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*Igor Krupnik, Michael A. Lang,  
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# Species Diversity and Distributions of Pelagic Calanoid Copepods from the Southern Ocean

*E. Taisoo Park and Frank D. Ferrari*

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**ABSTRACT.** In the Southern Ocean, 205 species of pelagic calanoid copepods have been reported from 57 genera and 21 families. Eight species are found in the coastal zone; 13 are epipelagic, and 184 are restricted to deepwater. All 8 coastal species and eight of 13 epipelagic species are endemic, with epipelagic species restricted to one water mass. Of the 184 deepwater species, 50 are endemic, and 24 occur south of the Antarctic Convergence. Most of the remaining 134 deepwater species are found throughout the oceans with 86% percent reported as far as the north temperate region. The deepwater genus *Paraeuchaeta* has the largest number of species in the Southern Ocean, 21; all are carnivores. *Scolecithricella* is also speciose with 16 species, and more specimens of these detritivores were collected. Species with a bipolar distribution are not as common as bipolar species pairs. A bipolar distribution may result from continuous extinction in middle and low latitudes of a wide spread deepwater species with shallow polar populations. Subsequent morphological divergence results in a bipolar species pair. Most of the numerically abundant calanoids in the Southern Ocean are endemics. Their closest relative usually is a rare species found in oligotrophic habitats throughout the oceans. Abundant endemics appear adapted to high primary and secondary productivity of the Southern Ocean. Pelagic endemicity may have resulted from splitting a widespread, oligotrophic species into a Southern Ocean population adapted to productive habitats, and a population, associated with low productivity that remains rare. The families Euchaetidae and Heterorhabdidae have a greater number of their endemic species in the Southern Ocean. A phylogeny of these families suggests that independent colonization by species from different genera was common. Thus, two building blocks for the evolution of the Southern Ocean pelagic fauna are independent colonization and adaptation to high productivity.

## INTRODUCTION

Copepods often are referred to as the insects of the seas. They certainly are comparable to insects in survival through deep time, ecological dominance, geographic range, and breadth of adaptive radiation (Schminke, 2007). However, they are not comparable to insects in numbers of species. Only 11,302 species of copepods were known to science toward the end of the last century (Humes, 1994), and 1,559 have been added since then. In contrast, the number of described insects approaches one million (Grimaldi and Engel, 2005). In terms of the number of individuals alive at any one time, however, copepods undoubtedly

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surpass the insects. Among the copepod orders, calanoid copepods contribute more numbers of individuals to the Earth's biomass, primarily because of their unique success in exploiting pelagic aquatic habitats. Calanoid copepods also are speciose; Bowman and Abele (1982) estimated 2,300 species of calanoids, and as of this writing, 525 species have been added. These calanoid species are placed in 313 nominal genera belonging to 45 families (F. D. Ferrari, personal database).

Knowledge about the distribution and diversity of calanoid copepods in the Southern Ocean has increased significantly over the past century (Razouls et al., 2000). Most of the calanoid copepods reported from the Southern Ocean have been collected from pelagic waters. However, more species new to science are now being described from waters immediately over the deep-sea floor of the Southern Ocean (Bradford and Wells, 1983; Hulsemann, 1985b; Schulz and Markhaseva, 2000; Schulz, 2004, 2006; Markhaseva and Schulz, 2006a; Markhaseva and Schulz, 2006b, 2007a, 2007b). The diversity of this benthopelagic calanoid fauna from other oceans (Grice, 1973; Markhaseva and Ferrari, 2006) suggests that the total calanoid diversity from this habitat of the Southern Ocean is significantly underestimated, and many new species are expected to be described. The present review then is restricted to pelagic calanoid copepods because the benthopelagic fauna has not been well surveyed and their species not as well known as pelagic calanoids.

Pelagic calanoid copepods are numerically the dominant species of the zooplankton community in the Southern Ocean (Foxton, 1956; Longhurst, 1985). Beginning with the *Challenger* expedition (1873–1876), many expeditions to the Southern Ocean have provided specimens for taxonomic studies of the calanoids. Early works by Brady (1883), based on the *Challenger* collections, Giesbrecht (1902), based on *Belgica* collections, Wolfenden (1905, 1906, 1911), based on the *Gauss* (German deep-sea expedition) collections, and Farran (1929), based on the British *Terra Nova* collections, led to the discovery of most of the numerically dominant and widespread pelagic calanoid species in the Southern Ocean. Several major national expeditions followed, such as the *Meteor* expedition, 1925–1927, the SS *Vikingen* expedition, 1929–1930, and the *Norvegia* expedition, 1930–1931. However, collections obtained by these expeditions were studied mainly to understand the vertical or seasonal distribution or other aspects of the biology of pelagic animals. Significant publications resulting from these studies include Hentschel (1936), Steuer and Hentschel (1937), and Ottestad (1932, 1936). In 1925 the British

*Discovery* Committee launched a program of extensive oceanographic research in the Southern Ocean, including intensive studies of the zooplankton fauna. Publications by Mackintosh (1934, 1937), Hardy and Gunther (1935), and Ommanney (1936) based on the *Discovery* collections are notable for their valuable contributions to the population biology of the numerically dominant calanoid copepods. Continued studies of the *Discovery* collections led to the publication of additional papers, such as Foxton (1956) about the zooplankton community and Andrew (1966) on the biology of *Calanoides acutus*, the dominant herbivore of the Southern Ocean.

Southern Ocean copepods became the subject of taxonomic studies once again toward the middle of the last century with two important monographs (Vervoort, 1951, 1957). These were the most comprehensive treatments published on pelagic calanoids, to that time, and began a new era of taxonomic analyses of Southern Ocean copepods. In these two studies, many previously known species of the Southern Ocean calanoids were completely and carefully redescribed, confusion regarding their identity was clarified, and occurrences of these species in other oceans were noted from the published literature. Two papers by Tanaka (1960, 1964) appeared soon afterward, reporting on the copepods collected by the Japanese Antarctic Expedition in 1957 and 1959. On the basis of collections made by the Soviet Antarctic expeditions, 1955–1958, Brodsky (1958, 1962, 1964, 1967) published several studies of the important herbivorous genus *Calanus*. More recently, important contributions to taxonomy of the Southern Ocean calanoids have been made by Bradford (1971, 1981) and Bradford and Wells (1983), reporting on calanoids found in the Ross Sea. Additionally, invaluable contributions have been made to the taxonomy of the important inshore genus *Drepanopus* by Bayly (1982) and Hulsemann (1985a, 1991).

Beginning in 1962, the U.S. Antarctic Research Program funded many oceanographic cruises to the Southern Ocean utilizing the USNS *Eltanin*. Samples taken with opening-closing Bé plankton nets and Isaacs-Kidd midwater trawls on these cruises were made available by the Smithsonian Institution for study through the Smithsonian Oceanographic Sorting Center. The exhaustive taxonomic works by Park (1978, 1980, 1982, 1983a, 1983b, 1988, 1993) are based almost exclusively on the midwater trawl samples collected during the *Eltanin* cruises, and these results significantly increased taxonomic understanding of most species of pelagic calanoids. Other studies based on the *Eltanin* samples include the following: Björnberg's (1968) work on the Megacalanidae; Heron and Bowman's

(1971) on postnaupliar developmental stages of three species belonging to the genera *Clausocalanus* and *Ctenocalanus*; Björnberg's (1973) survey of some copepods from the southeastern Pacific Ocean; Yamanaka's (1976) work on the distribution of some Eucalanidae, Aetideidae, and Euchaetidae; Fontaine's (1988) on the *antarctica* species group of the genus *Paraeuchaeta*; Markhaseva's (2001) on the genus *Metridia*; and Markhaseva and Ferrari's (2005) work on Southern Ocean species of *Lucicutia*. In addition, four exhaustive monographs have treated the taxonomy of a pelagic calanoid family throughout the world's oceans, and these also have contributed further to an understanding of the Southern Ocean fauna: Damkaer's (1975) work on the Spinocalanidae, Park's (1995) on the Euchaetidae, Markhaseva's (1996) on the Aetideidae, and Park's (2000) on the Heterorhabdidae. These monographs were based on specimens from an extensive set of samples from the world's oceans. As a result, the taxonomy and geographical range of most of the widespread species of these families are now well known.

Recently described new species of Southern Ocean calanoids are either pelagic species that previous authors failed to recognize as distinct from similar relatives, e.g., *Pleuromamma antarctica* Steuer, 1931 (see Ferrari and Saltzman, 1998), or species inhabiting extraordinary habitats seldom explored previously, like the water immediately above the seafloor. Bradford and Wells (1983) described the first benthopelagic calanoid copepods of the Southern Ocean, *Tharybis magna* and *Xanthocalanus harpagatus*, from a bait bottle. *Neoscolecithrix antarctica* was collected in small numbers in the Antarctic Sound adjacent to the Antarctic Peninsula by Hulsemann (1985b), who believed the species lived in close proximity to the seafloor. More recent additions to the benthopelagic calanoid fauna include *Parabradyidius angelikae* Schulz and Markhaseva, 2000, *Paraxantharus brittae* Schulz, 2006, and *Sensiava longiseta* Markhaseva and Schulz, 2006, each belonging to a new genus, and *Brachycalanus antarcticus* Schulz, 2005, *Scolecitrichopsis elenae* Schulz, 2005, *Byrathis arnei* Schulz, 2006, *Pseudeuchaeta arcuicornis* Markhaseva and Schulz, 2006, *Bradyetes curvicornis* Markhaseva and Schulz, 2006, *Brodskius abyssalis* Markhaseva and Schulz, 2007, *Rythabis assymetrica* Markhaseva and Schulz, 2007, and *Omorius curvispinus* Markhaseva and Schulz, 2007. These latter species were collected from the Weddell Sea, an arm of the Southern Ocean, and from the Scotia Sea.

In this paper, all relevant studies of the taxonomy of pelagic Southern Ocean calanoid copepods are reviewed. Lists are compiled of species, genera, and families, and the

geographical range within the Southern Ocean and relative abundance of each species are noted. Morphological differences are used to suggest evolutionary relationships among species. The distribution of all species is reviewed, and several generalized patterns are hypothesized. Of particular interest here are the species for which fewer than 50 specimens have been collected during the extensive history of surveys of the Southern Ocean pelagic fauna. The distribution of these rare, pelagic calanoids, almost all deepwater species, contributes favorably to an understanding of patterns of distribution and of speciation in the Southern Ocean.

## METHODS

Traditionally, the Southern Ocean has been described physiographically as including the ocean basins adjacent to the continent of Antarctica plus the following adjoining seas: Amundsen Sea, Bellingshausen Sea, Ross Sea, Weddell Sea, and the southern part of the Scotia Sea. In this review of pelagic calanoid copepods, the southern boundary of the Southern Ocean is defined physiographically by the Antarctic continent, but the northern boundary is defined hydrographically, by the average position of the Subtropical Convergence. The Subtropical Convergence is located around 40°S (Deacon 1934, 1937), where the surface temperature of the sea drops sharply from about 18°C to 10°C. In this review, then, the Southern Ocean includes both the Antarctic region and the subantarctic region. Antarctic and subantarctic regions are separated by the Antarctic Convergence, which is located around 55°S, where the sea surface temperature drops 3°C to 5°C over about 30 miles (48.3 km). Although the latitudinal positions of both the Subtropical Convergence, among the Atlantic, Pacific and Indian oceans, and the Antarctic Convergence, among the Atlantic, Pacific and Indian sectors of the Southern Ocean, may vary significantly, locally, these convergences seldom vary more than a degree of latitude from their mean position.

Studies of the distribution of organisms are one of the primary purposes of the discipline of taxonomy, and the scope and effectiveness of taxonomic studies is dictated by the availability of specimens. Like most pelagic organisms, calanoid copepods in the Southern Ocean have been collected mainly with tow nets operated aboard oceangoing ships, which usually sail to a preselected set of geographic positions in the ocean. Because of the physical isolation of the Southern Ocean, studies of its pelagic calanoid copepods have depended primarily on efforts of national

oceanographic expeditions, many of which routinely carried out sampling protocols for pelagic organisms.

The Isaacs-Kidd midwater trawls employed by the U.S. Antarctic Research Program were particularly effective in collecting large, pelagic copepods and significantly increased knowledge about the calanoid fauna. More than 1,000 midwater trawl samples were taken, and these samples are believed to have collected nearly all of the pelagic calanoid copepods in the water column; most of these species have been described (Park, 1978, 1980, 1982, 1983a, 1983b, 1988, 1993). The trawls were not fitted with a device to measure water flow through the mouth of the trawl, so no quantitative measure of the amount of water filtered by the trawl can be calculated for these samples. Sampling times, ranging from one to four hours, have allowed a calculation of the number of animals collected per unit time of trawl operation for the more abundant species, e.g., *Paraeuchaeta antarctica* (see Ferrari and Dojiri, 1987, as *Euchaeta antarctica*), but this measure is too coarse for the rare species that are the primary focus of this study.

The Isaacs-Kidd midwater trawls were quickly lowered to a specified deepest depth, obliquely towed at 3-5 knots to a specified shallowest depth, and then quickly retrieved to the surface again. It is not possible to determine the depth of collection for the specimens captured in a sample with this protocol. Furthermore, normally, only one trawl sample was collected at a station, and therefore, only one depth range was sampled at a particular location. As a result of these constraints, studies based on these samples cannot provide direct information about the vertical distribution of the calanoid species. However, by comparing the presence or absence of a species in samples taken to different greatest depths at different locations here or by calculating a frequency of occurrence for each sampled depth range relative to all trawls at that depth range (Yamanaka, 1976), it is possible to make a first-order determination of how deep a trawl has to be towed in order to collect a certain species.

Southern Ocean pelagic calanoids are categorized here in several different ways. Species collected in the vicinity of continental or insular land masses are inshore species, while species collected away from continental or insular land masses have been categorized to vertical zones as follows: epipelagic (0–200m), mesopelagic (200–1,000m), and bathypelagic (1,000–4,000). The term “deepwater” refers to the mesopelagic and bathypelagic zones together. In terms of abundance, species are categorized by the number of specimens collected or known from other expeditions: CC, very common (over 100 specimens found); C, common (between 99 and 50 specimens found); R, rare

(between 49 and 10); and RR, very rare (less than 10 specimens found). These are not counts per sample, but are all specimens known to science.

A large number of endemic species are found in the Southern Ocean, and these discoveries are placed within the context of endemism throughout the world's oceans for two well-studied families, Euchaetidae and Heterorhabdidae. To facilitate comparisons, four noncontiguous areas of interest were defined among the world's oceans: the Southern Ocean, the Arctic (including adjacent boreal seas of the Atlantic and Pacific oceans), the eastern Pacific Ocean (along the Pacific coasts of the Americas, including the boundary currents), and the Indo-West Pacific Ocean (in and around the Malay Archipelago). The latter three were chosen as areas of interest because most of the endemic species of Euchaetidae and Heterorhabdidae not found in the Southern Ocean occur in one of them. So, for example, the Atlantic Ocean was not considered an area of interest because its endemic species occur mainly toward its northern and southern boundaries, and these endemic species could be included in the Arctic Ocean and Southern Ocean areas, respectively. There are no a priori biological hypotheses that support these utilitarian areas of interest, although endemism is discussed in the context of high primary and secondary productivity.

Three broad feeding categories, herbivory, carnivory, and detritivory, are recognized for many pelagic calanoids. Food preferences of calanoid copepods have not been studied systematically, but the following publications supported the general feeding categories of these taxa: Mullin's (1967) work on the herbivory of Calanidae and Eucalanidae, Yen's (1983) on the carnivory of Euchaetidae, Ohtsuka et al.'s (1997) on the carnivory of derived Heterorhabdidae, Nishida and Ohtsuka's (1997) on the detritivory of Scolecitrichidae, and Itoh's (1970) and Matsuura and Nishida's (2000) on the carnivory of Augaptilidae. Studies of a few species of the large family Aetideidae (Robertson and Frost, 1977; Auel, 1999) have suggested that these species may be omnivores, but on the basis of the morphology of their mouthparts, they are considered carnivores here. Feeding is connected to environment through areas of high primary and secondary productivity, and here high primary and secondary productivity is equated with permanent, annually episodic upwelling areas. These areas of upwelling are associated with western boundary currents adjacent to all continents or are associated with three oceanic bands: trans-Southern Ocean, worldwide equatorial, and boreal Pacific (LaFond, 1966; Huber, 2002).

