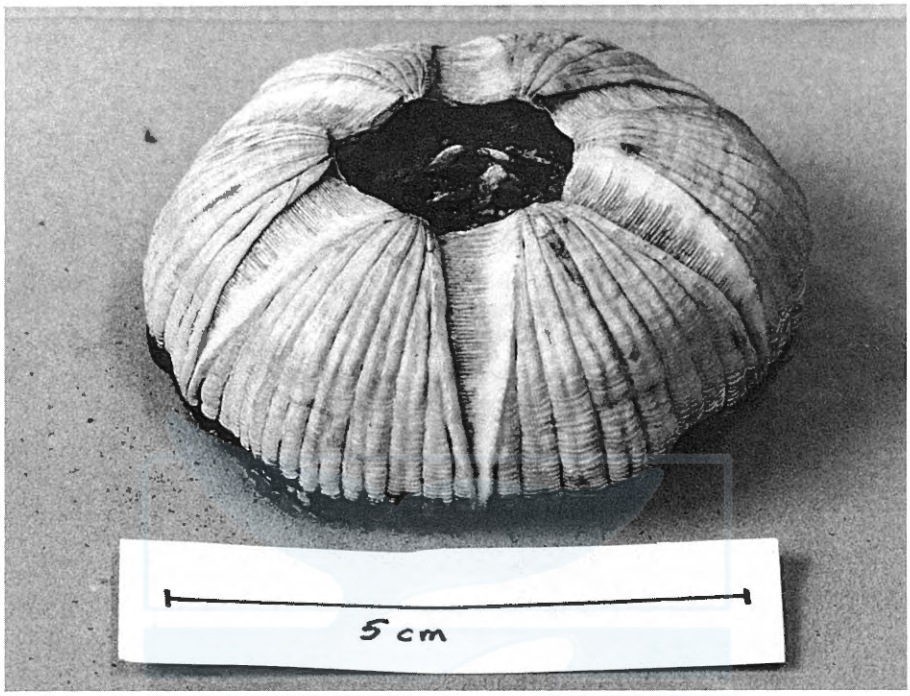

Fig. 7. *Cetopirus complanatus* labelled as *Coronula balaenaris* (from the collection of the British Museum, Natural History)

reported as only rarely occurring on the dorsal surface of humpbacks posterior to the blowholes (Tomilin, 1957), the closely related barnacle *Cryptolepas rhachianecti* "often form[s] a continuous mass on the dorsal aspect of the rostrum and the most anterior part of the back" of gray whale (Rice and Wolman, 1971:100). There was no indication that *Cryptolepas* had been present, but it is reasonable to conclude that *Coronula* could under special circumstances show the same distribution. Support for the hypothesis that the depressions were formed by barnacles comes from the relative abundance of depressions near the attached barnacles.

The whale's molt may be a mechanism by which the barnacles lose their attachment to the whale or it may simply facilitate this process. The right whale's molt has been described in Ling (1974), Reeves and Brownell (1982), and Payne *et al.* (1981). In the right whale we observed, the circular impressions were often contained within irregularly shaped patches of lightercolored skin where pieces of epidermis had sloughed off (see Fig. 1).

Our photographs did not show any *Tubicinella major* (Fig. 8), barnacles found often on right whales in the Southern Hemisphere. Because these barnacles are cryptically buried in the whale's epidermis among the callosities (Marloth, 1902), they may have been present although the species has not been reported from the North Pacific.

