

disturbance from vessels passage, and close approach by people, on Weddell seal behavior, distribution, and foraging are unknown. There is a risk of injury to a small number of animals from collision with boats or crushing from large vessel passage through ice fields. Currently, there are no reports of significant fisheries interactions, however, the development of new fisheries in Antarctic waters, particularly those targeting the Antarctic toothfish, could have an impact on Weddell seal nutrition, and potential operational interactions should be considered in the management plans.

**See Also the Following Articles**

Antarctic marine mammals ■ Earless seals ■ Pinniped Ecology ■ Pinniped Life History

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WHALE LICE

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Whale lice spend their entire lives clinging to their hosts. Each cetacean species or genus presents its own set of challenges, to which whale louse species and genera have adapted anatomically, physiologically and behaviorally. Whale lice differ radically in all these ways from their ancestors which did not live on whales. Thus like cetaceans themselves, whale lice have pushed the limits of extreme evolutionary “reinvention.”

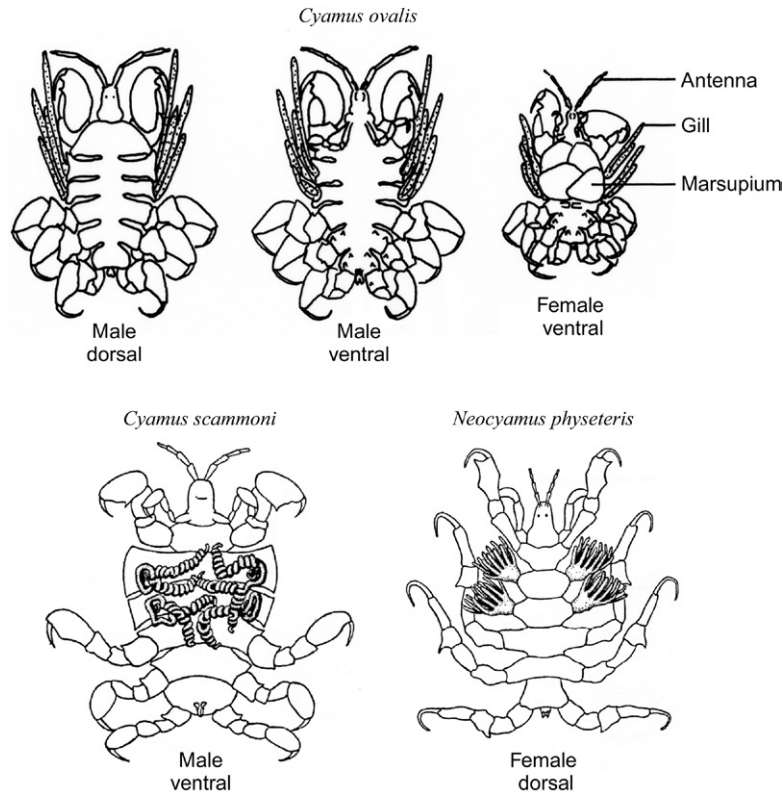
**I. Origin and Diversification of Whale Lice**

Whale lice are amphipod crustaceans; hence, they are “lice” only by analogy. Their overall appearance is unique (Fig. 1), but a close relationship with skeleton shrimp (Caprellidae) is indicated by some qualitative features of anatomy and by molecular data (Ito et al., 2011). Recent classifications place them in a family Cyamidae within a superfamily Caprelloidea and/or a suborder Caprellidea that includes Caprellidae and other families (Myers and Lowry, 2003).

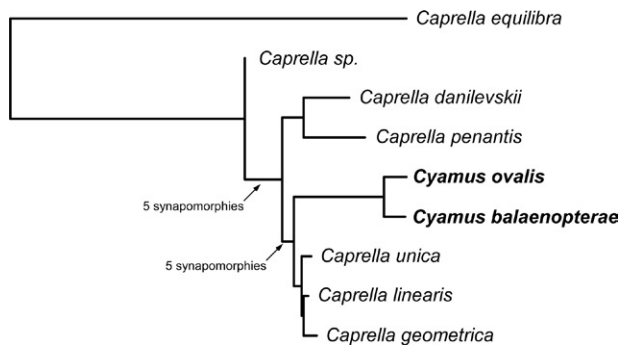
Most caprellids cling to seaweeds, corals, rocks, and similar substrates in near-shore environments where they capture very small prey (e.g., copepods) that currents bring their way (Caine, 1974, 1980; Watling and Carlton, 2007). It is likely that some ancestral caprellids transferred accidentally onto the ancestors of modern cetaceans which also lived in near-shore environments. A living model for this process was documented by Caine (1986) who found *Caprella andreae* on 96% of 138 loggerhead sea turtles examined in South Carolina and Florida. *C. andreae* is now known to be a globally distributed “rafter” that lives on at least two species of sea turtles and can also be found on floating human artifacts such as fishing gear (Cabezas et al., 2013). Almost all other caprellids appear to live on immobile hosts or objects.