Descriptions of the geographical distribution of a species beyond the Southern Ocean were initiated by dividing the world's oceans into the following regions, generally following Backus (1986): Antarctic (south of the Antarctic Convergence), subantarctic (between the Antarctic and Subtropical convergences), south temperate (Subtropical Convergence to Tropic of Capricorn, about 20°S), tropical (Tropic of Capricorn to Tropic of Cancer, about 20°N), north temperate (Tropic of Cancer to about 50°N), subarctic (boreal seas adjacent to the Arctic Ocean to the Arctic Circle at 66°N), and the region of the Arctic basin. Some of the boundaries of these areas correspond to hydrographic features, e.g., they are the surface manifestations of the boundaries of water masses. However, these boundaries have not been shown to describe the generalized distribution of deepwater animals, and, in fact, two other ways of explaining the distribution of deepwater animals are proposed here. Distribution records for the regions outside of the Southern Ocean are derived from the latest reference given to each species in Appendix 1. There has been no attempt to correct for differences in sampling intensity among these regions, although the south temperate region has been sampled least (only mentioned in reports by Grice and Hulsemann, 1968, and Björnberg, 1973), and the north temperate, subarctic, and Arctic have been sampled the most.

Most of the very common pelagic calanoids are usually widespread within the Southern Ocean and were discovered during the early expeditions that ended in the first part of the twentieth century. These species originally were described from specimens collected in the Southern Ocean rather than being inferred from descriptions of specimens from other oceans, and most of these species have been re-described once or twice since their original description. As a result, their taxonomy is stable, and their morphology and distribution within the Southern Ocean are relatively well known. Many deepwater calanoids also originally have been described from the Southern Ocean. Their morphology is well known, but most of these deepwater species are rare. As a result, information about their distribution, particularly beyond the Southern Ocean, remains limited. Occurrences of these rare deepwater calanoids are based on only a few specimens captured at only a small number of locations, but at least some of the occurrences beyond the Southern Ocean have been confirmed by direct comparison of specimens. In contrast, other rare deepwater species originally were described from oceans other than the Southern Ocean and only subsequently were recorded from the Southern Ocean. Because specimens of these rare species from the Southern Ocean have not been compared

to specimens from the type locality, their nominal attribution has yet to be verified.

In this study, the distribution ranges of many species outside the Southern Ocean are determined from information available in the literature. Observations about distributions that are accompanied by species descriptions are the usual source for these data. However, not all species descriptions in the literature are equally informative, and in some cases, it is not easy to determine the identity of all species reported under the same name. In the present study, the distribution range assigned for many of the rare or very rare species, especially for those reports of a few specimens from several localities, should be considered provisional. The definitive answer to the geographical distribution for these rare species must wait until their potential distribution range has been more extensively sampled.

For rare and, particularly, very rare species, specimens may not have been reported from all of the regions between the Southern Ocean and the region farthest north from which a species has been collected. Initially, a continuous deepwater distribution is assumed if a species is present in more than one nonadjacent region, although a possible origin for disjunct distributions is considered here within a larger context of the evolution of bipolar species pairs.

Because the northern boundary of the Southern Ocean is defined hydrographically, certain warm-water species have been reported as penetrating for a relatively short distance south into the subantarctic region, while some typically subantarctic species have often been found to extend north of 40°S in small numbers. If the number of these reports is small, an extension of the species range is not considered here. In this study, warm-water species included in the list as subantarctic species are those that have been reported several times, south of the Subtropical Convergence and close to the Antarctic Convergence. Problems have been resolved in a similar manner for range extensions of species between the Antarctic and subantarctic regions. The identification of a species as having an Antarctic distribution as opposed to a subantarctic distribution is based on the number of reports in one water mass relative to the number in the other water mass.

In this study, the morphological divergence of the exoskeleton among species is used as a first approximation to the degree of relatedness among species, with the understanding that allopatric sibling species may not undergo significant morphological divergence in the absence of a strong adaptive pressure and that secondary sex characters

of the exoskeleton are likely to diverge over a shorter period of time than the rest of the exoskeleton. Specimens from the wider geographical regions are reexamined for information regarding the morphological variation and distribution ranges of some of the species (T. Park, unpublished data).

The abundances found in Tables 1–7 are derived from Park (1978, 1980, 1982, 1983a, 1983b, 1988, 1993), who examined samples selected mainly from the *Eltanin* mid-water trawl collections available from the Smithsonian Oceanographic Sorting Center. The selection was made to cover as wide an area as possible, but only an aliquot of the original sample was examined systemically and consistently so that the sorted specimens reflect the relative abundance of the species in the sample in a general way. In this paper's introduction, counts of the number of species of copepods and of calanoid copepods were determined by using an online species database (The World of Copepods, National Museum of Natural History) to extend the counts of Humes (1994), beginning with the year 1993, and Bowman and Abele (1982), beginning with the year 1982.

### NUMBER SPECIES OF PELAGIC CALANOIDS FROM THE SOUTHERN OCEAN

Two hundred and five species of pelagic calanoid copepods (Appendix 1) in 57 genera from 21 families (Appendix 2) have been reported from the Southern Ocean. Among these, 8 (3.9%) species are coastal or inshore, 13 (6.3%) are epipelagic species, and 184 (89.8%) are deepwater species. Of the 57 genera of pelagic calanoids reported from the Southern Ocean, *Paraeuchaeta* is the most speciose genus with 21 species, followed by *Scolecithricella* (16 species), *Euaugaptilus* (14 species), *Scaphocalanus* (10 species), *Metridia* (9 species), *Pseudochirella* (9 species), *Gaetanus* (8 species), *Onchocalanus* (7 species), and *Lucicutia* (6 species). The 16 species included in the genus *Scolecithricella* are morphologically diverse, and recently, Vyshkvartzeva (2000) proposed to place the species of *Scolecithricella* in one of three genera. Although we are not comfortable with this proposal because the analysis was not exhaustive, acceptance would result in the following numbers from the Southern Ocean: *Scolecithricella* (9 species) and *Pseudoamallothrix* (6 species), with *S. pseudopropinqua* being moved to the genus *Amallothrix*.

Species of *Paraeuchaeta* (Euchaetidae) are deepwater calanoids, and some of them can be collected in large numbers in the Southern Ocean, e.g., *Paraeuchaeta antarctica*

(see Park, 1978; Ferrari and Dojiri, 1987) or *P. barbata*, *P. rasa*, and *P. biloba* (see Park, 1978). Feeding of a few species of *Paraeuchaeta* has been studied (Yen, 1983, 1991), and these species are known to be carnivores. On the basis of the similarity of feeding appendages among species, this feeding mode is assumed for all species of the genus. In the Southern Ocean, species of *Euaugaptilus* (Augaptilidae) are typically bathypelagic and thought to be carnivores on the basis of the structure of their feeding appendages (Itoh, 1970; Matsuura and Nishida, 2000); they have not been reported in large numbers. The family Aetideidae has the largest number of species (45) in the Southern Ocean, with almost 40% of its species belonging to two genera, *Pseudochirella* and *Gaetanus*; these species also are considered to be carnivores. The combined 80 species of *Paraeuchaeta*, *Euaugaptilus*, and Aetideidae, then, represent a significant contribution to carnivory in the Southern Ocean and so are believed to play a major role in the dynamics of the deepwater plankton community.

The Scolecitrichidae is the next most speciose family after Aetideidae. Among the 35 species of Scolecitrichidae, those in the genera *Scolecithricella* and *Scaphocalanus* make up 45% of the family in the Southern Ocean. Although the feeding niche of most species of Scolecitrichidae is not well known, derived chemosensory setae on maxilla 2 and maxilliped (Nishida and Ohtsuka, 1997) suggest that species of Scolecitrichidae are the major detritivores in the Southern Ocean. In contrast to carnivory and detritivory, herbivory in the Southern Ocean has been studied more extensively (Hardy and Gunther, 1935; Andrews, 1966). The herbivore fauna is structured by large numbers of individuals belonging to a few species in genera of two families: *Calanus* (three species) and *Calanoides* (one species) in Calanidae and *Eucalanus* (one species) and *Rhincalanus* (one species) in Eucalanidae.

Phylogenetic relationships among the congeneric species of the Southern Ocean have been proposed for two families that have been studied worldwide, Euchaetidae and Heterorhabdidae. Six monophyletic groups of species (species groups) of *Paraeuchaeta* have been identified (Park, 1995). One or more species in five of the six species groups of *Paraeuchaeta* are found in the Southern Ocean. One species group, the *antarctica* species group, consists of five species, and all of its species are limited to waters south of the Antarctic Convergence; this is the only species group of either family that is found only in the Southern Ocean. Three species in the *antarctica* species group of *Paraeuchaeta* appear to be restricted to waters along the edge of ice shelf of Antarctica, and all five may share



this same inshore habitat (Fontaine, 1988). Species of the *antarctica* species group are assumed to have evolved after the colonization of the Southern Ocean by a common ancestor (see the Evolution of the Pelagic Calanoid Fauna within the Southern Ocean section). Each species of *Paraeuchaeta* in the remaining four species groups represented in the Southern Ocean has its closest relative in other oceans, rather than the Southern Ocean, suggesting that the remaining species of *Paraeuchaeta* may have colonized the Antarctic region independently.

The family Heterorhabdidae is represented in the Southern Ocean by three genera, *Heterorhabdus*, *Heterostylites*, and *Paraheterorhabdus*. There are five species in the first genus; a single species in each of the last two genera is found in the Southern Ocean (Park, 2000). Four of the five species of *Heterorhabdus* belong to the same species group, the *abyssalis* species group, with 17 species. Two of the four species of this group, *H. spinosus* and *H. paraspinosus*, are morphologically quite similar, suggesting a recent speciation event within the Southern Ocean. The remaining two *Heterorhabdus* species of the *abyssalis* species group, *H. austrinus* and *H. pustulifer*, are morphologically dissimilar; they may have colonized the Southern Ocean independently from one another and from the pair *H. spinosus* and *H. paraspinosus*. The fifth species, *H. lobatus*, belongs to the *papilliger* species group along with five other species found in other oceans; along with *Paraheterorhabdus farrani* and *Heterostylites nigrotinctus*, *H. lobatus* represents an independent colonization.

### INSHORE CALANIDS ALONG CONTINENTAL AND INSULAR COASTS OF THE SOUTHERN OCEAN

Eight species of pelagic calanoids have been found exclusively in waters close to a land mass of the Southern Ocean (Table 1): three species of *Drepanopus* (*D. bispinosus*, *D. forcipatus*, and *D. pectinatus*), three species of *Paralabidocera* (*P. antarctica*, *P. grandispina*, and *P. separabilis*), and two species of *Stephos* (*S. longipes* and *S. antarcticus*). The three species of *Drepanopus* have been collected several times, and all three occasionally have been collected in very large numbers, so their distribution is well known. *Drepanopus bispinosus* has been reported, often as abundant, from inshore waters adjacent to the Vestfold Hills region of Antarctica (Bayly, 1982), and its population structure has been established (Bayly, 1986). *Drepanopus pectinatus* occurs close to shores of Crozet Island, Kerguelen Island, and

**TABLE 1.** Inshore pelagic calanoid copepods of the southern ocean. Ant, waters south of the Antarctic Convergence; S-Ant, waters between the Antarctic Convergence and the Subantarctic Convergence; CC, very common (over 100 specimens found); C, common (between 99 and 50 specimens found); R, rare (between 49 and 10 specimens found).

Species name	Distribution	Abundance
<i>Drepanopus bispinosus</i>	Ant	CC
<i>Drepanopus forcipatus</i>	S-Ant	CC
<i>Drepanopus pectinatus</i>	S-Ant	CC
<i>Paralabidocera antarctica</i>	Ant	C
<i>Paralabidocera grandispina</i>	Ant	R
<i>Paralabidocera separabilis</i>	Ant	R
<i>Stephos longipes</i>	Ant	C
<i>Stephos antarcticus</i>	Ant	R

Heard Island in the Indian Ocean sector of the Southern Ocean (Hulsemann, 1985a); some aspects of its biology also have been elucidated (Razouls and Razouls, 1990). *Drepanopus forcipatus* is restricted to Atlantic and Pacific coastal and shelf areas along southern South America, including the Falkland Islands, and around South Georgia Island (Hulsemann, 1985a); its copepodid stages have been described (Hulsemann, 1991).

The distributions of the remaining five inshore species are not as well known, and only *Paralabidocera antarctica* and *Stephos longipes* have been reported from more than one locality. *Paralabidocera antarctica* is now known to occur in small numbers in waters close to the shoreline at several locations, including the South Shetland Islands, the extreme south of the Ross Sea, two localities in the Atlantic Ocean sector of Antarctica, and one locality in the Indian Ocean sector of Antarctica (Vervoort, 1957). The species is believed to inhabit the surface water layers and is occasionally captured under the ice (Vervoort, 1951); development of its marine and lacustrine populations has been described (Swadling et al., 2004). *Paralabidocera grandispina* Waghorn, 1979 and *P. separabilis* Brodsky and Zvereva, 1976 are known only from their type localities, beneath the ice along the Pacific Ocean sector of Antarctica and near the shore of Antarctica in the Indian Ocean sector, respectively.

Of the two species of *Stephos*, *S. longipes* has been found close to or under the ice shelf in the Pacific and Indian ocean sectors of Antarctica including the Ross Sea, where it can be very abundant (Giesbrecht, 1902; Farran, 1929; Tanaka, 1960). Its associations with the ice and the open water have been described (Kurbjewit et al., 1993;

Schnack-Schiel et al., 1995). *Stephos antarcticus* is known only from its type locality, McMurdo Sound of the Ross Sea (Wolfenden, 1908). Most species of the genus *Stephos* are closely associated with the water immediately above the seafloor (Bradford-Grieve, 1999).

Among these eight species, the three species of *Drepanopus* and the three species of *Paralabidocera* clearly seem to be pelagic. The two species of *Stephos* appear to be ice oriented but are considered pelagic here. All of these inshore species are characteristically small in size, ranging from 0.85 to 2.80 mm in body length.

### EPIPELAGIC FAUNA OF THE SOUTHERN OCEAN

The epipelagic calanoid fauna of the Southern Ocean south of the Antarctic Convergence (Table 2) is relatively simple in species composition. There are five species, all are very common, and their combined biomass is unsurpassed by the epipelagic calanoid fauna of any other region of the world's oceans (Foxton, 1956). These five epipelagic species are, in order of abundance, *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus*, *Metridia gerlachei*,

and *Clausocalanus laticeps*. These are the copepods most often associated by planktonologists with the Southern Ocean. All were discovered during the early expeditions, and their taxonomy and distribution have been clearly and carefully defined. Although these five species are more abundant in waters south of the Antarctic Convergence, they also may be collected north of the convergence, but here they appear to be associated with the deeper Antarctic Intermediate Water. *Calanoides acutus* and, to a lesser extent, *Rhincalanus gigas* and *Calanus propinquus* are the dominant herbivores south of the Antarctic Convergence, and their role in that ecosystem is well known (Chiba et al., 2002; Pasternak and Schnack-Schiel, 2001).

The analogous epipelagic calanoids of the subantarctic region, between the Antarctic and Subtropical convergences, are *Calanus simillimus*, *Clausocalanus brevipes*, and *Ctenocalanus citer*. These three herbivores are very common in the subantarctic region, but they are not as numerous in these waters as the previous five epipelagic calanoids are south of the Antarctic Convergence. Furthermore, the Antarctic Convergence does not limit the southern boundary of the range of these three species as precisely as it limits the northern boundary of the previous five epipelagic calanoids. The population structure and life histories of the three have been described (Atkinson, 1991; Schnack-Schiel and Mizdalski, 1994).

There are three additional large-sized, epipelagic herbivores that may be collected in the subantarctic region as well as in the south temperate midlatitudes: *Calanus australis*, *Neocalanus tonsus*, and *Subeucalanus longiceps*. *Calanus australis* is known to be distributed along the southern coast of Chile, off Argentina, in New Zealand waters, and in southeastern Australian waters (Bradford-Grieve, 1994). Its distribution during summer has been investigated (Sabatini et al., 2000). *Neocalanus tonsus* is widely distributed in subantarctic waters but also may be found in the deepwater of the south temperate region; some aspects of its life history are known (Ohman et al., 1989). *Subeucalanus longiceps* (Subeucalanidae) occurs circumglobally in the subantarctic and temperate regions of the Southern Hemisphere. These three species are important herbivores in the subantarctic as well as the south temperate region.