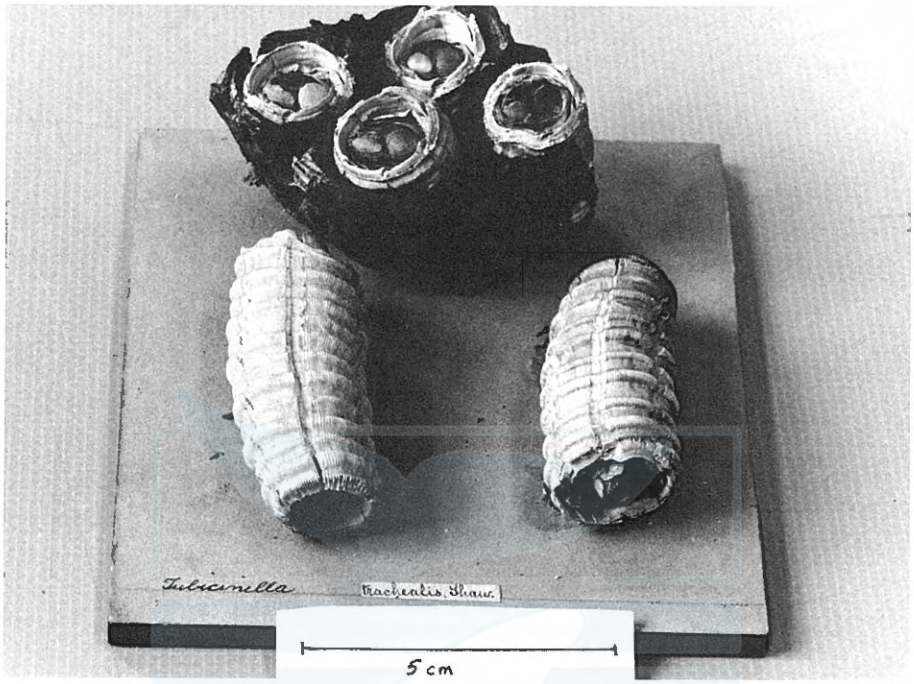

Fig. 8. *Tubicinella major*, species endemic to the right whale, shown embedded in a piece of right whale skin and in a lateral view detached from the whale skin (from the collection of the British Museum, Natural History).

Right whales are usually heavily infested with amphipods of the genus *Cyamus* ("whale lice") (Payne *et al.*, 1981; Reeves and Brownell, 1982). The resolution of our photographs was not adequate to detect individual cyamids, but cyamids appear to have been present on this animal. The small, aggregated, whitish objects concentrated around the dark callosities anterior to the blowholes visible in Figs 1 and 2 are probably cyamids. In the original color transparencies, these objects have a slight brownish tinge characteristic of cyamids.

The stalked barnacle *Conchoderma auritum* (Fig. 5) often attaches itself to the shell of *C. diadema* (Pilsbry, 1916; Cornwall, 1927, 1955; Tomilin, 1957; Newman and Ross, 1971). Because of the large size of *Conchoderma*, if present, it should have been easily detected but was not observed, indicating an absence of this species.

Little is known about the natural history of *Coronula diadema* or *C. reginae*. It is generally believed that most *C. diadema* have a lifespan of one year or less (Cornwall, 1955; Newman and Abbott, 1980). Nishiwaki (1959) found *Coronula* spp. on 211 of 212 humpback whales taken in the North Pacific during the months of January to April. He does not describe the relative size or abundance of these barnacles. Cornwall (1955:52) states that the barnacles "are mostly small

in the early summer months, but are considerably larger and many have dropped off or been rubbed off by the end of the summer." Off Madagascar, Angot (1951) reported that on humpbacks taken between mid-June and mid-August (the early southern winter) the *C. diadema* were all large, ranging in size from 2.5 cm to 5 cm in diameter, the latter size being more common. By mid-September, the adult barnacles had disappeared and the whales were covered with the free-swimming larvae of the barnacles beginning to attach themselves. By early October (southern spring), small sessile adult barnacles were well attached.

The life cycle of the closely related *Cryptolepas rhachianecti* is similar to that described above. Rice and Wolman (1971) found that almost all *Cryptolepas* were large on whales taken off California during the southbound migration. Whales taken during the northbound migration bore both large and small barnacles. Our sighting of the right whale occurred during the height of the gray whale's northward migration past Half Moon Bay which is at the south edge of Rice and Wolman's study area. All the barnacles visible in the photographs of the right whale were large. The small size of the larvae and young sessile adult forms would make them difficult to detect at a distance.

HISTORICAL RECORDS OF CORONINE BARNACLES ON RIGHT WHALES

As noted above, there are no reports of coronuline barnacles on right whales in recent literature reviews except Tomilin (1957) and Watson (1981). However, the older literature contains at least 22 such references. These records must be reviewed carefully to cull out those which describe, or appear to describe, callosities and cyamids rather than barnacles.

Callosities are large "wartlike excresences" well described in Ridewood (1901) and Payne *et al.* (1981). In their gross morphology, the jagged projections of epidermis which form a callosity resemble a group of barnacles. They are usually present on the rostrum, behind the blowholes, and on the lower jaw (Reeves and Brownell, 1982; Payne *et al.*, 1981). Callosities are visible in Figs 1 and 2.