The caprellids are an old radiation with 100 recognized genera and more than 200 species in the single genus *Caprella* (WoRMS: <http://www.marinespecies.org/>). The cyamids are much less diverse, with six genera containing roughly 40 species, more than half of them in the genus *Cyamus* (WoRMS; Leung 1967; Margolis





**Figure 1** Three cyamid species from right, gray, and sperm whales, respectively. The spiral gills of *C. scammoni* and the fringed gills of *N. physeteris* are unusual. Redrawn from Rowntree, V.J., 1996. Feeding, distribution, and reproductive behavior of cyamids (Crustacea: Amphipoda) living on humpback and right whales. *Can. J. Zool.* 74, 103–109 (© Canadian Science Publishing or its licensors) and Leung, Y.-M., 1967. An illustrated key to the species of whale-lice (Amphipoda, Cyamidae), ectoparasites of Cetacea, with a guide to the literature. *Crustaceana* 12, 279–291.



**Figure 2** Phylogeny of some caprellids and two cyamids inferred from 18S rRNA gene sequences. Ingroups containing the cyamids are supported by a total of 10 shared, derived nucleotide states. Sequences are from GenBank except those for *Caprella* sp., *C. penantis*, and *Cyamus ovalis*, which are unpublished data of the authors.

et al., 2000; Martin and Haney, 2007). And cyamids are a young radiation, having evolved on Cetacea. Thus rather than being a sister-family to Caprellidae, Cyamidae might be expected to comprise a lineage within the Caprellidae. Consistent with this hypothesis, a preliminary analysis of 18S rRNA gene sequences places the genus *Cyamus* within the genus *Caprella* (Fig. 2).

Given the intimate and obligate relationships of cyamids with their hosts, and the fact that some whales carry several cyamid species, why are there fewer species of whale lice than of whales? One reason for their limited diversity may be that sets of closely related and ecologically similar cetacean species (e.g., rorquals, and some

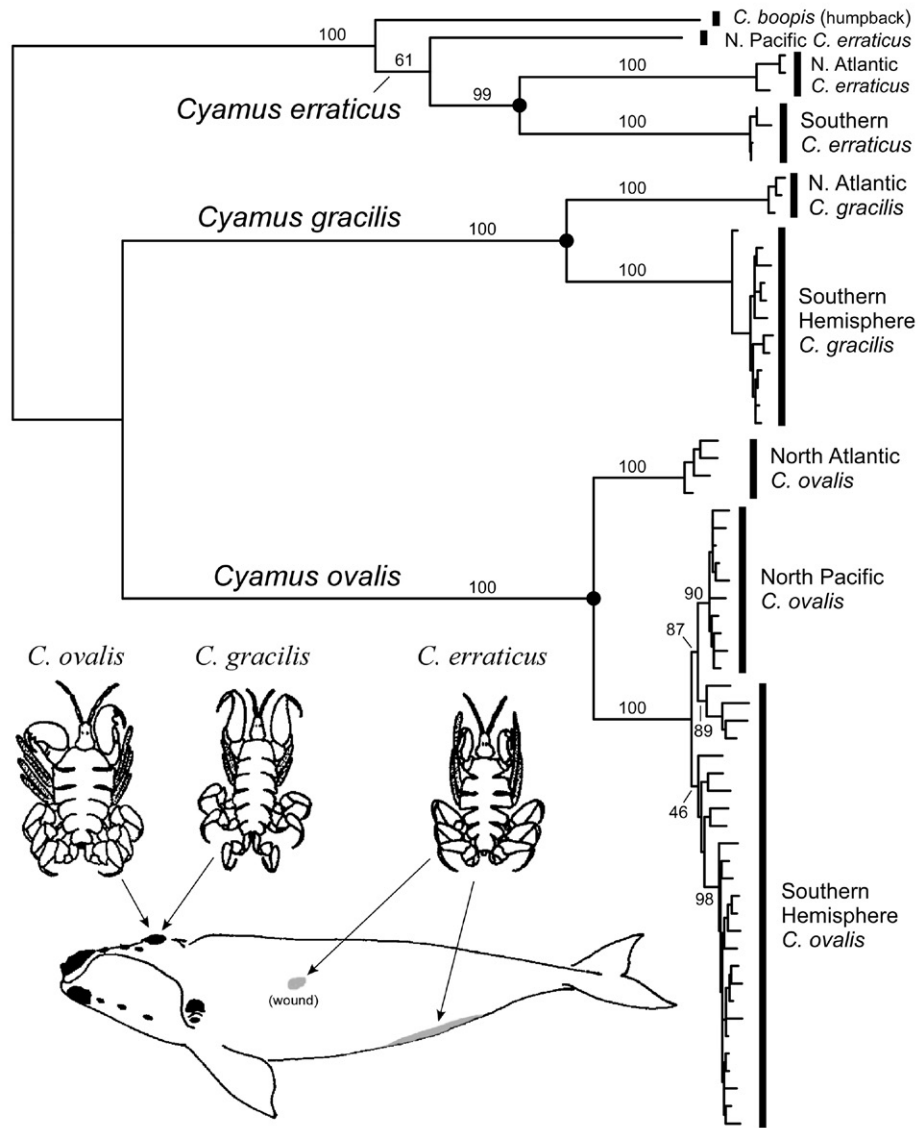
groups of small toothed whales) present what amounts to a single resource from a cyamid's point of view.