Two small-sized, epipelagic herbivores, *Clausocalanus parapergens* and *Ctenocalanus vanus*, are found in subantarctic waters. *Clausocalanus parapergens* has been reported as far north as the subtropical convergence (Frost and Fleminger, 1968). Specimens referred to as *Ctenocalanus vanus* from the Southern Ocean by Farran (1929) and Vervoort (1951, 1957) are *Ctenocalanus citer* (T. Park,

**TABLE 2.** Epipelagic calanoid copepods of the Southern Ocean. CC, very common (over 100 specimens found); C, common (between 99 and 50 specimens found).

Species name	Abundance
Species endemic to Antarctic waters	
<i>Calanoides acutus</i>	CC
<i>Calanus propinquus</i>	CC
<i>Clausocalanus laticeps</i>	CC
<i>Metridia gerlachei</i>	CC
<i>Rhincalanus gigas</i>	CC
Species endemic to subantarctic waters	
<i>Calanus simillimus</i>	CC
<i>Clausocalanus brevipes</i>	CC
<i>Ctenocalanus citer</i>	C
Species ranging from subantarctic water to south temperate region	
<i>Calanus australis</i>	C
<i>Neocalanus tonsus</i>	C
<i>Subeucalanus longiceps</i>	C
Species ranging from subantarctic waters to north temperate region	
<i>Eucalanus hyalinus</i>	C
<i>Rhincalanus nasutus</i>	C

unpublished observations); this species is restricted to the Southern Ocean.

Calanids like *Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus*, *Calanus australis*, and *Neocalanus tonsus* as well as eucalanids like *Rhincalanus gigas* and subeucalanids like *Subeucalanus longiceps* are considered epipelagic here because they spend their juvenile and adult life in near-surface waters. However, during seasonal episodes of low primary productivity, some late juvenile stages of the populations of each of these species descend to mesopelagic depths (Vervoort, 1957) to diapause.

Two epipelagic calanoid species, *Eucalanus hyalinus* and *Rhincalanus nasutus*, do not occur in large numbers in the subantarctic region. North of the Subtropical Convergence, they often are encountered in warmer waters, and they have been collected in the north temperate region. Their taxonomy and distribution are well understood. Usually, only a few specimens are collected in pelagic samples from the Southern Ocean, and here these species are considered to be associated with habitats of low primary productivity.

In summary, 13 calanoid species contribute to the epipelagic fauna of the Southern Ocean. Five of them are endemic south of the Antarctic Convergence and are very common throughout this region. Three species are endemic to the subantarctic region and occur throughout that region. However, the subantarctic endemics are not as numerous as the five species endemic to the Antarctic region in midwater trawl samples. Three more epipelagic calanoid species occur widely in the subantarctic and temperate regions of the Southern Hemisphere. They are either common in productive coastal upwelling areas or are circumglobal in the West Wind Drift of the Southern Hemisphere. The broadest latitudinal range exhibited by subantarctic epipelagic calanoids is that of the two species of Eucalanidae that have been collected from the subantarctic region to the north temperate region.

## DEEPWATER CALANIDS RESTRICTED TO THE SOUTHERN OCEAN

Among the 184 species of deepwater calanoids found in the Southern Ocean, 50 species were originally described from the Southern Ocean and, to date, are known exclusively from there (Table 3). Twenty-four of these deepwater calanoids originally were described from waters south of the Antarctic Convergence and subsequently have been found exclusively in those waters; they are endemics of the Antarctic region. Of these 24 Antarctic endemics, six

species have a distinctly localized distribution, occurring almost exclusively along the ice edge of Antarctica. There are four closely related species of the *antarctica* species group of *Paraeuchaeta*, plus one species each of *Aetideopsis* and *Chiridiella*. All six species have strongly built bodies and limbs and a well-sclerotized exoskeleton; they are presumed to be carnivores. *Chiridiella megadactyla* was described from a single female collected close to the edge of the Ross Ice Shelf and has not been found again. *Aetideopsis antarctica*, a rare species, was collected initially from waters beneath the edge of the Ross Ice Shelf (Wolfenden, 1908); it subsequently has been found several other times from the same habitat. Three of the four species of the *antarctica* species group of *Paraeuchaeta*, *P. austrina*, *P. erebi*, and *P. tycodesma*, have also been reported only a few times and collected only in small numbers. *Paraeuchaeta similis*, the fourth species of the group, has occasionally been reported to be quite common under the ice (Bradford, 1981), unlike the above three congeners of its species group, which are rare. However, *P. similis* also may be collected in the deeper layer of warm water (Vervoort, 1965b), well away from the ice edge. Here it occasionally may co-occur with *P. antarctica* (see Ferrari and Dojiri, 1987), the fifth species of the group (Fontaine, 1988; Park, 1995). The three ice edge species of *Paraeuchaeta*, together with *P. similis* and *P. antarctica*, a species endemic to and abundant throughout Antarctic and the subantarctic regions (Park, 1978; Marín and Antezana, 1985; Ferrari and Dojiri, 1987), form the group of closely related species. Despite this close relationship, all five of these species have been collected a number of times in the same midwater trawl from waters adjacent to the ice edge.

Four other species, *Batheuchaeta antarctica*, *B. pubescens*, *Pseudochirella formosa*, and *Onchocalanus subcristatus*, were initially described from deep water south of the Antarctic Convergence. All have been collected only once, and each is known only from one or two specimens. The first three are aetideids and are presumed to be carnivores; the last belongs to Phaennidae, a family of detritivores related to the Scolecitrichidae. These four species and the earlier mentioned *Chiridiella megadactyla* remain so poorly known that their taxonomic status and distribution cannot be confirmed.

Among the 24 species endemic to the Antarctic region, the remaining 14 species have been collected widely south of the Antarctic Convergence and, except for *Euaugaptilus austrinus* and *Landrumius antarcticus*, are either common or very common, so their taxonomy and distribution have been well established. Among them are three species of small calanoid copepods, *Scaphocalanus vervoorti*,

TABLE 3. Abundances of deepwater calanoid species endemic to the Southern Ocean. CC, very common; C, common; R, rare; RR, very rare.

Species name	Abundance	Species name	Abundance
Species occurring along the ice edge of Antarctica (6 spp.)		Species occurring in both Antarctic and subantarctic waters (19 spp.)	
<i>Aetideopsis antarctica</i>	R	<i>Aetideus australis</i>	C
<i>Chiridiella megadactyla</i>	R	<i>Candacia maxima</i>	R
<i>Paraeuchaeta austrina</i>	R	<i>Cephalophanes frigidus</i>	C
<i>Paraeuchaeta erebi</i>	R	<i>Heterorhabdus pustulifer</i>	C
<i>Paraeuchaeta similis</i>	C	<i>Heterorhabdus austrinus</i>	C
<i>Paraeuchaeta tycodesma</i>	R	<i>Heterostylites nigrotinctus</i>	R
Species occurring widely in Antarctic waters (14 spp.)		<i>Metridia pseudoasymmetrica</i>	R
<i>Euaugaptilus antarcticus</i>	CC	<i>Paraeuchaeta antarctica</i>	CC
<i>Euaugaptilus austrinus</i>	R	<i>Paraeuchaeta biloba</i>	CC
<i>Euchirella rostromagna</i>	CC	<i>Paraeuchaeta dactylifera</i>	C
<i>Haloptilus ocellatus</i>	CC	<i>Paraeuchaeta parvula</i>	C
<i>Landrumius antarcticus</i>	R	<i>Paraeuchaeta rasa</i>	CC
<i>Onchocalanus magnus</i>	C	<i>Paraheterorhabdus farrani</i>	C
<i>Onchocalanus wolfendeni</i>	C	<i>Pleuromamma antarctica</i>	C
<i>Paraeuchaeta eltaninae</i>	C	<i>Pseudochirella mausoni</i>	C
<i>Scaphocalanus antarcticus</i>	CC	<i>Scaphocalanus farrani</i>	CC
<i>Scaphocalanus subbrevicornis</i>	CC	<i>Scaphocalanus parantarcticus</i>	CC
<i>Scaphocalanus verwoorti</i>	CC	<i>Scolecithricella dentipes</i>	CC
<i>Scolecithricella cenotelis</i>	CC	<i>Scolecithricella schizosoma</i>	CC
<i>Scolecithricella verwoorti</i>	C	Species endemic to subantarctic waters (7 spp.)	
<i>Spinocalanus terranova</i>	C	<i>Aetideopsis tumorosa</i>	R
Species known from 1 or 2 specimens in Antarctic waters (4 spp.)		<i>Bathycalanus eltaninae</i>	R
<i>Batheuchaeta antarctica</i>	RR	<i>Bathycalanus unicornis</i>	R
<i>Batheuchaeta pubescens</i>	RR	<i>Bradycalanus enormis</i>	R
<i>Onchocalanus subcristatus</i>	RR	<i>Bathycalanus inflatus</i>	R
<i>Pseudochirella formosa</i>	RR	<i>Bradycalanus pseudotypicus</i>	R
		<i>Candacia cheirura</i>	C

*Scolecithricella cenotelis*, and *Scaphocalanus subbrevicornis*, that may occur in particularly large numbers in waters close to continent, where they may be encountered in relatively shallow water (Park, 1980, 1982). These small, abundant species all belong to the family Scolecitrichidae and are presumed to be detritivores. Two other small, common, pelagic calanoids, *Scolecithricella verwoorti* and *Spinocalanus terranova*, are found exclusively in the Antarctic region but in relatively smaller numbers than the first three. The former is a scolecitrichid. *Spinocalanus terranova* belongs to the Spinocalanidae; its trophic niche is not known.

Of the remaining nine deepwater species restricted to waters south of the Antarctic Convergence, all are relatively large calanoids. They can be divided into two groups. Four species are very common; in order of the number of specimens collected they are *Euchirella rostromagna*, *Haloptilus ocellatus*, *Scaphocalanus antarcticus*, and *Euaugaptilus antarcticus*. Three species are common, *Onchocalanus wolfendeni*, *Paraeuchaeta eltaninae*, and *Onchocalanus*

*magnus*, and two species are rare, *Euaugaptilus austrinus* and *Landrumius antarcticus*. These large species are taxonomically diverse and belong to five calanoid families (Appendix 2).

There are 19 endemic species of calanoid copepods that have been found in both the Antarctic and the subantarctic regions, i.e., south of the Subtropical Convergence. Most prominent among them are five species of *Paraeuchaeta*: *P. antarctica*, *P. biloba*, *P. rasa*, *P. parvula*, and *P. dactylifera*. *Paraeuchaeta antarctica* and *P. rasa* are among the most abundant carnivorous calanoids of the Southern Ocean. They are usually encountered south of the Antarctic Convergence but may be collected in small numbers to the north in open waters; *P. antarctica* has also been reported as far north as the Chilean fjords (Marín and Antezana, 1985). *Paraeuchaeta biloba* can be collected immediately adjacent to, and on either side of, the Antarctic Convergence. A unique record of the co-occurrence of these three species of *Paraeuchaeta* is from a deep midwater trawl sample (0–1,295 m) taken

off Uruguay (34°43'S, 49°28'W to 34°51'S, 49°44'W) in the southwestern Atlantic north of the Subtropical Convergence (Park, 1978).

*Paraeuchaeta parvula*, like *P. biloba*, has also been collected both north and south of the Antarctic Convergence. *Paraeuchaeta dactylifera* has only been found in relatively small numbers and usually in the subantarctic region; two specimens captured well south of the Antarctic Convergence (Park, 1978) are exceptions. Two aetideid species, *Aetideus australis* and *Pseudochirella mawsoni*, can also be found both north and south of the Antarctic Convergence. *Aetideus australis* has been collected more often in waters north of the convergence than south. *Pseudochirella mawsoni* has been reported from numerous localities in the Southern Ocean and has been collected in large numbers in midwater trawls immediately north of convergence. Both species are presumed to be carnivores.

Four very common scolecitrichid species are endemic to the Southern Ocean. *Scolecithricella dentipes* and *Scaphocalanus farrani* are found throughout the Antarctic and subantarctic regions, where they may be numerous in some samples. *Scaphocalanus parantarcticus* and *Scolecithricella schizosoma* are also distributed throughout the Southern Ocean and may be very common but are found in smaller numbers than the first two.

There are four species of the family Heterorhabdidae that are well-known endemics of the Southern Ocean: *Heterorhabdus pustulifer*, *H. austrinus*, *Heterostylites nigrotinctus*, and *Paraheterorhabdus farrani*. *Paraheterorhabdus farrani* is common and has been collected throughout the Southern Ocean; *Heterorhabdus pustulifer* and *H. austrinus* are also common, while *Heterostylites nigrotinctus* is rare. Among the remaining 4 of the 19 endemic species reported from both Antarctic and subantarctic regions, three rare species, *Candacia maxima*, *Cephalophanes frigidus*, and *Metridia pseudoasymmetrica*, and the common *Pleuromamma antarctica* are not often encountered in samples. However, there are enough records to suggest that these species are limited to the Southern Ocean.

There are seven deepwater species that have been found only in the subantarctic region (Table 3). Six of them, *Aetideopsis tumerosa*, *Bathycalanus eltaninae*, *B. unicornis*, *Bradycalanus enormis*, *B. inflatus*, and *B. pseudotypicus*, are known from a few localities and only a few specimens; their distribution cannot be determined with certainty. Of these six species, the latter five belong to the family Megacalanidae; *Aetideopsis tumerosa* is an aetideid. The seventh species, *Candacia cheirura*, has been collected often enough to be considered the only species of Candaciidae restricted to the subantarctic region. It is

common and has been hypothesized to be restricted to mesopelagic waters of the West Wind Drift (Verwoort, 1957), also called the Antarctic Circumpolar Current, which is the dominant circulation feature of the Southern Ocean.

In summary, among the 50 deepwater calanoid copepod species found exclusively in the Southern Ocean, six species occur close to the continent. Although these species have been captured in relatively small numbers, they may have been undersampled due to the difficulty in collecting with a midwater trawl in deepwater close to the continent. Among these six species, the closely related *Paraeuchaeta austrina*, *P. erebi*, and *P. tycodesma*, all members of the *antarctica* species group, appear to be restricted to the same habitat. Of the 18 species found in open waters south of the Antarctic Convergence, four were originally described from one or two specimens collected in a single sample, have not been rediscovered, and remain poorly known. The remaining 14 species can be regarded as typical endemics of the Antarctic deep water. Except for two relatively rare species, they are common or very common in waters south of the Antarctic Convergence. Nineteen of the 50 Southern Ocean deepwater species are typical endemics of the region as a whole, and most of them have been collected from many localities throughout the Southern Ocean. Seven of these species have only been found in the subantarctic region. Their distributions are based on a small number of specimens and therefore are insufficiently known. *Candacia cheirura* is an exception; it is a common endemic of the subantarctic region.

## DEEPWATER CALANIDS FROM ANTARCTIC WATERS REPORTED NORTH OF THE SUBTROPICAL CONVERGENCE

A total of 127 deepwater species of pelagic calanoid copepods have been reported from the Southern Ocean south of the Antarctic Convergence. Twenty-four of those species are limited to this region (see the Deepwater Calanoids Restricted to the Southern Ocean section), and 19 species have been found northward, into the subantarctic region, with their distribution terminating at the Subtropical Convergence. Thus, 43 of these 127 deepwater species collected south of the Antarctic Convergence are endemic to the Southern Ocean.

The remaining 84 species have been reported beyond the Subtropical Convergence to varying degrees. Seven (8%) of these species have been collected in the south temperate region, adjacent to the Southern Ocean (Table 4), and five (6%) species have been collected as far north as

**TABLE 4.** Abundances and locations of deepwater calanoid species collected south of the Antarctic Convergence that occur north of the Subtropical Convergence. 1, south temperate; 2, tropical; 3, north temperate; 4, subarctic; 5, Arctic basin. Abundance in Southern Ocean: CC, very common; C, common; R, rare; RR, very rare. A “+” indicates presence.