Typically, the large callosities are covered by hundreds, or thousands, of cyamids, causing the callosities to appear light-colored, making them not only about the same size and shape as a group of barnacles, but also the same color (see Payne (1976:335) for a close-up photograph of a callosity covered with cyamids with the epidermal projections misidentified as barnacles). All right whales, but no bowheads (*Balaena mysticetus*), have callosities.

Right whale callosities are unique structures, and to a lay observer callosities probably appear more analogous to humpback whale barnacles then to the epidermal tissue of other marine mammals. For example, author and whaler Melville (1851:432) described in *Moby Dick* the large callosity at the end of a right whale's rostrum as "this strange, crested, comb-like incrustation on the top of the mass — this green barnacled thing." Lay

observers' use of barnacles as a metaphor to describe callosities with cyamids was often interpreted literally by 19th century scientists lacking personal experience with right whales, resulting in much confusion.

This confusion not only affected knowledge of barnacle distribution; but also significantly delayed recognition of the right whale as a species distinct from the bowhead, and generated erroneous reports of barnacles on right whales. Apparently none of the zoologists writing before 1870 had personally seen a right whale. They based their papers on review only of pieces of baleen and bone, and the stories and drawings of biologically untrained whalers. Not until Scammon (1874) is there a good description of the callosities of a right whale in the Western scientific literature.

One cause for the taxonomic confusion was the rarity of right whales in the eastern North Atlantic by the late 18th and early 19th centuries. Many whalers never caught one (Reeves, 1982). The main target of the contemporary whaling industry was the bowhead with which taxonomists were familiar. So these scientists interpreted whalers' reports of a second, rare, smaller balaenid species with shorter baleen in the North Atlantic as simply representing unusually small bowheads. Most scientists did not recognize the right whale as a species distinct from the bowhead until the 1830's, after the discovery of the right whale grounds in the Southern Hemisphere. The taxonomic debate on classification of the North Atlantic right whale continued until the late 1800's and is well recorded in Allen (1908). What is striking was the willingness of these 19th century scientists to describe without qualification the whalers' reports of barnacle-like growths on right whales as being unquestionably *Coronula* spp.

As a guide to the confusing names applied to right whales and barnacles in this older literature, a selective list of synonyms is presented in Table 2. The current names of barnacles used in this paper follow the taxonomy of Newman and Ross (1976).

A second source of ambiguity in the older records stems from the possibility that general references to barnacles on right whales refer to *Tubicinella major* (Fig. 8) rather than *Coronula* spp. The former species has been reported only on right whales and, with two exceptions, only in the Southern Hemisphere (Marloth, 1902; Pilsbry, 1916; Barnard, 1924). There are two old vague reports of *Tubicinella* being found in the North Atlantic, one on a stranded whale in 1650 from the Faroe Islands (Worm, 1655 cited in Pilsbry, 1916) and one prior to 1850 (Gruvel, 1903). *Tubicinella* occurs typically in among the callosities.

RECORDS OF *CORONULA* SPP. AND UNSPECIFIED BARNACLES

One of the earliest references in the scientific literature to barnacles on right whales occurs in Scoresby (1820). Apparently Scoresby never personally saw a right whale. He believed that the "Nordkaper", as the right whale was called,

TABLE 2. SELECTIVE SYNONYMY OF WHALE AND BARNACLE SPECIES

Current Name	Synonym
Eubalaena glacialis	Right whale, Nordkaper, Sarde, sletbag, *Balaena glacialis, B. biscayensis, B. japonica, B. antarctica, B. australis.*
Balaena mysticetus	Bowhead whale, Greenland whale, Arctic right whale.
Coronula diadema	*Lepas diadema, L. balaenaris, Diadema japonica, D. californica, Coronula biscayensis.*
Coronula reginae	No synonyms (Often not distinguished from *Coronula diadema*)
Cetopirus complanatus	*Coronula complanata, Coronula balaenaris, C. darwini, Lepas balaenaris, Balanus polythalamius complanatus*

was merely a type of bowhead (which he called "mysticetus"). In his review of whales in the North Atlantic, Scoresby describes a "mysticetus" which occurs along the coasts of Africa and South America, within the range of the right whale, but not the bowhead. He wrote that "one striking difference, possibly the effect of situation and climate, is that the mysticetus found in southern regions, is often covered with barnacles (Lepas Diadema [= *C. diadema*] &c) while those of the arctic seas are free from these shellfish." (p. 473). Scoresby makes no mention of the callosities on these southern whales. Apparently he mistook descriptions of callosities for barnacles.