Another reason may be that we currently recognize only a fraction of the cyamids that exist. They are tiny passengers on hosts that may be more than a thousand times longer and a billion times more massive than themselves. On some cetaceans there are few cyamid individuals per whale and they make themselves inconspicuous by sheltering in crevices. Also, some cyamid species remain morphologically indistinguishable from each other after millions of years of separation (Fig. 3; Kaliszewska et al., 2005). Thus new species and new host associations are still being discovered (Haney et al. 2004, Martínez et al., 2008).

## II. Life History

As they transitioned from being typical caprellids to being whale lice, cyamids changed dramatically in morphology and behavior. While maintaining a similar distribution of body lengths (typically 6–20 mm, with adult males larger than females), they became vastly wider and dorsoventrally flattened, with stout grasping appendages tipped with exceedingly sharp, recurved claws that enable them to resist the many forces that constantly threaten their grip on the whale (Fig. 1). This is a matter of life and death: if they wash off, they are effectively doomed.

Cyamids eat the dead outer layer of their host's skin (Rowntree, 1983, 1996) and possibly other foods that adhere to the skin such as bacteria and algae, which could complement a monotonous diet of keratin. However, the stable-isotopic signatures of whale lice are very similar to those of host skin. This indicates that most of the carbon and nitrogen atoms in a whale louse come from its whale (Schell et al., 2000).



**Figure 3** A gene genealogy of mitochondrial sequences from the three right whale cyamid “species.” The nominally conspecific populations from different hemispheres are all deeply reciprocally monophyletic, except that the North Pacific *Cyamus ovalis* clade is contained within southern *C. ovalis*, as discussed in the text. Redrawn from Kaliszewska, Z.A., Seger, J., Rowntree, V.J., Barco, S.G., Benegas, R., Best, P.B., et al., 2005. Population histories of right whales (Cetacea: Eubalaena) inferred from mitochondrial sequence diversities and divergences of their whale lice (Amphipoda: Cyamus). *Mol. Ecol.* 14, 3439–3456.

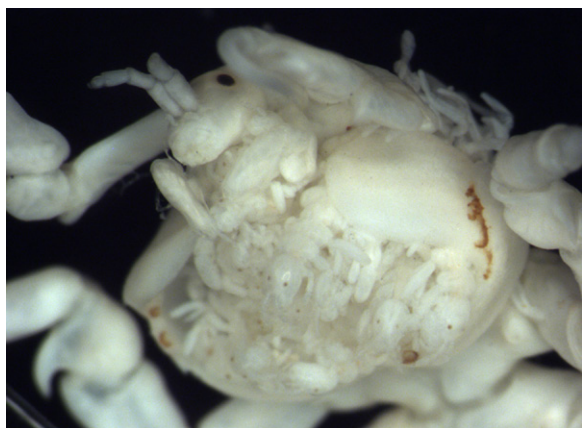
As in caprellids, males consort with gravid females, holding on to a female’s gills with their front legs and hovering over her for days. Also like caprellids, females protect their eggs, embryos, and even juveniles large enough to have fed on whale skin, in a “marsupium” derived from the gill bases (Figs 1 and 4). Broods begin with up to several hundred eggs in some species. This immense fertility implies that juvenile mortality rates can be very high.