Species name	Abundance	Region				
		1	2	3	4	5
Species ranging from Antarctic waters to the south temperate region (7 spp.)						
<i>Euaugaptilus hadrocephalus</i>	RR	+				
<i>Euaugaptilus perasetosus</i>	R	+				
<i>Onchocalanus paratrigoniceps</i>	R	+				
<i>Paraenchaeta regalis</i>	CC	+				
<i>Pseudochirella hirsuta</i>	C	+				
<i>Scolecithricella hadrosoma</i>	R	+				
<i>Scolecithricella parafalcifer</i>	R	+				
Species ranging from Antarctic waters to tropical region (5 spp.)						
<i>Cornucalanus robustus</i>	CC	+	+			
<i>Farrania frigida</i>	R	+	+			
<i>Lucicutia bradyana</i>	R	+	+			
<i>Paraenchaeta abbreviata</i>	R	+	+			
<i>Scaphocalanus major</i>	R	+	+			
Species ranging from Antarctic waters to north temperate region (29 spp.)						
<i>Bathenchaeta lamellata</i>	R	+	+			
<i>Bathenchaeta peculiaris</i>	R	+	+			
<i>Bathycalanus bradyi</i>	R	+	+			
<i>Chiridiella subaequalis</i>	R			+		
<i>Chiridius polaris</i>	R			+		
<i>Cornucalanus chelifer</i>	CC	+	+			
<i>Cornucalanus simplex</i>	R	+	+			
<i>Euaugaptilus bullifer</i>	R	+	+			
<i>Euaugaptilus magna</i>	C	+	+			
<i>Euaugaptilus maxillaris</i>	R	+	+			
<i>Euaugaptilus nodifrons</i>	C	+	+			
<i>Gaetanus antarcticus</i>	R	+	+			
<i>Gaetanus paracurvicornis</i>	R	+	+			
<i>Haloptilus fons</i>	R	+	+			
<i>Haloptilus oxycephalus</i>	CC	+	+			
<i>Lophobrix humilifrons</i>	R	+	+			
<i>Metridia ferrarii</i>	R	+	+			
<i>Onchocalanus cristatus</i>	R	+	+			
<i>Onchocalanus hirtipes</i>	R	+	+			
<i>Onchocalanus trigoniceps</i>	R	+	+			
<i>Scaphocalanus elongatus</i>	C	+	+			
<i>Scolecithricella altera</i>	R	+	+			
<i>Scolecithricella emarginata</i>	CC	+	+			
<i>Scolecithricella obtusifrons</i>	R	+	+			
<i>Scolecithricella ovata</i>	C	+	+			
<i>Talacalanus greeni</i>	R	+	+			
<i>Valdiviella oligarbra</i>	R	+	+			
<i>Valdiviella brevicornis</i>	R	+	+			
<i>Valdiviella insignis</i>	R	+	+			

(continued)



the tropical region. There are records of 29 species (35%) from the Southern Ocean as far north as the north temperate region and reports of 30 species (36%) as far north as the subarctic seas (Table 5). Thirteen species (15%) have been collected as far north as the Arctic Ocean.

Five (71%) of the seven species ranging from the Antarctic region to the south temperate region are rare or very rare (Table 4). *Euaugaptilus hadrocephalus*, *E. perasetosus*, *Onchocalanus paratrigoniceps*, *Scolecithricella hadrosoma*, and *S. parafalcifer* originally were described from a few specimens and have not been collected again; they are poorly known. Two species, *Paraeuchaeta regalis* and *Pseudochirella hirsuta*, have been collected from many localities throughout the subantarctic region, and specimens have been found in small numbers from samples both northward in the south temperate region and southward into Antarctic regions. *Paraeuchaeta regalis*, like its euchaetid congeners, is probably a carnivore; *Pseudochirella hirsuta*, an actideid, is also presumed to be carnivorous on the basis of the size and structure of its feeding appendages.

Of the five Southern Ocean species that have been collected into the deepwater of the tropical region (Table 4), *Farrania frigida*, *Lucicutia bradyana*, *Paraeuchaeta abbreviata*, and *Scaphocalanus major* are rare (80%) and remain poorly known; their records are based on a small number of specimens collected from a few widely separated localities. Only one of the five species, *Cornucalanus robustus*, occurs throughout the Southern Ocean; Park (1983b) recovered it from 37 deepwater stations in the Antarctic and subantarctic regions. Vervoort (1965a) identified five specimens, including two juvenile copepods in the deep water of the Gulf of Guinea in the tropical Atlantic, and this remained the only record from outside the Southern Ocean until Björnberg (1973) reported it in the southeastern Pacific Ocean.

All 29 Southern Ocean species collected as far north as the north temperate region (Table 4) appear to be bathypelagic, found between 1,000 and 4,000 m. Twenty-two (76%) of these are rare in the Southern Ocean. Among the remaining seven species, six are either common or very common (number in the parenthesis is the number of specimens found in the Southern Ocean): *Haloptilus oxycephalus* (388), *Scolecithricella emarginata* (226), *Cornucalanus chelififer* (111), *Scolecithricella ovata* (76), *Euaugaptilus nodifrons* (71), and *Scaphocalanus elongatus* (63). *Scolecithricella emarginata* and *Cornucalanus chelififer* are very common in the Southern Ocean. *Haloptilus oxycephalus* is very common and *Euaugaptilus nodifrons* is common in the Southern Ocean, but only a few specimens of either species have been collected in the subantarctic, south temperate, or tropical regions. *Scolecithricella ovata* and *Scapho-*

*calanus elongatus* are common in the subantarctic region. Forty-four specimens of the seventh species, *Euaugaptilus magnus*, have been recovered from the Southern Ocean, but most of these are from the subantarctic region. It is categorized here as rare but is still better represented than the other 22 rare species.

Thirty species reported from Antarctic region also have been collected in the subarctic region (Table 4). All of them are bathypelagic, and 87% are rare. The remaining four species are common or very common in the Southern Ocean (number in the parenthesis is the number of specimens found in the Southern Ocean by T. Park): *Scolecithricella minor* (1,728), *Racovitzanus antarcticus* (1,077), *Scolecithricella valida* (74), and *Pseudochirella obtusa* (52). A greater number of specimens of *Scolecithricella minor* than any other species of this genus was encountered in the Southern Ocean. Specimens were more likely to be collected in water close to the continent, where the species occasionally has been reported from the epipelagic zone. *Racovitzanus antarcticus* is more likely to be encountered in the Antarctic region although it also occurs in waters immediately north of the Antarctic Convergence and beyond. *Scolecithricella valida* was found widely throughout the Southern Ocean. *Pseudochirella obtusa* was recorded from the Antarctic region by Park (1978) as *Pseudochirella polyspina*.

Thirteen species (Table 4) from the Antarctic region have also been collected in the Arctic region (Arctic Ocean basin). They are all bathypelagic, and 77% are rare except for the following three very common species (number in parenthesis is the number of specimens found in the Southern Ocean by T. Park): *Paraeuchaeta barbata* (462), *Gaetanus tenuispinus* (414), and *Gaetanus brevispinus* (150). The northern and southern polar populations of the species now known as *Paraeuchaeta barbata* at one time were considered to be a bipolar species, *Euchaeta farrani* (see Farran, 1929; Vervoort, 1957). Later, *Euchaeta farrani* was synonymized with *Euchaeta barbata* by Park (1978). *Euchaeta barbata* was then considered to have a wide distribution throughout the deep water of the world's oceans, as recorded under that name by Mauchline (1992) and later as *Paraeuchaeta barbata* by Park (1995). Throughout the Southern Ocean, *P. barbata* is very common in deep water. *Gaetanus tenuispinus* is very common south of the Antarctic Convergence. Specimens of the third very common species, *Gaetanus brevispinus* Sars, 1900, were initially described from the Southern Ocean as *Gaidius intermedius* Wolfenden, 1905, but specimens of this species now are considered to belong to *Gaetanus brevispinus* (see Markhaseva, 1996). *Gaetanus brevispinus* is most often encountered in large numbers south of the Antarctic Convergence.



**TABLE 5.** Abundances and locations of subantarctic deepwater calanoid species absent south of the Antarctic Convergence that occur north of the Subtropical Convergence. 1, south temperate; 2, tropical; 3, north temperate; 4, subarctic; 5, Arctic basin. Abundance in Southern Ocean: CC, very common; C, common; R, rare. A “+” indicates presence.

Species name	Abundance	Region				
		1	2	3	4	5
Species ranging from subantarctic to south temperate region (6 spp.)						
<i>Euaugaptilus aliquantus</i>	R	+				
<i>Euaugaptilus brevirostratus</i>	R	+				
<i>Heterorhabdus spinosus</i>	CC	+				
<i>Heterorhabdus paraspinosus</i>	C	+				
<i>Paraeuchaeta exigua</i>	C	+				
<i>Scolecithricella pseudopropinqua</i>	R	+				
Species ranging from subantarctic to tropical region (2 spp.)						
<i>Euchirella similis</i>	R	+	+			
<i>Landrumius gigas</i>	R	+	+			
Species ranging from subantarctic to north temperate region (31 spp.)						
<i>Aetideus arcuatus</i>	R	+	+	+		
<i>Euaugaptilus angustus</i>	R		+	+		
<i>Euaugaptilus gibbus</i>	R		+	+		
<i>Euaugaptilus laticeps</i>	R	+	+	+		
<i>Euaugaptilus oblongus</i>	R			+		
<i>Euchirella rostrata</i>	R	+	+	+		
<i>Gaetanus minor</i>	R	+	+	+		
<i>Gaetanus pileatus</i>	R	+	+	+		
<i>Heterorhabdus lobatus</i>	C	+	+	+		
<i>Lophothrix frontalis</i>	C	+	+	+		
<i>Metridia lucens</i>	R	+	+	+		
<i>Metridia venusta</i>	R	+	+	+		
<i>Paraeuchaeta comosa</i>	R	+	+	+		
<i>Paraeuchaeta pseudotonsa</i>	C	+	+	+		
<i>Paraeuchaeta sarsi</i>	R	+	+	+		
<i>Paraeuchaeta scotti</i>	R	+	+	+		
<i>Pleuromamma abdominalis</i>	R	+	+	+		
<i>Pleuromamma peseki</i>	R	+	+	+		
<i>Pleuromamma quadrungulata</i>	R	+	+	+		
<i>Pleuromamma xiphias</i>	R	+	+	+		
<i>Scaphocalanus cristatus</i>	R			+		
<i>Scaphocalanus echinatus</i>	CC	+	+	+		
<i>Scaphocalanus medius</i>	C		+	+		
<i>Scolecithricella dentata</i>	R	+	+	+		
<i>Scolecithricella profunda</i>	R	+	+	+		
<i>Scolecithricella vittata</i>	R	+	+	+		
<i>Scottocalanus securifrons</i>	C	+	+	+		
<i>Scottocalanus helena</i>	R	+	+	+		
<i>Undeuchaeta major</i>	R	+	+	+		
<i>Undeuchaeta plumosa</i>	R	+	+	+		
<i>Valdiviella minor</i>	R	+	+	+		
Species ranging from subantarctic to subarctic waters (10 spp.)						
<i>Centraugaptilus rattrayi</i>	R	+	+	+	+	
<i>Chirundina streetsii</i>	R	+	+	+	+	
<i>Disseta palumbii</i>	R	+	+	+	+	
<i>Euchirella maxima</i>	R	+	+	+	+	
<i>Gaetanus kruppii</i>	R	+	+	+	+	
<i>Gaetanus latifrons</i>	R	+	+	+	+	
<i>Metridia brevicauda</i>	R	+	+	+	+	
<i>Paraeuchaeta hansenii</i>	R	+	+	+	+	
<i>Scottocalanus thorii</i>	R			+	+	
<i>Undinella brevipes</i>	R			+	+	
Species ranging from subantarctic to Arctic basin (1 sp.)						
<i>Parabeterorhabdus compactus</i>	R	+	+	+		+

In summary, there are 84 species of deepwater calanoid copepods that occur south of the Antarctic Convergence and have also been reported northward to different degrees; 86% of these species have been reported at least as far north as the north temperate region. Two of the seven species occurring from the Antarctic region to the south temperate region are common or very common in the Southern Ocean, while one of the five species found from the Antarctic region north to the tropical region is very common in the Southern Ocean. Seven of the 29 species reported from the Antarctic region and the north temperate region are common or very common in the Southern Ocean. Four of the 30 species from the Antarctic region and reported as far north as the subarctic region are common or very common in the Southern Ocean. Only 3 of the 13 species found in the Arctic Ocean are common or very common in the Southern Ocean. These observations suggest that most (80%) of the rare or very rare deepwater species occurring in the Antarctic region appear to be distributed widely throughout the world's oceans, where they also are rare or very rare deepwater species. However, there are a small number (17) of deepwater species that may be collected in large numbers in the Southern Ocean that are widely distributed and rare or very rare outside of the Southern Ocean.

In contrast to the epipelagic calanoid community, the deepwater pelagic calanoid community of the Southern Ocean is represented by a very diverse group of species. Many of the endemic species collected in the Southern Ocean are common or very common there, apparently having adapted to the high primary and secondary productivity (Park, 1994). Interestingly, a few of the species collected in other regions are also very common in the Southern Ocean, although they are known from only a few specimens throughout the rest of their range. These species appear to be capable of surviving in habitats of low productivity, and yet they can maintain larger populations in some eutrophic habitats like the Southern Ocean. This small number of deepwater species of pelagic calanoid copepods may also be well adapted to high primary and secondary productivity of the Southern Ocean, and this adaptation may result in relatively larger numbers of specimens (Park, 1994).

### **SUBANTARCTIC DEEPWATER CALANOIDS REPORTED NORTH OF THE SUBTROPICAL CONVERGENCE**

Of the 167 deepwater calanoid species found in the subantarctic region, between the Antarctic Convergence and Subtropical Convergence, seven are endemic to that

region; 110 species were also collected south of the Antarctic Convergence. The remaining 50 species are not collected south of the Antarctic Convergence, but their distribution does extend north of the Subtropical Convergence (Table 5). Six species (12%) can be found in the south temperate region, and two (4%) have been collected in the tropical region. There are records of 31 species (62%) in the north temperate region, 10 species (20%) in the subarctic region, and 1 species (2%) from the Arctic basin.

Of the six species ranging from the subantarctic to the south temperate regions, *Heterorhabdus spinosus* is very common, and *H. paraspinosus* and *Paraeuchaeta exigua* are common in the subantarctic region. The two species of *Heterorhabdus* occur together and have been collected from only three other widely separated areas: off the west coast of South Africa, off the southern west coast of Chile, and off the east coast of New Zealand and in the Tasman Sea. *Paraeuchaeta exigua* has been found in four widely separated areas: the eastern and the western parts of the South Atlantic Ocean, the Tasman Sea, and the western Indian Ocean, where it is very common (Park, 1995). These three species apparently are associated with habitats of high secondary productivity, especially coastal upwelling systems. The remaining three species have been found only once and remain poorly known.

Only two species, *Euchirella similis* and *Landrumius gigas*, have been reported from the subantarctic region to the tropical region. They are very rare in the subantarctic region and remain poorly known. All 31 species ranging from the subantarctic region to the north temperate region were originally described from the low or middle latitudes and subsequently have been reported from the subantarctic region. All are believed to be mesopelagic or bathypelagic except for two relatively shallow living species, *Scolecithricella dentata* and *Scolecithricella vitata*. Twenty-five of the species are rare in the subantarctic region, and five species, *Scottocalanus securifrons*, *Paraeuchaeta pseudotonsa*, *Lophothrix frontalis*, *Scaphocalanus medius*, and *Heterorhabdus lobatus*, are common. Only *Scaphocalanus echinatus* is very common in the subantarctic region.

Ten of the subantarctic species have been found as far north as the subarctic region. They are all rare deepwater calanoids. *Paraheterorhabdus compactus* is the only species known to occur from the subantarctic region north to the Arctic basin; it is bathypelagic and occurs in small numbers throughout its range (Park, 2000).

In summary, there are 50 species that are absent south of the Antarctic Convergence but are found in the subantarctic region and northward to varying degrees. Eighty-

four percent of these species have been reported to at least the north temperate region. Eighty-two percent are rare; the exceptions are three of six species occurring in the subantarctic and south temperate regions, where they are common in the productive coastal waters, and 6 of 31 species found from the subantarctic to the north temperate regions. These latter six are common or very common in productive the subantarctic region.