Nine years later, Brandt and Ratzeburg (1829) mention barnacles occurring on right whales. Although their article is cited as authority for the occurrence of *Coronula* barnacles on right whales by both Eschricht and Reinhardt (1866) and Tomilin (1957), the two references in Brandt and Ratzeburg's book to barnacles on right whales are minor, undocumented notes. The first merely paraphrases Scoresby's (1820) comment about southern "mysticetus". The second, in a footnote on page 126, states, without giving a source, that balaenid whales from the east coast of North America are reported to have "head decorations" of *Lepas* (=*Coronula*? =*Cetopirus*?) barnacles. It appears that neither author had firsthand experience with right whales. Brandt and Ratzeburg make no mention of callosities on these whales.

Another early reference to barnacles on right whales occurs in Siebold's (1844) *Fauna Japonica*. Siebold repeats Scoresby's (1820) observation that the southern balaenid whales were "recouverte de bernaches" (covered with barnacles), characteristics which he says are shared by the Japanese right whale, but not the bowhead. Siebold's study contains two good drawings of a right whale done from a porcelain model of a freshly killed whale (plates 28, 29). These drawings show small callosities at the tip of the rostrum and above the eye, typical locations, but show no barnacles. Siebold probably confused callosities with barnacles. This porcelain model is mentioned again by Holder

(1883:127) who cites Siebold for the proposition that the right whale "is subject to cirripeds."

In 1855, a crew member of an American whaling ship described in his diary right whales as having "on the end of their nose...a bunch of barnacles about 18 inches wide. This the whalemen call his bonnet – and when you see a whale just rising out of water it has the appearance of a rock – the barnacles are enormous – as much as two inches deep – the boys often roast them and eat them the same as oysters." (Weir, 1977). Whether this refers to the callosities or barnacles is unclear.

A more extensive discussion of barnacles is found in the monograph on bowheads by Eschricht and Reinhardt (1866). They refer to the "very well authenticated fact of the Nordkaper [North Atlantic right whale] being infested with coronulas" (p. 45) as well as the "indisputable fact" of *Coronula* barnacles being "inseparable from right whales in the Southern Hemisphere" (p. 45). They go on to argue that the presence of *Coronula* barnacles on the North Atlantic right whale and their absence on bowheads supports their conclusion that the two whales constitute separate species (pp. 39, 44–45). Surprisingly, in the extensive discussion of the Nordkaper's field marks, they make no mention of the species's most obvious fieldmark – its callosities.

Eschricht and Reinhardt's descriptions of right whales are not based on firsthand observations of any intact specimens, but on their interpretation of earlier commentaries. Four references, one of which is Brandt and Ratzeburg (1829), are cited to support the contention that *Coronula* barnacles are a fieldmark of the Nordkaper.

The second reference is to an early commentary on whaling near Spitzbergen (Edge, 1625). Edge describes whalers hunting a balaenid whale of smaller size with shorter baleen than the typical bowhead. He describes this animal as having "naturally growing upon his back white things like unto barnacles." (p. 471). Without discussion of their reasons, Eschricht and Reinhardt (1866) conclude that this indisputably is a reference to *Coronula* barnacles on a right whale.

Eschricht and Reinhardt's third reference appears to be to a 17th century account of whaling written in Latin by Icelandic clergymen (Allen, 1908). The passage quoted from this early commentary simply refers to a type of right whale which has "asperis testis," which can be translated as "rough shellfish," adorning its back in a pattern similar to that of a garland of roses or a group of stars. This could easily be an interpretation of a whaler's description of callosities covered by whale lice.

Eschricht and Reinhardt's (1866:35) fourth record is of a right whale captured in 1778 or 1779 by a Danish whaling ship in the western North Atlantic. They state that "the head [of the whale was reported to be]... infested with such a multitude of Cirripeds that it would have been easy, according to the statement of the captain, to gather a whole sackful of these 'white patches' as he called them." This report is supplemented by the statement that

Chemnitz and Martini (1790) confirmed the specimens obtained were coronuline barnacles. This record is discussed in more detail *infra* in the later section on records of *Cetopirus complanatus*.