Most individual cyamids spend their entire life on their whale of birth. However, if every individual did that they would go extinct, because every whale will eventually die. The evolutionary payoff can be huge for colonizing an empty whale “island,” or even one that has been colonized by relatively few unrelated founders (Hamilton and May, 1977). Thus cyamids are expected to be willing to transfer between whales that touch each other, even when doing so is risky. Such opportunities arise, first, when mother whales give birth and nurse their calves. For example, *Cyamus erraticus* concentrates in the genital and mammary slits of right whales and rapidly

colonizes young calves, covering parts of their heads in dense swarms. Later, as the calf’s callosities develop, the callosity specialists *C. ovalis* and *C. gracilis* move in and *C. erraticus* retreats to places where it enjoys a competitive advantage (Fig. 3).

### III. Whales as Mobile Islands

The vertical transfer of cyamids from female whales onto their offspring is easy to see, but how much horizontal exchange occurs later, between unrelated whales? Kaliszewska et al. (2005) found very high levels of haplotype diversity within the cyamid populations on individual right whales, and low levels of differentiation between them ( $F_{st}$  values between 0 and 0.05). These numbers imply that at least a few cyamids immigrate onto a typical right whale in each cyamid generation. Right whales do not have family-based social groups, but they interact frequently on their nursery grounds, and apparently their whale lice often seize those opportunities to move.



**Figure 4** A female *Neocyamus physeteris* with offspring that appear to be well beyond first instar, still occupying her marsupium.

Whales, especially young ones, sometimes interact with whales of other species, and this can lead to “inappropriate” cyamid exchanges—usually a tragic mistake for the migrant cyamids, but occasionally giving rise to new species (for example, *Cyamus ceti* on the bowhead whale, which appears to be derived from *C. ceti* on the gray whale). As this scenario would predict, the three nominal species on right whales are *not* each other’s closest relatives, nor are the three different species that live on gray whales.

Remarkably, there is *no* differentiation between the regional cyamid populations on right whales off Argentina, South Africa, and Australia ( $F_{st} = 0$ ), even though the whale populations are differentiated (Kaliszewska et al., 2005). This lack of structure would be expected if whales from different subpopulations occasionally met on feeding grounds and exchanged cyamids, or if they migrated between subpopulations even rarely, in which case an entire cyamid “city” would also migrate.

In striking contrast to the lack of genetic structure within Southern Hemisphere right whale cyamids, there are deep splits between the nominally conspecific cyamid populations on either side of the equator, indicating no exchange in the Atlantic for the last few million years. There is a slight exception to this pattern in the Pacific: the mitochondrial genealogy of North Pacific *Cyamus ovalis* is contained within the southern *C. ovalis* genealogy, implying that a southern whale visited the North Pacific several hundred thousand years ago and introduced a mitochondrial genome that swept through North Pacific *C. ovalis* (Fig. 3).

Northern and southern right whale cyamids share the same names because they show no obvious differences, yet their genes say they have been separated for most of the Pliocene—nearly as long as humans and chimpanzees. This implies that they were well tuned for life on their right whale hosts before they stopped crossing the equator several million years ago, and that since then they have experienced very little pressure to change. This extreme conservatism, recently, seems out of character for the descendants of caprellids that changed themselves almost beyond recognition, very rapidly, when they first took up whale riding.

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Parasites

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## WHALING, ABORIGINAL AND WESTERN TRADITIONAL

RICHARD ELLIS

### I. Humans Meet Whales

One of the earliest records of man’s interactions with whales can be found in the chronicles of the conquests of Alexander the Great, which took place in the 4th century BC, and were transcribed some 300 years later by the Greek historian Arrian, probably of sperm whales (*Physeter macrocephalus*), but also baleen whales, as being