### SOUTHERN OCEAN CALANIDS WITH A BIPOLAR DISTRIBUTION

There are nine pelagic calanoids whose distribution can be described as bipolar (Table 6). *Aetideopsis minor*, *Pseudochirella spectabilis*, and *Spinocalanus antarcticus* are found south of the Antarctic Convergence and in the Arctic basin (Table 4); *Aetideopsis rostrata* and *Pseudochirella batillipa* are found south of the Antarctic Convergence, in the Arctic basin and its adjacent boreal seas (Table 4); *Metridia ornata* and *Racovitzanus antarcticus* are found south of the Antarctic Convergence and in boreal seas adjacent to the Arctic basin (Table 4); *Batheuchaeta peculiaris* and *Chiridius polaris* are found both north and south of the Antarctic Convergence and in boreal seas adjacent to the Arctic basin. Eight of these nine species are rare or very rare deepwater species in both polar areas, and three of those eight have been found in the subarctic region but not in the Arctic Ocean basin. The ninth species, *Racovitzanus antarcticus*, is very common in the waters south of the Antarctic Convergence and has been described as common in the boreal seas adjacent to the Arctic basin (Brodsky, 1950).

Park (1983a) examined specimens of *R. antarcticus* from the northern Pacific Ocean and found that they are identical to those from the Southern Ocean in anatomical details of the exoskeleton. In the Southern Ocean, the number of *R. antarcticus* collected appears to decrease rather abruptly with distance northward from the Antarctic Convergence, and there is some evidence that the species may be found in deeper waters north of the convergence but within the Southern Ocean (Park, 1983a). In the Northern Hemisphere, *R. antarcticus* seems to inhabit the mesopelagic zone (200–1,000 m).

Two hypotheses can be suggested to explain the distribution of *R. antarcticus*. The polar populations may be connected through very deep living populations in the north temperate, tropical, and south temperate regions at depths not adequately sampled to date. This connection would mediate gene flow through the undetected deepwater populations in the temperate and tropical regions and would result in the stable morphological similarity between specimens from the Southern and Northern hemispheres. A similar scenario may explain the apparent bipolar distribution of remaining eight deepwater calanoid copepods that are rare or very rare: at high latitudes they inhabit shallower depths, where individuals can be captured more easily, perhaps because secondary productivity is higher. At lower latitudes, populations are found much deeper and are not as readily collected. The alternate hypothesis is of incipient speciation from a previously more broadly distributed deepwater species that is no longer connected through temperate and tropical deepwater populations (see the Comparative Endemicity of the Southern Ocean Fauna section). Morphological similarity in this case is transitory because the absence of gene flow between the polar populations is expected to result in morphological divergence.

The remaining eight rare species have come to be recognized as having a bipolar distribution in one of three ways. *Aetideopsis minor*, *Chiridius polaris*, *Pseudochirella batillipa*, and *Spinocalanus antarcticus* originally were described from the Southern Ocean and subsequently reported from the Northern Hemisphere. *Spinocalanus antarcticus* was discovered in the Arctic Ocean (Damkaer, 1975), while *Aetideopsis minor*, *Chiridius polaris*, and *Pseudochirella batillipa* recently have been recorded for the first time beyond their type locality, in the Arctic Ocean and adjacent boreal seas (Markhaseva, 1996). Two species, *Batheuchaeta peculiaris* and *Metridia ornata*, originally were described from localities adjacent to the Arctic Ocean; subsequently, they were reported from the Southern Ocean, for the first time outside their type locality, by Markhaseva (1996, 2001). Finally, two species were

TABLE 6. Nine Calanoid species with a bipolar distribution.

Species name	Distribution
<i>Aetideopsis minor</i>	Antarctic (61°–69°S), Arctic basin
<i>Aetideopsis rostrata</i>	Antarctic, Arctic and boreal seas
<i>Batheuchaeta peculiaris</i>	Antarctic (63°S), boreal region (45°–46°N)
<i>Chiridius polaris</i>	Antarctic (53°–68°S), boreal region (44°–46°N)
<i>Metridia ornata</i>	Antarctic (55°–70°S), boreal region (38°–57°N)
<i>Pseudochirella batillipa</i>	Antarctic (53°–66°S), 86°N and 44°–46°N
<i>Pseudochirella spectabilis</i>	Antarctic (61°–68°S), Arctic basin
<i>Racovitzanus antarcticus</i>	Southern Ocean, boreal seas
<i>Spinocalanus antarcticus</i>	Antarctic, Arctic basin

recognized to be bipolar when specimens from southern and northern localities, originally considered different species, subsequently were proposed to be identical. *Aetideopsis inflata*, originally described from the Antarctic region, was synonymized with the subarctic species *Aetideopsis rostrata* (see Markhaseva, 1996), so *Aetideopsis rostrata* is now a bipolar species. Similarly, *Pseudochirella elongata*, also originally described from the Antarctic region, was synonymized with the Arctic species *Pseudochirella spectabilis* (see Markhaseva, 1996); the latter species now has a bipolar distribution. The geographical distribution of these rare species, as inferred from a small number of specimens and from a limited number of localities, however, may not be completely understood.

It is worth noting that some species of pelagic calanoid copepods previously regarded as having disjunct populations in the Southern and Arctic oceans have not subsequently been found to be bipolar. Rather, the northern and southern populations have been recognized as two separate species. As examples, the southern population previously referred to as *Calanus finmarchicus* is now *Calanus australis*; the northern population previously known as *Neocalanus tonsus* is now *Neocalanus plumchrus*; the southern population originally known as *Scaphocalanus brevicornis* is now *Scaphocalanus farrani*. The first two species are epipelagic herbivores; the third is a deepwater detritivore. The taxonomic history of *Paraeuchaeta barbata* is informative but more complex (see the Deepwater Calanoids from Antarctic Waters Reported North of the Antarctic Convergence section). This species originally was described as *Euchaeta farrani* from the Norwegian Sea by With (1915); subsequently, it was recorded from the Antarctic region by Farran (1929) and Vervoort (1957) and proposed by them to be a species with a bipolar distribution. As described more completely above (see the Deepwater Calanoids from Antarctic Waters Reported North of the Antarctic Convergence section), these specimens have been recognized by Park (1995) as belonging to *P. barbata*, a deepwater carnivore, now understood to be distributed throughout the world's oceans.

In summary, taxonomic analyses have reversed initial inferences of a bipolar distribution for *Calanus finmarchicus*, *Neocalanus tonsus*, and *Scaphocalanus brevicornis*. However, taxonomic analyses have established a bipolar distribution for the rare and very rare deepwater species *Aetideopsis rostrata*, *Aetideopsis minor*, *Chiridius polaris*, *Pseudochirella spectabilis*, and *Pseudochirella batillipa*. The distribution of the very common *P. barbata* offers reasons for caution in hypothesizing a bipolar distribution for rare and very rare deepwater species.

## VERY COMMON PELAGIC CALANOIDS AND AREAS OF HIGH PRODUCTIVITY

All of the very common epipelagic calanoids of the Southern Ocean are herbivores (Table 2). In order of abundance, they are *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus*, *Calanus simillimus*, *Metridia gerlachiei*, *Clausocalanus laticeps*, and *Clausocalanus brevipes*. These epipelagic calanoids are endemic to the Southern Ocean and appear to have successfully adapted to the high primary productivity there. The eutrophic conditions there may also be responsible for the high numbers of individuals of these endemic herbivores. The seven epipelagic species together make up the enormous secondary biomass of the Southern Ocean, a secondary biomass that is unsurpassed in any other region of the world's oceans (Foxton, 1956).

Among the deepwater calanoids of the Southern Ocean, there are 26 species (Table 7) from the studies of Park (1978, 1980, 1982, 1983a, 1983b, 1988, 1993) that are represented by more than 100 individuals and are considered very common. A majority, 14 of 26 species, of these very common deepwater calanoids are limited in their distribution to the Southern Ocean. Among the 14 very common deepwater endemic species, eight belong to two genera in the family Scolecitrichidae (five species of *Scaphocalanus* and three of *Scolecithricella*); all are detritivores. These are followed, in order of abundance, by three species of *Paraeuchaeta* in the Euchaetidae.

Twelve very common species are more widely distributed, found northward at varying distances beyond the Subtropical Convergence. Four species have been found as far north as the north temperate region, one has been found in the subarctic region, and three other deepwater species have a range extending into the Arctic Ocean. *Racovitzanus antarcticus* has a bipolar distribution. Most of these very common species, then, are either endemic to the Southern Ocean (14 species) or have a broad distribution extending north of the tropical region (9 species).

Among the 26 common deepwater calanoids of the Southern Ocean, 12 species belong to the family Scolecitrichidae (six species of *Scaphocalanus*, five species of *Scolecithricella*, and one species of *Racovitzanus*). The family is followed, in order of number of species, by the families Euchaetidae, with five species all belonging to the genus *Paraeuchaeta*; Aetideidae, with three species (two of *Gaetanus* and one *Euchirella*); Augaptilidae, also with three species (two *Haloptilus* and one *Euaugaptilus*); Phaennidae, with two species (both *Cornucalanus*); and Heterorhabdidae, with one species belonging to the genus *Heterorhabdus*.

TABLE 7. Very common deepwater calanoid species of the Southern Ocean (26 spp.).

Species name	Number of specimens
Species endemic to the Southern Ocean (14 spp.)	
<i>Euaugaptilus antarcticus</i>	136
<i>Euchirella rostromagna</i>	182
<i>Haloptilus ocellatus</i>	152
<i>Paraeuchaeta antarctica</i>	602
<i>Paraeuchaeta biloba</i>	370
<i>Paraeuchaeta rasa</i>	546
<i>Scaphocalanus antarcticus</i>	130
<i>Scaphocalanus farrani</i>	1,271
<i>Scaphocalanus parantarcticus</i>	289
<i>Scaphocalanus subbrevicornis</i>	188
<i>Scaphocalanus vervoorti</i>	1,936
<i>Scolecithricella cenotelis</i>	929
<i>Scolecithricella dentipes</i>	1,603
<i>Scolecithricella schizosoma</i>	151
Species ranging from the Southern Ocean to south temperate region (2 spp.)	
<i>Paraeuchaeta regalis</i>	109
<i>Heterorhabdus spinosus</i>	243
Species ranging from the Southern Ocean to the tropical region (1 sp.)	
<i>Cornucalanus robustus</i>	161
Species ranging from the Southern Ocean to the north temperate region (4 spp.)	
<i>Haloptilus oxycephalus</i>	388
<i>Scolecithricella emarginata</i>	226
<i>Cornucalanus chelifera</i>	111
<i>Scaphocalanus echinatus</i>	114
Species ranging from the Southern Ocean to the subarctic region (1 sp.)	
<i>Scolecithricella minor</i>	1,728
Species ranging from the Southern Ocean to the Arctic basin (3 spp.)	
<i>Gaetanus brevispinus</i>	150
<i>Gaetanus tenuispinus</i>	414
<i>Paraeuchaeta barbata</i>	462
Species with a bipolar distribution (1 sp.)	
<i>Racovitzanus antarcticus</i>	1,077

The 12 scolecitrichid species together were represented by 9,642 individuals from the Southern Ocean, and the five *Paraeuchaeta* species were represented by 2,089 individuals. Three aetideid species and three augaptilids were represented by 746 and 676 individuals, respectively.

On the basis of the relatively large number of specimens of *Paraeuchaeta*, Aetideidae, Heterorhabdidae, and Augaptilidae that are carnivores, all of these species are presumed to be well adapted to the high secondary productivity resulting from the large populations of epipelagic

herbivores in the Southern Ocean. Species of Scolecitrichidae play a major ecological role as pelagic detritivores in the Southern Ocean, just as species of Scolecitrichidae and related bradfordian families of calanoids play a similar role (detritivory) in the deepwater benthopelagic habitat of other oceans (Markhaseva and Ferrari, 2006). Because of their relatively small body size, scolecitrichids may also serve as a food source for carnivorous calanoids like species of *Paraeuchaeta*, the aetideids, and the augaptilids during periods when the juvenile stages of herbivores are unavailable as prey for these carnivores.

These conclusions are reinforced by restricting observations to the 10 species represented in the Southern Ocean by more than 400 individuals (with number of individuals in parenthesis): *Scaphocalanus vervoorti* (1,936), *Scolecithricella minor* (1,728), *S. dentipes* (1,603), *Scaphocalanus farrani* (1,271), *Racovitzanus antarcticus* (1,077), *Scolecithricella cenotelis* (929), *Paraeuchaeta antarctica* (602), *Paraeuchaeta rasa* (546), *Paraeuchaeta barbata* (462), and *Gaetanus tenuispinus* (414). Four of the scolecitrichid species, *Scaphocalanus vervoorti*, *S. farrani*, *Scolecithricella dentipes*, and *S. cenotelis*, and two of the euchaetid species, *Paraeuchaeta antarctica* and *P. rasa*, are endemic to the Southern Ocean. The range of the very common *Scolecithricella minor* extends into the subarctic region, while *Paraeuchaeta barbata* and *Gaetanus tenuispinus* have been collected as far north as the Arctic basin. The scolecitrichid *Racovitzanus antarcticus* is also among the most common species in the Southern Ocean but exhibits a bipolar distribution, occurring in boreal waters adjacent to the Arctic basin. These 10 very common species either are endemic to the Southern Ocean (*Scaphocalanus vervoorti*, *Scolecithricella dentipes*, *Scaphocalanus farrani*, *Scolecithricella cenotelis*, *Paraeuchaeta antarctica*, and *Paraeuchaeta rasa*) or have a distribution that extends as far north as the subarctic region or Arctic basin (*Scolecithricella minor*, *Racovitzanus antarctica*, *Paraeuchaeta barbata*, and *Gaetanus tenuispinus*). None of the very common deepwater Southern Ocean pelagic calanoids have distributions that extend only to the south temperate region to the tropical region.

Within the Southern Ocean the abundance and distribution of deepwater calanoids are believed to be determined, for the most part, by the availability of food rather than their adaptation to nonbiological environmental parameters such as water temperature (Park, 1994). Whether these eutrophic species are endemics or not, they are restricted to water of high primary and secondary productivity. They can be expected to be common or very common due to their adaptations for exploiting

the available food sources associated with that habitat. In contrast, oligotrophic species in the Southern Ocean are not presumed to be adapted to waters of high productivity. Their distribution is expected to be worldwide because they are capable of surviving at most levels of food resources anywhere in the world's oceans. However, oligotrophic species are expected to be rare or very rare in most regions of the world's oceans. With these constraints, a distribution of common or very common species is expected to be limited to the highly productive Southern Ocean; this is observed about half the time. Fourteen of the 26 common or very common species of the Southern Ocean are endemic.

As noted, among the 10 most numerous of the very common species found in the Southern Ocean, six are endemic. Of the remaining four species represented by more than 400 specimens in the Southern Ocean, *Scolecithricella minor*, *Gaetanus tenuispinus*, and *Paraeuchaeta barbata* have been reported throughout the world's oceans, while *Racovitzanus antarctica* appears to have a bipolar distribution, restricted to the Southern Ocean and to the subarctic region (boreal seas adjacent to the Arctic Ocean). The distribution of *Scolecithricella minor* and *Gaetanus tenuispinus* outside the Southern Ocean is based on literature records. Until these records can be verified by direct comparison of specimens, the relationship of the Southern Ocean specimens to specimens collected elsewhere remains tentative, and we are unable to contribute more to the nature of these distributions.

The distribution of *Paraeuchaeta barbata* has become clearer in recent years and can also be understood within the context of the association of this abundant species with areas of high primary and secondary productivity. The polar populations of *Paraeuchaeta barbata* were once regarded as a separate, bipolar species (see the Deepwater Calanoids from Antarctic Waters Reported north of the Antarctic Convergence section). When Park (1995) restudied the various populations by analyzing a large number of specimens collected throughout the world's oceans, he found that specimens exhibited a considerable but continuous variation in size. As a result of this analysis and an earlier restricted analysis (Mauchline, 1992), body size was rejected as species-specific character state for *P. barbata*.

This considerable and continuous variation in body size of *P. barbata* was subsequently reexamined in association with the distribution of this species (T. Park, unpublished observations). Large-sized individuals occur not only at the high latitudes of both hemispheres but also along the west coast of the Americas in areas associated

with significant coastal upwelling systems. Large individuals also were recorded in the Malay Archipelago and along the east coast of Japan up to Kuril and Kamchatka; these are also seasonally episodic areas of upwelling. Coastal upwelling systems along the west coast of the Americas and the east coast of Japan result in high primary and secondary productivity, which, in turn, may explain the larger-size individuals of *P. barbata* in these areas. The smallest individuals of *P. barbata* are found in the middle of the North Atlantic, an oligotrophic habitat.