In his short review of parasites on whales, Beneden (1870) refers to several species of barnacles occurring on right whales in different oceans – *Coronula biscayensis* (=*Coronula diadema*) in the North Atlantic, *Coronula balaenaris* (=*Cetopirus complanatus*?) in the southern seas, and *Diadema japonica* (=*C. diadema*) in the North Pacific. None of these reports is based on firsthand observations by Beneden. The occurrence of barnacles on right whales in the North Atlantic is based on only one thirdhand report from shore whalers. The Southern Hemisphere barnacles are discussed in the following section on *Cetopirus complanatus*.

In the North Pacific, Beneden's conclusion is based entirely on a drawing of a barnacle which appears in a Japanese book on whales and whaling. Beneden does not give a citation for the book, but it is probably Oyamada Tomokiyo's book "Isanatori Ekotoba", published in Japanese in 1829. No English translation was widely available until 1983 (Matthews and Pilleri, 1983). In this recent translation (Yamada, 1983), both the author's name and the book's title are allegedly mistranslated (Omura in press).

The two volumes of the Isanatori Ekotoba contain a detailed and insightful record of Japanese whaling on the west coast of Kyushu, Japan. Right whales were a primary target of this fishery (Omura in press), and the book contains accurate drawings of details of the right whale's anatomy with notes accompanying the drawings. Of particular interest to this study are two drawings in plate 4 of volume II. Along with drawings of the baleen, blubber, and "bonnet" of a right whale are two sets of detailed drawings of barnacles. One of these sets of barnacles is identified in the notes as being a "Sessile barnacle" which "is as large as a sake cup. It is like those living on the sea shore; its shape is pentagonal or hexagonal. Its shell is hard and white. The flesh is edible. It attaches itself to the Right whale like the stalked barnacle." (Yamada 1983:84) The three barnacles pictured closely resemble *Coronula* spp. One has the barrel-like shape of *C. diadema*; one appears flattened like *C. reginae*; and the third is intermediate in form.

The second set of pictures are of stalked barnacles resembling *Conchoderma auritum*. The accompanying note describes them as "Stalked barnacle. Kaki, literally, oyster. The barnacle is four to five inches long with soft, light pink skin; it is used for food. All the white spots on the skin of the Right whale are attached barnacles." This is the only record of a stalked barnacle occurring on a right whale. However, *Conchoderma auritum* is commonly found on humpbacks and is often attached to a *Coronula diadema* (Newman and Abbott, 1980). The described abundance of the stalked barnacles is surprising and is more suggestive of the abundance and distribution of cyamids than barnacles.

The general detail and accuracy of the drawings and notes strongly suggests that Tomokiyo made firsthand observations of right whales and of

coronuline barnacles on right whales. There is also one picture of a whale louse (*Cyamus* spp.) which is separately identified making it unlikely that either set of barnacles were misidentified cyamids.

The next reference to barnacles on right whales occurs in Holder (1883:106) who describes secondhand a right whale which stranded on the New Jersey coast as "having but few molluscan parasites." He also writes (p. 118) that "The species is said to bear a 'bonnet' on its snout...seemingly covered by parasitic molluscs." At that time cirripeds were considered molluscs rather than crustaceans. Both of these references appear to be to cyamids on the callosities. Holder did not personally see any right whale.

In his monograph on whales, True (1904) suggests that right whales carry cirripeds. He describes certain "white spots" reported around the tips and surface of the pectoral flipper, the tip of the flukes, the "bonnet", and the genitals as being due to parasitic cirripeds as in the humpback whale. This speculation is not based on firsthand observation. The areas described frequently have white coloration in the absence of barnacles (Andrews, 1908; Omura *et al.*, 1969; Reeves and Brownell, 1982).

An unexpected reference to barnacles appears in a guide written for visitors to the British Museum of Natural History. In this guide, Lydekker (1909:15) describes the skeleton and model of a North Atlantic right whale in museum including the callosity known as the "bonnet", then states that the species "is further characterised by the frequent presence upon its skin of parasitic barnacles (*Coronula*), which are never found on the Greenland Whale." No further explanation is given.

In 1916, R.C. Andrews, assistant curator of mammals at the American Museum of Natural History, wrote: "on the extreme end of the snout the right whale always has an oval roughened area, some two feet in length, called the 'bonnet'. This growth is produced by whale lice (*Cyamus*) and barnacles (*Coronula*), and although it is never absent in this species it is not found on the bowhead." (Andrews, 1916:248). Andrews (1908, 1916) had observed at least one right whale in the North Atlantic firsthand, but his statement seems to be based on previous literature rather than his own observations. This also appears to be a description of the whale's callosities.

Barnard (1924) states that there are specimens of *Coronula diadema* in the South Africa Museum labelled as having been taken from a right whale (S.A.M. Nos. 1323-5, A229, A305). He provides no further details. A review of these and other specimens in the museum revealed only two specimens (No. 1325) from Simon's Town, South Africa (34°S, 18°30'E) labelled as being from a right whale. Barnard's reference to A229 appears to be a typographical error for A299. This latter specimen is probably from a humpback whale, and A305 is labelled as being from a humpback whale. For the other *Coronula* and *Cetopirus* specimens in the museum, no host species is identified (P. Best, pers. comm.).

Freund (1932) states that in addition to cyamids, *Coronula biscayensis* [=*C.*

diadema] is found sometimes on the heads of right whales in large amounts. No further information and no source for this statement is provided.

Matthews (1938), in his study of southern right whales, notes that in addition to cyamids, cirripeds were recorded from one whale which was described by the person who made the observation as having "a mass of encrusted barnacles and lice on the side of the chin." This may simply be another reference to the whale's callosities.

Tomilin (1957:39) states without elaboration that *Coronula* barnacles are not found on bowheads, but "thrive on the warm-loving Black Right whale *Eubalaena glacialis*." He reports these barnacles occurring on right whales in all oceans. Tomilin gives no indication that he personally observed barnacles on right whales. His comments appear to be based primarily, if not entirely, on the article by Brandt and Ratzeburg (1829) discussed above.

Leatherwood *et al.* (1976:52) state in their field guide to North Atlantic cetaceans: "Yellow-brown lice and, less frequently, barnacles grow on the callosities [of the right whale]." No further comments are made and no source is given for this statement. In a companion field guide to Eastern North Pacific cetaceans Leatherwood *et al.* (1982:67) describe the callosities on the right whale's head with no mention of barnacles then state the skin on the right whale's "broad back is free of callosities and generally free of barnacles." No reason is given for why the absence of barnacles was so qualified.

RECORDS OF CETOPIRUS COMPLANATUS

Much less is known about *Cetopirus complanatus* than about either *Coronula diadema* or *C. reginae*. There is one documented record of *C. complanatus* for which the host is described as a right whale (Darwin, 1854). All other museum specimens of this barnacle refer to its host as a whale without describing the particular species (Murray, 1896:449; Gruvel, 1905; Pilsbry, 1916; Barnard, 1924; Newman and Ross, 1976).

Few specimens of this species are in scientific collections (Nilsson-Cantell, 1938; Stubbings, 1967) and those in collections have minimal information on their labels. This species has a particularly long and confusing taxonomic history (Pilsbry, 1916; Newman and Ross, 1976). Its similarity to *Coronula diadema*, and particularly to *C. reginae*, combined with the abbreviated descriptions of early records of coronuline barnacles on right whales, renders many early records highly ambiguous.

Cetopirus complanatus's reported distribution includes the coasts of Chile, South Africa, Australia, and Tasmania (Newman and Ross, 1976). There is one report of this barnacle from Kerguelen Island off the coast of Norway mentioned in Gruvel (1903), and Pilsbry (1916). Nilsson-Cantell (1931) lists two specimens reportedly from the North Atlantic in the collection of the Natural History Museum of Basel. However, this species is not described from the North Atlantic in a later report (Nilsson-Cantell, 1978). There are

no reports from the North Pacific.

As noted above, *C. complanatus* closely resembles *C. reginae*, and the two species are difficult, if not impossible, to distinguish from a distance. *C. complanatus* is also closely related taxonomically to *Coronula*. Indeed, most early taxonomists, including Darwin (1854) and Pilsbry (1916), did not distinguish *Cetopirus* as a separate genus. So, many of the early references to *Coronula* barnacles on right whales may be to *Cetopirus* rather than *Coronula*.

The first suggestion in the literature that *Cetopirus* may occur on right whales is in Eschricht and Reinhardt (1866:35–36). They describe a barnacle taken from a right whale in the North Atlantic as being identified by Chemnitz and Martini (1790) as *Balanus polythalamius complanatus*, which as Chemnitz and Martini (1790) use it is apparently synonymous with *Cetopirus complanatus* (Pilsbry, 1916). A barnacle expert wishing to pursue this record is referred to Eschricht and Reinhardt (1866:35,36 fn.1) and Pilsbry (1916:277–78).