Species like *P. barbata*, which are distributed throughout the world's oceans, may have become very common in the Southern Ocean and other areas of seasonally episodic upwelling by taking advantage of the high secondary productivity of eutrophic habitats; individuals of this species are also larger in these habitats as a result of the availability of prey. In contrast, away from areas of high productivity, few specimens are collected, and individuals are smaller in size.

## COMPARATIVE ENDEMICITY OF THE SOUTHERN OCEAN FAUNA

The pelagic calanoid families Euchaetidae and Heterorhabdidae have been studied throughout the world's oceans (Park, 1995, 2000). From these publications, the number of endemic species belonging to these two families from the Southern Ocean can be compared to the number of endemics from three other areas of interest of the world's oceans: Arctic-boreal (including the adjacent boreal seas of the Atlantic and Pacific Oceans), Indo-West Pacific, and eastern Pacific. The Southern Ocean, with 10 endemic species of *Paraeuchaeta*, has the highest number for that genus (Table 8), followed by the Arctic Ocean, with seven endemic species of *Paraeuchaeta*, and the Indo-West Pacific and the eastern Pacific, each with four endemic species. Twenty-three of the 25 endemic species of *Paraeuchaeta* referred to above are bathypelagic; the exceptions are the Indo-West Pacific epipelagic species *Paraeuchaeta russelli* and *P. simplex*.

Six of the 10 Southern Ocean endemics, *P. antarctica*, *P. biloba*, *P. dactylifera*, *P. eltaninae*, *P. parvula*, and *P. rasa*, have been found in large numbers. *Paraeuchaeta australina*, *P. erebi*, and *P. tycodesma* have not been collected in large numbers, but they appear to be restricted to the ice edge along Antarctica. This habitat may not have been adequately sampled with midwater trawls, and as a result, these species may be underrepresented in trawl samples. *Paraeuchaeta similis* and *P. antarctica* have a broader dis-

TABLE 8. Endemic species of *Paraeuchaeta* and Heterorhabdidae found in four different areas of interest. A “+” indicates presence.

Species	Area of interest			
	Southern Ocean	Arctic-boreal	Eastern Pacific	Indo-West Pacific
<i>Paraeuchaeta antarctica</i>	+			
<i>P. austrina</i>	+			
<i>P. biloba</i>	+			
<i>P. dactylifera</i>	+			
<i>P. eltaninae</i>	+			
<i>P. erebi</i>	+			
<i>P. parvula</i>	+			
<i>P. rasa</i>	+			
<i>P. similis</i>	+			
<i>P. tycodesma</i>	+			
<i>P. birostrata</i>		+		
<i>P. brevirostris</i>		+		
<i>P. elongata</i>		+		
<i>P. glacialis</i>		+		
<i>P. norvegica</i>		+		
<i>P. polaris</i>		+		
<i>P. rubra</i>		+		
<i>P. californica</i>			+	
<i>P. copleyae</i>			+	
<i>P. grandiremis</i>			+	
<i>P. papilliger</i>			+	
<i>P. eminens</i>				+
<i>P. investigatoris</i>				+
<i>P. russelli</i>				+
<i>P. simplex</i>				+
<i>Heterorhabdus austrinus</i>	+			
<i>H. pustulifer</i>	+			
<i>H. spinosus</i>	+			
<i>H. paraspinosus</i>	+			
<i>Heterostylites nigrotinctus</i>	+			
<i>Paraheterorhabdus farrani</i>	+			
<i>Heterorhabdus fistulosus</i>		+		
<i>H. norvegicus</i>		+		
<i>H. tanneri</i>		+		
<i>Paraheterorhabdus longispinus</i>		+		
<i>Heterorhabdus abyssalis</i>			+	
<i>H. americanus</i>			+	
<i>H. prolixus</i>			+	
<i>H. quadrilobus</i>			+	
<i>Heterostylites echinatus</i>			+	

tribution within the Southern Ocean, but only *P. antarctica* has been collected in large numbers.

The endemic species of the Arctic Ocean, including adjacent boreal waters, and the endemics of the eastern Pacific have also been found in large numbers. These species are all believed to inhabit waters of high primary and secondary productivity, where endemism may have developed as an adaptation to these eutrophic habitats (Park, 1994). Of the four endemics of the Indo-West Pacific, *Paraeuchaeta russelli* and *P. simplex* are neritic, inhabit-

ing relatively shallow water. *Paraeuchaeta eminens* and *P. investigatoris* are deepwater species. All four species are common in waters of the Malay Archipelago, an area with relatively high primary and secondary productivity. High primary and secondary productivity, rather than a habitats abiological attributes, appears to have been the primary determinant for the evolution of endemism among these species of *Paraeuchaeta*.

Within the family Heterorhabdidae, six species are endemic to the Southern Ocean as compared to five endemic

species in the eastern Pacific. Four species are restricted to the Arctic-boreal area, including three species endemic to the boreal Pacific and one endemic species found in the boreal Atlantic. No endemic species of Heterorhabdidae is found in the Indo-West Pacific. All of the heterorhabdid species discussed here are assumed to be carnivores, with the exception of *Heterostylites echinatus* (see Ohtsuka et al., 1997), and carnivory is assumed to have arisen from suspension feeding within the Heterorhabdidae only once (Ohtsuka et al., 1997).

The highest number of endemic heterorhabdid species, like the number of endemics of *Paraeuchaeta*, is found in the Southern Ocean. However, in contrast to species of *Paraeuchaeta*, of the six Southern Ocean endemic heterorhabdids, only *Heterorhabdus spinosus* is found in large numbers; it is common in coastal waters. Beyond the Southern Ocean, among the four endemic species of the Arctic and boreal seas, *Heterorhabdus norvegicus* is very common in the boreal Atlantic. *Heterorhabdus fistulosus*, *H. tanneri*, and *Paraheterorhabdus longispinus* are very common along the coasts of the boreal Pacific, and all occur in large numbers in some localities. Among the five endemic species of Heterorhabdidae in the eastern Pacific, all are limited in their distribution to waters close to the coasts of Americas, in areas of coastal upwelling, where they have been found in large numbers. One explanation for the different occurrences of *Paraeuchaeta* and heterorhabdid endemics in the Southern Ocean is that the heterorhabdids may be relatively late colonizers of the Southern Ocean; species of *Paraeuchaeta* may already have established themselves as the dominant carnivores before colonization of the Southern Ocean by species of Heterorhabdidae.

In summary, within the two families of pelagic calanoids that have been studied worldwide, the highest number of endemic species is found in the Southern Ocean. All Southern Ocean endemics of *Paraeuchaeta* are found in large numbers, except for *P. similis* and three species found near the ice edge adjacent to Antarctica where these ice edge species may have been undersampled. In contrast, the six endemic species of Heterorhabdidae found in the Southern Ocean are rare. However, beyond the Southern Ocean the endemics of both families of carnivores are associated with the waters of high primary and secondary productivity, where they may be collected in large numbers. On the basis of these observations, the endemism of many of the very common bathypelagic calanoids of the Southern Ocean, like the endemism of Southern Ocean epipelagic calanoids, is suggested to have resulted from the adaptation to conditions of high primary and secondary productivity.

## EVOLUTION OF THE PELAGIC CALANOID FAUNA WITHIN THE SOUTHERN OCEAN

Among the 184 deepwater calanoid species found in the Southern Ocean, 50 species (27%) occur exclusively in the Southern Ocean; 20 of those species (40%) are rare or very rare (Table 3). Several factors may be responsible for the evolution of the deepwater pelagic calanoid fauna, restraining their dispersal throughout the deepwater of the world's oceans and selecting for this endemism. Water temperature, as represented by the rather abrupt changes at the Antarctic Convergence or the Subtropical Convergence, is unlikely to affect the structure or the distribution of the deepwater calanoids because water temperatures below 1,000 m are uniformly cold within the Southern Ocean, and this uniformly cold deepwater is continuous with the deepwater of the adjacent Pacific, Atlantic, and Indian oceans. The proposed relationship between habitat productivity and endemism may be a more useful initial condition. The majority (60%) of deepwater endemic species of the Southern Ocean are common or very common. As mentioned earlier, this may be the product of the high primary and secondary productivity of the Southern Ocean, especially south of the Antarctic Convergence, resulting in the evolution and adaptation of an oligotrophic species to this eutrophic habitat. Endemism of deepwater pelagic calanoids in the Southern Ocean, therefore, is hypothesized to have evolved as rare species that are widely distributed in oligotrophic habitats throughout the world's oceans became adapted to exploit high primary and secondary productive habitats (Park, 1994); these adaptations have resulted in an increased population size of the eutrophic species.

A second explanatory condition for the evolution of the pelagic, marine calanoid fauna in the Southern Ocean depends on whether polar species within a single genus are monophyletic, having evolved from a single ancestral species that initially colonized the Southern Ocean, or polyphyletic, with each species having evolved independently from an ancestor distributed outside of the Southern Ocean or by evolving from more than one initially colonized ancestral species. There is evidence that supports this latter model of independent colonizations for Southern Ocean endemic species of the families Euchaetidae and Heterorhabdidae (see the Comparative Endemism of the Southern Ocean Fauna section), although the situation is more complex for the *antarctica* species group of *Paraeuchaeta*.

Further evidence can be found in the phenomenon of sibling species pairs. When morphological details are closely compared, one species often can be found outside the Southern Ocean that is very similar to each Southern



Ocean endemic. These two species, the Southern Ocean endemic and its closest relative outside of the Southern Ocean, are referred to here as a sibling species pair. Fifteen endemics among the 17 sibling species pairs (Figure 1) have an allopatric distribution, rather than being sympat-

ric with its closest relative. In addition, the *antarctica* species group of *Paraeuchaeta* is also allopatric with its most closely related congener, *P. bisinuata*. The only exception is the pair *Haloptilus ocellatus* and *H. oxycephalus*; these two species may be considered allopatric but with a narrow

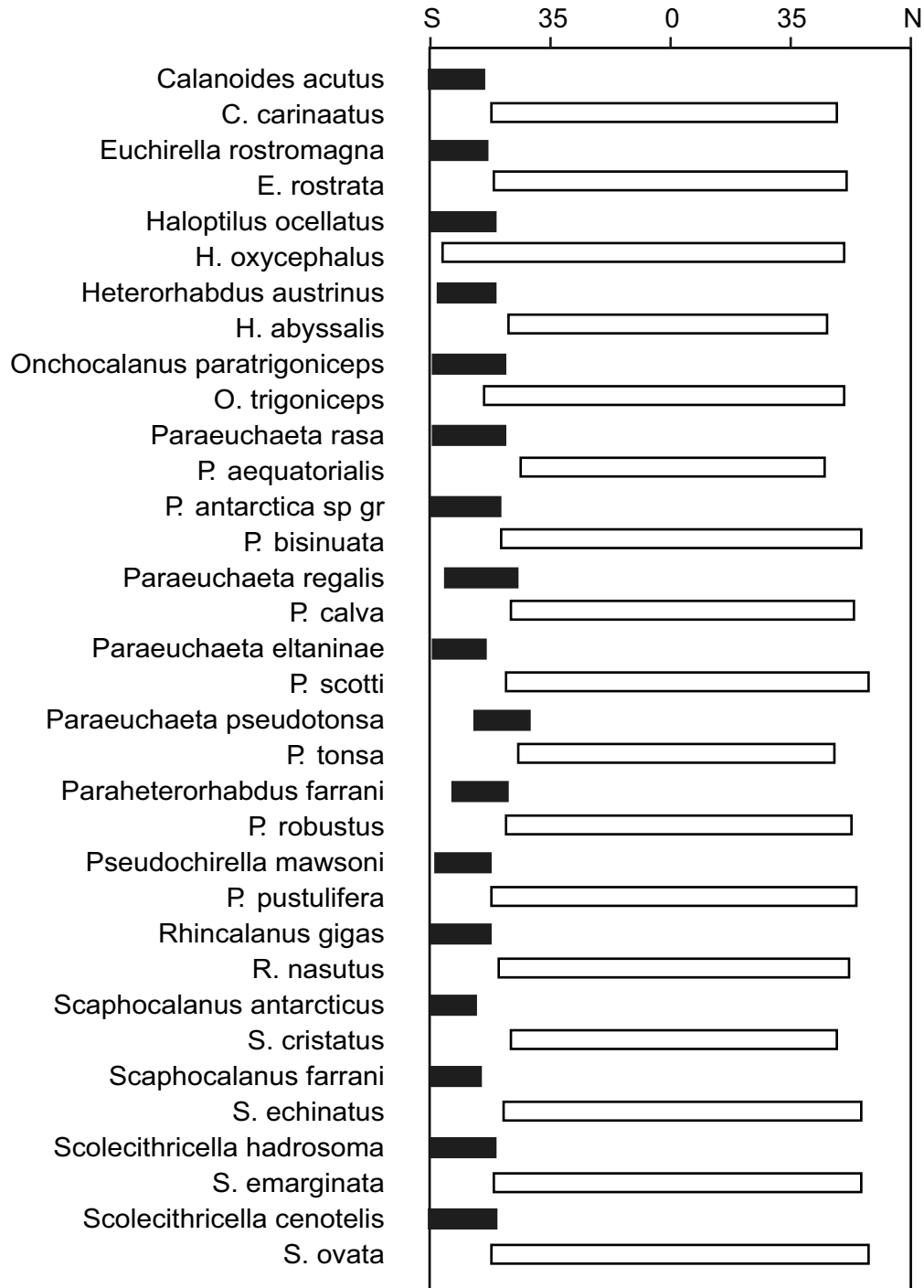


FIGURE 1. Distribution of selected pelagic calanoids of the Southern Ocean and their closest relatives.

zone of overlap. For many common or very common deep-water calanoid species that are endemic to the Southern Ocean (Figure 1, Tables 4, 5), the closest relative is not found in the Southern Ocean, is widely distributed, is rare, and is usually associated with oligotrophic habitats. Examples of these deepwater sibling species pairs (Southern Ocean species first) include (Figure 1) *Euchirella rostromagna* and *E. rostrata*, *Paraeuchaeta pseudotonsa* and *P. tonsa*, *P. antarctica* and *P. bisinuata*, *Scaphocalanus cristatus* and *S. antarcticus*, and *Paraheterorhabdus farrani* and *P. robustus*. The members of some sibling species pairs are so similar to each other morphologically that, originally, they were regarded as the same species, e.g., *Paraeuchaeta tonsa* and *P. pseudotonsa* or *Euchirella rostrata* and *E. rostromagna*. In addition to being more numerous, the Southern Ocean endemics are usually larger in size than their smaller, rare, cosmopolitan counterparts. Between members of the deepwater pairs, the common or very common endemics adapted to the eutrophic habitat of the Southern Ocean are hypothesized to have evolved from a rare widespread species adapted to oligotrophic habitats (Park, 1994). This evolutionary event has resulted in two closely related species, a sibling species pair with the species outside of the Southern Ocean remaining adapted to an oligotrophic environment and the Southern Ocean species adapted to high-productivity habitats. In view of the close morphological similarity between the species of a sibling species pair, this process seems to have a relatively short evolutionary history. However, this hypothesis does not imply that all pairs evolved about the same time.

The situation for *Paraeuchaeta antarctica* appears to be more complicated than a case of a simple sibling species pair. *Paraeuchaeta antarctica* is a very common predator and is morphologically similar to four other endemic species, *P. similis*, *P. austrina*, *P. erebi*, and *P. tycodesma*. These five endemic species make up the *antarctica* species group (Fontaine, 1988). All five of these species can be found to occur sympatrically adjacent to the ice edge of Antarctica. *Paraeuchaeta austrina*, *P. erebi*, and *P. tycodesma* are restricted to this habitat, while *P. antarctica* and *P. similis* may be found throughout the Southern Ocean. The most similar congener, and presumed closest relative, of the *antarctica* species group is *P. bisinuata*. *Paraeuchaeta bisinuata* is a rare deepwater species found in all the world's oceans except the Southern Ocean. *Paraeuchaeta bisinuata* and the common ancestor of the *antarctica* species group are hypothesized to have been a sibling species pair. The common ancestor of the *antarctica* species group is assumed to have colonized the Southern Ocean, eventually adapting and being confined to the eutrophic habitat.