The second report of *Cetopirus* on right whales is in Darwin's (1854) monograph on cirripeds. He describes *C. complanatus* as *Coronula balaenaris*. Darwin does not usually specify the host species of the barnacles he examined, but he does so in this case, stating that *Cetopirus* "seems often to be associated with *Tubicinella*. Some specimens thus associated, sent by Mr Bennet to Professor Owen were said to have been attached to the *Balaena australis*" (=*Eubalaena glacialis*) (p. 417). As noted in Table 1, *Tubicinella* has only been reported from the right whale, supporting Bennet's description of the host as a right whale.

Beneden's (1870) statement that *Coronula balaenaris* (=*C. complanatus*) occurs on all the whales in the temperate regions of the Southern Hemisphere is suspect. He describes these barnacles attached to the base of the whale's flippers, but then comments that the barnacles sent to museums in Europe were rarely labeled with the host whale species. Given these statements, it appears likely that the barnacles Beneden refers to are *Coronula* spp. and came from humpback, not right, whales.

Watson (1981) refers to *Coronula balaenaris* (=*Cetopirus complanatus*) as occurring on right whales as an endemic species. He does not give a source for this statement and offers no supporting evidence.

DISCUSSION

There have been few observations of right whales in the last hundred years, particularly few in the North Pacific (Omura *et al.*, 1969; Scarff, in press). In no case have coronuline barnacles been reported in the articles describing the sighting (Andrews, 1908; Collett, 1909; Omura, 1958; Klumov, 1962; Omura *et al.*, 1969; Payne *et al.*, 1981). Barnacles are not visible in the published photographs of any recent sightings (Payne, 1972, 1974, 1976; Gilmore, 1978; Leatherwood *et al.*, 1976; Woodhouse and Strickley, 1982; Reeves *et al.*, 1983). Recent detailed observations of right whales in the western North

Atlantic (Reeves *et al.*, 1983; D. Spero, pers. comm.; S. Kraus, pers. comm.) and in the South Atlantic off Argentina (Payne *et al.*, 1981; R. Payne, pers. comm.) have also failed to result in sightings of barnacles. There are also no recent observations of coronuline barnacles (other than *Tubicinella*) on right whales off the coast of South Africa (P. Best, pers. comm.).

The absence of barnacles in recent sightings and their presence in our sightings form a context in which earlier reports may be viewed. Many of these reports, particularly Scoresby (1820), Brandt and Ratzeburg (1829), Siebold (1844), Eschricht and Reinhardt (1866), and Holder (1883), are probably inaccurate descriptions of the callosities. The reports of Beneden (1870), Tomilin (1957), and Watson (1981) are unconvincing because of their vagueness and secondhand nature.

This leaves only four records: two of *C. diadema* (Yamada, 1829; Barnard, 1924) and two of *Cetopirus complantus* (Darwin, 1854; Chemnitz and Martini (1790) quoted in Eschricht and Reinhardt, 1866). These reports seem reliable. In each case the barnacle was described by an expert and the only question of reliability concerns the description of the whale host. In the case of Darwin (1854), the presence of *Tubicinella* on the same piece of skin with *Cetopirus* serves as an independent check on the host identity. Barnard's record is less compelling, but there is no question regarding the presence of a coronuline barnacle; the only uncertainty involves the identity of the host species. There is no reason other than the rarity of the record to doubt the accuracy of the museum tag because right whales do occur along the South African coast.

Two questions arise from the present observations. First, if coronuline barnacles can occur on right whales, why have there been so few recent observations of these barnacles on this species of whale? Second, where and how did this whale become associated with these barnacles?

In response to the first question, one argument involves the alleged lack of overlap in the winter ranges of coronuline barnacles and right whales. The absence of coronuline barnacles on the arctic bowhead whale (Tomilin, 1957; Marquette, 1977) and their presence on humpback and gray whales, species with more tropical winter ranges, is used to support this view. Nishiwaki (1972:12) states that "Black right whales simply do not migrate into warm water where the larvae of these barnacles is abundant." The opposite view is expressed by Tomilin (1957).

Another factor which may be important is the relative thickness of the epidermis of right whales. Darwin (1854) and Marloth (1902) have described in detail the manner in which coronuline barnacles attach themselves to whales. In the case of *Coronula* spp. and *Cetopirus*, the papillae of the whale's epidermis are pulled up into the ventral, external cavity in the barnacle's shell to form an adhesive seal. The whale's epidermis also grows over the lateral and dorsal surfaces of the barnacle to varying degrees among the barnacle species rather than being sheared by the basel edge of the barnacle's shell. In discussing scars on a right whale, Omura *et al.* (1969:34) mention that the black epidermis

of this species is approximately 15 mm thick. In contrast, in balaenopterid whales, it is only 5 mm thick, or less (Ling, 1974:16). The right whale's thicker epidermis may make it more difficult for the barnacle larvae to attach themselves initially to right whales than to humpback, and it may also be more difficult for the barnacle to maintain its attachment.

The evidence of barnacles on right whales in the early literature is so scant that the barnacles, if they occurred, were no longer common by the early 1800's, even on the unexploited populations of whales in the Pacific and Southern Hemisphere. The barnacles may require dense aggregations of whales as they occur off South Africa and Argentina in order for the nauplia to attach each year. The more dispersed wintering right whales in the Northern Hemisphere may not have consistently achieved the minimum population density necessary for perpetuation of barnacles. The reduction in total population size caused by whaling may have resulted in the extinction of local barnacle populations in the Northern Hemisphere.

About the question of how this whale acquired the barnacles, a clue may be found in the life history of *Coronula* barnacles. The young barnacles probably attached themselves to this whale during late winter 1981, or possibly during winter 1980. At that time the whale must have been in a region where free-swimming larvae of *Coronula* barnacles occurred. Individual free-swimming nauplia may remain in the water for two to four weeks (W. Newman, pers. comm.). Because *Coronula* barnacles have been seen most frequently on humpback whales, at some point during the winter the right whale was most probably in waters recently travelled by humpback whales.

Until recently, such a hypothesis would have seemed improbable because of the separate winter ranges of the two whale species. The known wintering grounds of humpback whales in the eastern North Atlantic are near the Hawaiian Islands (20°N) (Rice and Wolman, 1971) and off the coast of Mexico (20°N)(Rice, 1978). The winter distribution of right whales has traditionally been thought to be north of this latitude. There are very few sightings of right whales in the eastern North Pacific between November and March and most of these were made north of 40°N (Maury, 1852; Townsend, 1935; Scarff, in press). Historically, in the western North Pacific, right whales were found as far south as 30°N (Maury, 1852; Townsend, 1935), although more recently they have been observed only rarely south of 40°N (Omura *et al.*, 1969).

Sightings of right whales off the California coast are rare, the species' wintering grounds in the North Pacific apparently being elsewhere (Scarff, in press). However, there have been recent sightings of three right whales south of 30°N in the eastern North Pacific. On March 11, 1956, two right whales were observed off Baja California at 26°N (Rice and Fiscus, 1968). In 1979, a single right whale was observed on three occasions on March 25 and April 10 in the Hawaiian Islands at 20°N (Rowntree *et al.*, 1980; Herman *et al.*, 1980). Of particular note is that during all three observations, this latter right whale was interacting with humpbacks. The photographs of the right whale

we observed off Half Moon Bay were compared with photographs of the animal seen off Hawaii, and because of the presence of a white blaze on the animal seen near Hawaii and its absence on the animal from Half Moon Bay, these appear to be two different individuals.

It is possible that before their decimation by whalers, some right whales migrated further toward the equator than they currently appear to do. There is some indication that a similar phenomenon may have occurred off South Africa (Best, 1981). Perhaps also some humpback whales, perhaps juvenile animals, wintered further north resulting in overlap of the winter distribution of these two species. If either occurred, the early accounts of coronuline barnacles on right whales may be accurate.

Another possibility is that the right whale picked up the barnacles as a result of association with a whale of a species other than humpback, most probably a sperm whale (*Physeter macrocephalus*), but possibly another species (see Table 1). In October 1963, a right whale was observed swimming with two sperm whales off the coast of South Africa (Best, 1970). A second line of support for this hypothesis comes from the observation that two species of cyamid which are typically host specific have been reported on both right and sperm whales (Rowntree, 1984; Best, 1970; Reeves *et al.*, 1983).

In either case, the sighting of a right whale with humpbacks in Hawaii in 1979 and the sighting of another right whale in 1982 with barnacles typically found on humpbacks, suggest that researchers studying humpbacks on their winter grounds should be alert to the possible presence of right whales in the area.

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