All of its descendants, including *P. austrina*, *P. erebi*, and *P. tycodesma*, which are associated with waters adjacent to the ice edge, and the more broadly distributed *P. similis* and *P. antarctica*, are restricted to the Southern Ocean. *Paraeuchaeta bisinuata*, the cosmopolitan species of the original pair, remains associated with oligotrophic habitats throughout the world's oceans.

To summarize, the evolution of deepwater endemic species of the Southern Ocean can be hypothesized from an ordered set of changes in distribution and subsequent morphological divergence in the following way: (1) beginning with a rare, widely distributed species adapted to oligotrophic habitats, e.g., *Augaptilus glacialis*, (2) a Southern Ocean population becomes associated with its eutrophic habitat and becomes separated from the rare, widely distributed, oligotrophic species; (3) the Southern Ocean endemic population adapts to this eutrophic habitat, and its population size increases. It diverges from the rare, widely distributed, oligotrophic species, resulting in a sibling species pair, e.g., *Scolecithricella farrani* and *S. echinates*.

Another type of species pair identified in this study requires different explanatory conditions about the evolution of the Southern Ocean fauna. A bipolar species pair consists of two morphologically similar species, presumed closest relatives, one that is endemic to the Southern Ocean and a second that is endemic to the Arctic Ocean and adjacent boreal waters. Several endemic species of the Southern Ocean have a morphologically similar congener in the Arctic region (Table 7, Figure 2). The morphological similarities between the members are so close that some of the pairs were recognized as separate species only recently, e.g., the Southern Ocean *Scaphocalanus farrani* was separated from *S. brevicornis* by Park (1982). In general, the number of morphological differences is few and the degree of the morphological divergence is slight between members of these southern and northern oceanic pairs, e.g., *Paraheterorhabdus farrani* and *P. longispinus*, *Scaphocalanus parantarcticus* and *S. acrocephalus*, and *Paraeuchaeta regalis* and *P. polaris*. The extent of the morphological similarity between these polar species suggests that they may have been derived from a common ancestor (see below), although this does not imply that all pairs have evolved about the same time.

The evolution of deepwater bipolar species pairs can be hypothesized from an ordered set of changes in distribution and subsequent morphological divergence in the following way. Beginning with a widely distributed deepwater species with shallow populations in the Southern Ocean and Arctic Ocean, e.g., *Paraeuchaeta barbata*, (1)

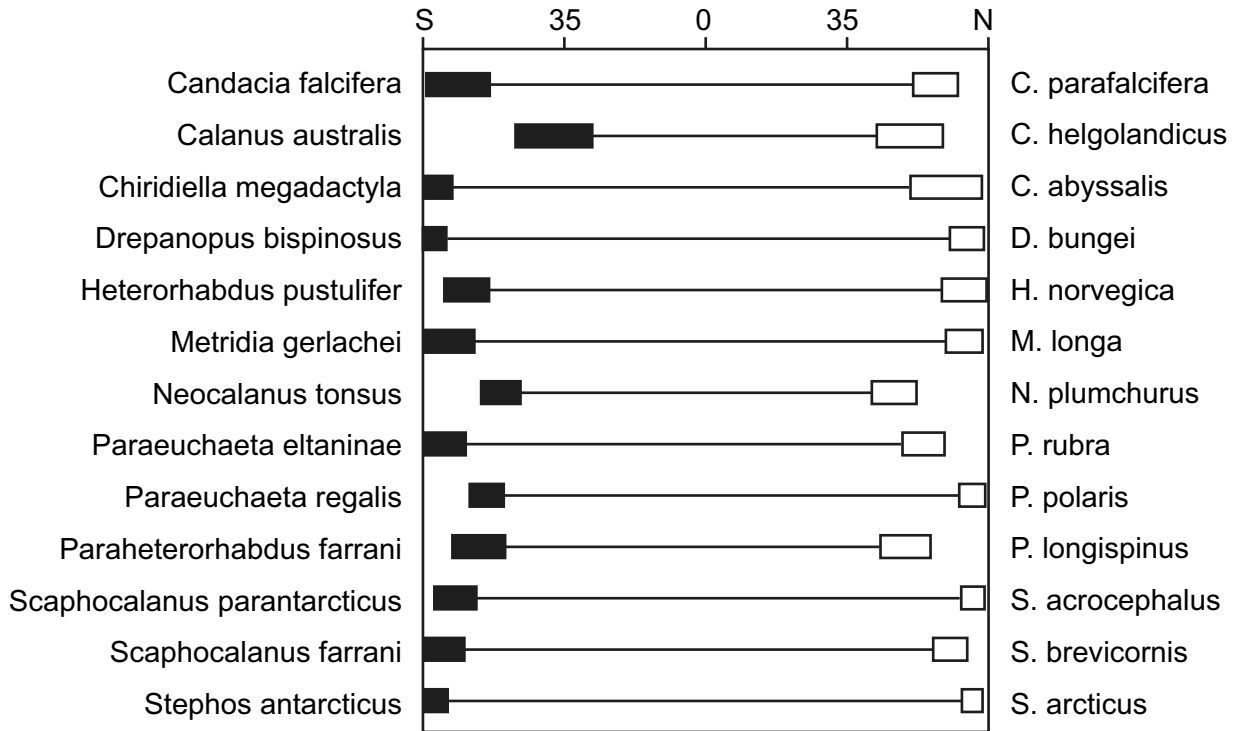


FIGURE 2. Distribution of selected pelagic calanoids of the Southern Ocean and their closest relatives in the subarctic region or the Arctic Ocean.

deepwater middle- and low-latitude populations become extinct over varying periods of time, resulting in a non-uniform distribution, e.g., *Batheuchaeta peculiaris*, (2) complete middle- and low-latitude extinctions eventually result in a species with a bipolar distribution, e.g., *Pseudochirella spectabilis*, and (3) subsequent morphological divergence of the bipolar populations results in a bipolar pair of species, e.g., *Paraeuchaeta regalis* and *P. polaris*.

The evolution of epipelagic calanoids of the Southern Ocean differs in some respects from deepwater pelagic calanoids. Throughout the world's oceans, there are many epipelagic marine calanoids whose distribution is confined to a water mass or current system within an ocean basin and sometimes very narrowly within that basin. Often, such distributions appear to be restricted to a zone of latitudes, although the causes may be related to specific nutrient and temperature regimes (Reid et al., 1978). Epipelagic species from the low or middle latitudes provide many examples of zonally distributed species (Frost and Fleminger, 1968). The circumpolar distributions of the epipelagic endemics of the Southern Ocean, *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus*, *Metridia gerlachei*, *Clausocalanus laticeps*, *Calanus simillimus*, *Clausocalanus bre-*

*vipes*, and *Ctenocalanus citer*, can be interpreted as zonal distributions. The first five are restricted to waters south of the Antarctic Convergence; the last three are restricted to waters south of the Subtropical Convergence and north of the Antarctic Convergence (Table 2). These two sets of epipelagic species may be adapted to the two different zones of cold water bounded by Antarctic Convergence and Subtropical Convergence, as well as by the unique primary productivity of the Southern Ocean.

In the Southern Ocean, the evolution of epipelagic calanoids shares some common attributes with deepwater pelagic calanoids. High primary productivity may have enabled the evolution of epipelagic species; all five endemic epipelagic species found south of the Antarctic Convergence are endemic herbivores utilizing the region's high primary productivity; all are very common. Three of the eight subantarctic epipelagic species are also endemic herbivores and are common or very common. Sibling species pairs can be found among epipelagic species as well as deepwater species, e.g., *Calanoides acutus* and *C. carinatus* or *Rhincalanus gigas* and *R. nasutus*. In contrast to deepwater sibling species pairs, both members of an epipelagic pair often are common or very common (Figure 1).

Epipelagic, bipolar species pairs have also been identified, e.g., *Calanus australis* and *C. helgolandicus* and *Neocalanus tonsus* and *N. plumchrus*.

The evolution of coastal species in the Southern Ocean may reflect processes similar to the model for the deepwater bipolar species pairs. Several species of coastal genera, such as *Drepanopus* and *Stephos*, are present in the Southern Ocean and the Arctic Ocean. However, the morphological differences between the Southern Ocean and the Arctic Ocean members are more extensive than those found between members of the oceanic genera of bipolar species pairs. The Southern Ocean coastal species *Drepanopus pectinatus*, *D. bispinosus*, and *D. forcipatus* and *Stephos longipes* and *S. antarcticus* are readily distinguished from their congeners *D. bungei* and *D. furcatus* and *S. arcticus* and its six relatives in the Arctic Ocean. In contrast, the Southern Ocean species of oceanic genera are difficult to distinguish from their Arctic and boreal congeners because they are very similar morphologically. Apparently, the species of these coastal pelagic genera may have had a different evolutionary history and perhaps a different biogeographical history than the oceanic pelagic calanoid species, although similar processes may have affected both groups. High productivity may have played an important role in the structure of the nearshore fauna because five of eight coastal species endemic to the Southern Ocean (Table 1) are common or very common.

The situation for *Paralabidocera antarctica*, *P. grandispina*, and *P. separabilis* requires further consideration. The genus *Paralabidocera*, an acartiid restricted to the Southern Hemisphere, is one of only five pelagic marine genera that are limited to one of the two hemispheres. The others are *Epilabidocera*, a pontellid, *Eurytemora*, a temorid, *Jashnovia*, an aetideid, and *Pseudocalanus*, a clausocalanid, and these four are limited to the Northern Hemisphere. Species of these genera are found in estuarine or inshore waters or in the neritic zone of the oceans. Each of these genera has a morphologically similar genus, and presumed closest relative (T. Park, unpublished data), distributed broadly throughout the world: species of *Paralabidocera* are similar to those of *Acartia*, species of *Epilabidocera* to *Labidocera*, *Eurytemora* to *Temora*, *Jashnovia* to *Gaetanus*, and *Pseudocalanus* to *Clausocalanus*. As a result, it seems reasonable to assume that the species of *Paralabidocera* have evolved from a cosmopolitan acartiid ancestor. In general, morphological differences between each limited genus and its cosmopolitan relative are not as great as between each limited genus and its remaining confamilial relatives, so that morphological

differences between species of *Paralabidocera* and *Acartia* are not as great as between *Paralabidocera* and species of *Acartiella* and *Paracartia*. The evolution of *Paralabidocera*, then, may be a relatively recent event within the Southern Ocean.

In summary, most genera of pelagic marine calanoid copepods found in the Southern Ocean are also found north of the Southern Ocean; *Paralabidocera*, restricted to the Southern Hemisphere, may be an exception. Many species of pelagic calanoid copepods endemic to the Southern Ocean are common or very common, reflecting their adaptation to the eutrophic environment there. The closest relative of many Southern Ocean species is usually a widely distributed congener adapted to waters of low primary and secondary productivity whose range does not extend into the Southern Ocean. These observations suggest that Southern Ocean endemics evolved from a common oligotrophic ancestor that split into two populations. The widely distributed daughter species retained its adaptation to oligotrophic habitats; the Southern Ocean endemic daughter became adapted to the eutrophic environment of the Southern Ocean. The *antarctica* species group of *Paraeuchaeta* appears to be monophyletic and may have subsequently evolved from a common Southern Ocean eutrophic daughter population after its initial split from an ancestor, similar to *P. bisinuata*, which is associated with oligotrophic habitats. Therefore, most Southern Ocean endemic species appear to have evolved after the Southern Ocean became an area of high primary and secondary productivity. High productivity is assumed to have developed with a strong circumpolar current following the separation of Antarctica from Australia. A hypothesis structuring the benthopelagic calanoid fauna from the divergence in feeding appendages differentially adapted for detritivory (Markhaseva and Ferrari, 2006) shares the same phenomenon, adaptation to diversity in food availability as an evolutionary cause of species diversity.

Another hypothesis to explain the endemism of the Southern Ocean involves species that contribute to bipolar species pairs. These may have evolved from a widely distributed deepwater species with shallow polar populations whose intervening deepwater populations subsequently became extinct, leaving a species with a bipolar distribution. The two populations then diverged. In this model, bipolar species are transient natural phenomena. Finally, this review provides no unequivocal support for zonal distributions for mesopelagic or bathypelagic calanoid species. In general, mesopelagic or bathypelagic calanoids appear to

occur broadly throughout the world's oceans and are unrestricted latitudinally or longitudinally.

## FUTURE CONSIDERATIONS

Seventy-seven pelagic, marine calanoid copepods had been reported from the Southern Ocean prior to 1950. Vervoort (1951, 1957) added 26 species, bringing the total number to 103. A total of 117 calanoid species were known before Park (1978, 1980, 1982, 1983a, 1983b, 1988, 1993, 2000) added 73 species. During this period, a few other authors added several species, so that the total reached 201 species by the end of the century. Recently, three species of *Metridia* and one species of *Lucicutia* have been added (Markhaseva, 2001; Markhaseva and Ferrari, 2005), bringing the total to 205 species.

The midwater trawls employed by the U.S. Antarctic Research Program have been very effective in sampling the large pelagic copepods of the Southern Ocean. There can be very few pelagic species left to be collected with sampling gear of this kind of device. However, fine-mesh samples, less than 100 micrometers, taken with traditional sampling gear like the conical plankton net may add new pelagic species or new records of pelagic species already known from other areas of the world's oceans.

With new sampling methods capable of reaching unexplored habitats, more species of calanoids, many expected to be new to science, can be anticipated to increase the Southern Ocean fauna of calanoid copepods. Waters immediately above the seabed, where new benthopelagic calanoid copepods have only recently been collected and studied carefully, are an example. The diverse fauna of this habitat has been very poorly sampled, and lists of new species and new records are in a growth phase. However, new species and new records of benthopelagic copepods are not expected to effect the conclusions drawn here about pelagic calanoids.

Beginning with the studies by Vervoort (1950, 1951, 1957), the species descriptions available in the literature for the Southern Ocean calanoids have been based on the complete morphology of the exoskeleton. Generally, these descriptions are of excellent quality, and the observations are easily repeatable with newly collected specimens. Most of the species discovered earlier have been redescribed in detail by subsequent authors, making the identification of specimens of those species reliable. However, the zoogeographic distribution of most species, particularly in areas outside of the Southern Ocean, needs significant

attention. Information about the vertical distribution of many species, except for the very common ones, remains insufficient. Finally, the population structure, particularly for nauplii, remains poorly known. These problems can be addressed with contemporary sampling gear but will require the kind of intellectual curiosity which drove the early exploration of the Southern Ocean by the U.S. Antarctic Research Program.

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## APPENDIX 1

This appendix contains a list of pelagic calanoid copepod species, alphabetical by genus and then species, reported from the Southern Ocean. Each species name includes the author and date of publication of the original species description. The author and date entry listed below a species name is the latest taxonomic reference to the species. Abbreviations for distributions are as follows: Ant, Antarctic; sAnt, subantarctic; Stemp, south temperate; Trop, tropical; Ntemp, north temperate; sArc, subarctic; Arc, Arctic.

- Aetideopsis antarctica* (Wolfenden, 1908): Ant  
*Faroella antarctica* Wolfenden, 1908:39, pl. 2, figs. 1–4.  
*Aetideopsis antarctica* Bradford, 1971:18, figs. 31–48.
- Aetideopsis minor* (Wolfenden, 1911): Ant, Arc  
*Faroella minor* Wolfenden, 1911:214.  
*Aetideopsis minor* Park, 1978:115–118, figs. 8–9; Markhaseva, 1996:32, figs. 20–21.
- Aetideopsis multiserrata* (Wolfenden, 1904): Ant, sArc  
*Faroella multiserrata* Wolfenden, 1904:117, pl. 9, figs. 26–28.  
*Aetideopsis multiserrata* Park, 1978:111–115, figs. 6–7; Markhaseva, 1996:37, figs. 22–23.
- Aetideopsis rostrata* Sars, 1903: Ant, sArc, Arc  
*Aetideopsis rostrata* Sars, 1903:160, pls. 4, 5; Markhaseva, 1996:42, figs. 26–28.  
*Aetideopsis inflata* Park, 1978:118–122, figs. 11–12.
- Aetideopsis tumorosa* Bradford, 1969: sAnt  
*Aetideopsis tumorosa* Bradford, 1969:74, figs. 1–28; Park, 1978:118, fig. 10; Markhaseva, 1996:42, fig. 29.
- Aetideus arcuatus* (Vervoort, 1949): sAnt, Ntemp  
*Snelliaetideus arcuatus* Vervoort, 1949:4, fig. 1; Park, 1978:108–111, figs. 4–5.  
*Aetideus arcuatus* Markhaseva, 1996:14, fig. 3.
- Aetideus australis* (Vervoort, 1957): Ant, sAnt  
*Euaetideus australis* Vervoort, 1957:46, figs. 16–19, 20a; Park, 1978:105–108, figs. 2–3.
- Arietellus simplex* Sars, 1905: Ant, sArc  
*Arietellus simplex* Sars, 1905:5, 22; 1925:334, pl. 120, figs. 7–12; Vervoort, 1957:141.
- Augaptilus glacialis* Sars, 1900: Ant, Arc  
*Augaptilus glacialis* Sars, 1900:88, pls. 26, 27; 1925:254, pl. 76, figs. 1–6; Vervoort, 1951:144, figs. 80, 81.
- Batheuchaeta antarctica* Markhaseva, 1986: Ant  
*Batheuchaeta antarctica* Markhaseva, 1986:848, fig. 6; 1996:53, fig. 34.

- Batheuchaeta lamellata* Brodsky, 1950: Ant-Ntemp  
*Batheuchaeta lamellata* Brodsky, 1950:189, figs. 106–107; Markhaseva, 1996:57–58.
- Batheuchaeta peculiaris* Markhaseva, 1983: Ant-Ntemp  
*Batheuchaeta peculiaris* Markhaseva, 1983:1740, fig. 1; 1996:58, figs. 41–42.
- Batheuchaeta pubescens* Markhaseva, 1986: Ant  
*Batheuchaeta pubescens* Markhaseva, 1986:846, fig. 5; 1996:58, fig. 43.
- Bathycalanus bradyi* (Wolfenden, 1905): Ant-Ntemp  
*Megacalanus bradyi* Wolfenden, 1905:1–3, pl. 1, figs. 1–6.  
*Bathycalanus maximus* Wolfenden, 1911:198, pl. 23, figs. 1–7, text fig. 2.  
*Bathycalanus bradyi* Vervoort, 1957:32, fig. 7.
- Bathycalanus eltaninae* Björnberg, 1968: sAnt  
*Bathycalanus eltaninae* Björnberg, 1968:75, figs. 15–41.
- Bathycalanus inflatus* Björnberg, 1968: sAnt  
*Bathycalanus inflatus* Björnberg, 1968:81, figs. 42–54.
- Bathycalanus unicornis* Björnberg, 1968: sAnt  
*Bathycalanus unicornis* Björnberg, 1968:73, figs. 1–14.
- Bradycalanus enormis* Björnberg, 1968: sAnt  
*Bradycalanus enormis* Björnberg, 1968:85, figs. 64–77.
- Bradycalanus pseudotypicus* Björnberg, 1968: sAnt  
*Bradycalanus pseudotypicus* Björnberg, 1968:82, figs. 55–63, 78.
- Calanoides acutus* (Giesbrecht, 1902): Ant  
*Calanoides acutus* Giesbrecht, 1902:17, pl. 1, figs. 10–14; Vervoort, 1951:42, figs. 25–33.
- Calanus australis* Brodsky, 1959: sAnt-Stemp  
*Calanus australis* Brodsky, 1959:1539–1542, pl. 1, figs. 9–12; pl. 2, figs. 4, 8, 10, 11; pl. 3, figs. 11, 13, 14; pl. 4, figs. 8, 9.
- Calanus propinquus* Brady, 1883: Ant  
*Calanus propinquus* Brady, 1883:34, pl. 2, figs. 1–7; pl. 14, figs. 10–11; Vervoort, 1951:27, figs. 14–24.
- Calanus simillimus* Giesbrecht, 1902: sAnt  
*Calanus simillimus* Giesbrecht, 1902:16, fig. 9; Vervoort, 1951:11, figs. 3–14.
- Candacia cheirura* Cleve, 1904: sAnt  
*Candacia cheirura* Cleve, 1904:180, 186, 198, pl. 1, figs. 1–6; pl. 2, figs. 7–10; Farran, 1929:273, fig. 29; Vervoort, 1957:142.
- Candacia falcifera* Farran, 1929: Ant-sArc  
*Candacia falcifera* Farran, 1929:270, fig. 28; Vervoort, 1957:142, fig. 132.
- Candacia maxima* Vervoort, 1957: Ant-sAnt  
*Candacia maxima* Vervoort, 1957:142–144, figs.132–138.
- Centraugaptilus rattrayi* (Scott, 1894): sAnt-sArc  
*Augaptilus rattrayi* Scott, 1894:36, pl. 2, figs. 25–37.  
*Centraugaptilus rattrayi* Sars, 1925:304, pl. 106; Hardy and Gunther, 1935:183.
- Cephalophanes frigidus* Wolfenden, 1911: Ant-sAnt  
*Cephalophanes frigidus* Wolfenden, 1911:284–285, fig. 46; Park, 1983b:321–325, figs. 3–4.
- Chiridiella megadactyla* Bradford, 1971: Ant  
*Chiridiella megadactyla* Bradford, 1971:19–20, figs. 49–60.
- Chiridiella subaequalis* Grice and Hulsemann, 1965: Ant-Ntemp  
*Chiridiella subaequalis* Grice and Hulsemann, 1965:231–235, fig. 10a–l; Markhaseva, 1996:108, fig. 82.
- Chiridius gracilis* Farran, 1908: sAnt-sArc  
*Chiridius gracilis* Farran, 1908:30, pl. 2, figs. 1–3; Park, 1978:122–124, fig. 13; Markhaseva, 1996:111, figs. 83–84.
- Chiridius polaris* Wolfenden, 1911: Ant, Ntemp  
*Chiridius polaris* Wolfenden, 1911:211, text fig. 6, pl. 24, figs. 9–12; Markhaseva, 1996:119, figs. 94–97.  
*Chiridius subantarcticus* Park, 1978:125–127, fig. 14.
- Chirundina streetsii* Giesbrecht, 1895: sAnt-sArc  
*Chirundina streetsii* Giesbrecht, 1895:249, pl. 1, figs. 5–10; Park, 1978:179, figs. 52–53.
- Clausocalanus brevipes* Frost and Fleminger, 1968: sAnt  
*Clausocalanus brevipes* Frost and Fleminger, 1968:70, figs. 56–59.
- Clausocalanus brevipes* Farran, 1929: Ant  
*Clausocalanus laticeps* Farran, 1929:224, fig. 4; Frost and Fleminger, 1968:42, figs. 24–28.
- Cornucalanus chelifer* (Thompson, 1903): Ant-Ntemp  
*Scolecithrix chelifer* Thompson, 1903:21, pl. 5, figs. 1–9; Park, 1983b:352–357, figs. 23–26.
- Cornucalanus robustus* Vervoort, 1957: Ant-Trop  
*Cornucalanus robustus* Vervoort, 1957:88–91, figs. 71–76; Park, 1983:358–363, figs. 27–30.
- Cornucalanus simplex* Wolfenden, 1905: Ant-Ntemp  
*Cornucalanus simplex* Wolfenden, 1905:22; Park, 1983b:364–365, fig. 31.
- Ctenocalanus citer* Heron and Bowman, 1971: sAnt  
*Ctenocalanus citer* Heron and Bowman, 1971:142, figs. 1, 16–18, 31–36, 54–58, 71–77, 94–99, 130–150.  
*Ctenocalanus vanus* Vervoort, 1951:59–61; 1957:37.
- Disseta palumbii* Giesbrecht, 1889: sAnt-sArc  
*Disseta palumbii* Giesbrecht, 1889a:812; 1893:369, pl. 29, figs. 2, 8, 14, 19, 23–25, 27; pl. 38, fig. 44; Park, 2000:14–18, figs. 1–3.
- Drepanopus bispinosus* Bayly, 1982: Ant  
*Drepanopus bispinosus* Bayly, 1982:165, figs. 2a–2h, 3a–3f.
- Drepanopus forcipatus* Giesbrecht, 1888: sAnt  
*Drepanopus forcipatus* Giesbrecht, 1888:335; Hulsemann, 1985:911, figs. 2–4, 6–8, 10, 12, 14, 16–20, 23, 24, 27–29, 32–33.
- Drepanopus pectinatus* Brady, 1883: sAnt  
*Drepanopus pectinatus* Brady, 1883:77, pl. 24, figs. 1–11; Hulsemann, 1985a:910, figs. 1, 5, 9, 11, 13, 15, 21, 22, 25, 26, 30, 31.
- Euaugaptilus aliquantus* Park, 1993: sAnt-Stemp  
*Euaugaptilus aliquantus* Park, 1993:13–14, figs. 7–8.
- Euaugaptilus angustus* (Sars, 1905): sAnt-Ntemp  
*Augaptilus angustus* Sars, 1905:10–11.  
*Euaugaptilus angustus* Sars, 1925:281–282, pl. 91; Park, 1993:27–30, figs. 19–20.
- Euaugaptilus antarcticus* Wolfenden, 1911: Ant  
*Euaugaptilus antarcticus* Wolfenden, 1911:334–336, fig. 70, pl. 36, figs. 6–7; Park, 1993:32–37, figs. 23–25.
- Euaugaptilus austrinus* Park, 1993: Ant  
*Euaugaptilus austrinus* Park, 1993:37–41, figs. 26–28.
- Euaugaptilus brevirostratus* Park, 1993: sAnt-Stemp  
*Euaugaptilus brevirostratus* Park, 1993:19–22, figs. 12–14.
- Euaugaptilus bullifer* (Giesbrecht, 1889): Ant-Ntemp  
*Augaptilus bullifer* Giesbrecht, 1889a:813; 1893:400, pl. 28, figs. 6, 21, 24; pl. 39, fig. 46.  
*Euaugaptilus bullifer* (Giesbrecht, 1889); Park, 1993:22–25, figs. 15–16.
- Euaugaptilus gibbus* (Wolfenden, 1904): sAnt-Ntemp  
*Augaptilus gibbus* Wolfenden, 1904:122; 1911:337–339, fig. 72, pl. 37, figs. 2–3.  
*Euaugaptilus gibbus* (Wolfenden, 1904); Park, 1993:25–27, figs. 17–18.
- Euaugaptilus hadrocephalus* Park, 1993: Ant-Stemp  
*Euaugaptilus hadrocephalus* Park, 1993:6–9, figs. 3, 4.
- Euaugaptilus laticeps* (Sars, 1905): sAnt-Ntemp  
*Augaptilus laticeps* Sars, 1905b:11.  
*Euaugaptilus laticeps* Sars, 1925:264–265, pl. 80; Park, 1993:30–32, figs. 21–22.
- Euaugaptilus magnus* (Wolfenden, 1904): Ant-Ntemp  
*Augaptilus magnus* Wolfenden, 1904:111, 122, 142, 145; Wolfenden 1911:341–343, fig. 74, pl. 37, figs. 4–9.  
*Euaugaptilus magnus* Park, 1993:41–44, figs. 29–30.
- Euaugaptilus maxillaris* Sars, 1920: Ant-Ntemp  
*Euaugaptilus maxillaris* Sars, 1920:15; 1925:287–288, pl. 95; Park, 1993:5–6, figs. 1–2.

- Euaugaptilus nodifrons* (Sars, 1905): Ant-Ntemp  
*Augaptilus nodifrons* Sars, 1905b:13–14.  
*Euaugaptilus nodifrons* Sars, 1925:267–269, pl. 82; Park, 1993:14–19, figs. 9–11.
- Euaugaptilus oblongus* (Sars, 1905): sAnt-Ntemp  
*Augaptilus oblongus* Sars, 1905b:11.  
*Euaugaptilus oblongus* Sars, 1925:266–267, pl. 81; Park, 1993:44–47, figs. 31–32.
- Euaugaptilus perasetosus* Park, 1993: Ant-Stemp  
*Euaugaptilus perasetosus* Park, 1993:9–13, figs. 5–6.
- Eucalanus hyalinus* (Claus, 1866): sAnt-Ntemp  
*Calanella hyaline* Claus, 1866:8.  
*Eucalanus hyalinus* Bradford–Grieve, 1994:76, figs. 42, 88.
- Euchirella maxima* Wolfenden, 1905: sAnt-sArc  
*Euchirella maxima* Wolfenden, 1905:18, pl. 6, figs. 9–11; Park, 1978:149–151, fig. 30.
- Euchirella rostrata* (Claus, 1866): sAnt-Ntemp  
*Undina rostrata* Claus, 1866:11, pl. 1, fig. 2.  
*Euchirella rostrata* Park, 1978:147–149, fig. 29.
- Euchirella rostromagna* Wolfenden, 1911: Ant  
*Euchirella rostromagna* Wolfenden, 1911:235; Park, 1978:151–155, figs. 31–34.
- Euchirella similis* Wolfenden, 1911: sAnt-Trop  
*Euchirella similis* Wolfenden, 1911:238, text fig. 23, pl. 28, figs. 1–2; Park, 1978:155–158, figs. 35–36.
- Farrania frigida* (Wolfenden, 1911): Ant-Trop  
*Drepanopsis frigida* Wolfenden, 1911:245, text fig. 29; Vervoort, 1951:61, figs. 34–39.  
*Farrania frigida* Vervoort, 1957:38–39.
- Gaetanus antarcticus* Wolfenden, 1905: Ant-Ntemp  
*Gaetanus antarcticus* Wolfenden, 1905:7, pl. 3, fig. 1; Park, 1978:141–144, figs. 25, 26; Markhaseva, 1996:178, figs. 138–139.
- Gaetanus brevispinus* (Sars, 1900): Ant-Arc  
*Chiridius brevispinus* Sars, 1900:68, pl. 19; Markhaseva, 1996:187–195, figs. 149–152.  
*Gaidius intermedius* Wolfenden, 1905:6, pl. 3, figs. 4–5; Park, 1978:131–136, figs. 18–20.
- Gaetanus kruppii* Giesbrecht, 1903: sAnt-sArc  
*Gaetanus kruppii* Giesbrecht, 1903:22; Park, 1978:136–139, figs. 21–22; Markhaseva, 1996:196–201, figs. 157–158.
- Gaetanus latifrons* Sars, 1905: sAnt-sArc  
*Gaetanus latifrons* Sars, 1905a: 4, 11; Vervoort, 1957:61–62; Markhaseva, 1996, p.201–204, figs. 159–160.
- Gaetanus minor* Farran, 1905: sAnt-Ntemp  
*Gaetanus minor* Farran, 1905:34, pl. 5; Park, 1978:144–147, figs. 27–28; Markhaseva, 1996:205–206, fig. 164.
- Gaetanus paracurvicornis* Brodsky, 1950: Ant-Ntemp  
*Gaetanus paracurvicornis* Brodsky, 1950:167, fig. 84; Markhaseva, 1996:211, fig. 167.
- Gaetanus pileatus* Farran, 1903: sAnt-Ntemp  
*Gaetanus pileatus* Farran, 1903:16, pl. 17, figs. 1–11; Park, 1978:139–141, figs. 23–24; Markhaseva, 1996:211–212, figs. 168–169.
- Gaetanus tenuispinus* (Sars, 1900): Ant-Arc  
*Chiridius tenuispinus* Sars, 1900:67, pl. 18.  
*Gaidius tenuispinus* Park, 1978, pp.127–131, figs. 15–17.  
*Gaetanus tenuispinus* Markhaseva, 1996:221–225, figs. 177–178.
- Haloptilus fons* Farran, 1908: Ant-Ntemp  
*Haloptilus fons* Farran, 1908:69–71, pl. 7, figs. 11–15; Park, 1988:3–4, figs. 1–2.
- Haloptilus longicirrus* Brodsky, 1950: Ant-sArc  
*Haloptilus longicirrus* Brodsky, 1950:363–364, fig. 254; Park, 1988:21–22, fig. 13.
- Haloptilus ocellatus* Wolfenden, 1905: Ant  
*Haloptilus ocellatus* Wolfenden, 1905:14–15, pl. 5; Park, 1988:4–9, figs. 3–4.
- Haloptilus oxycephalus* (Giesbrecht, 1889): Ant-Ntemp  
*Hemicalanus oxycephalus* Giesbrecht, 1889a:813; Giesbrecht, 1893:384, pl. 42, figs. 16, 23.  
*Haloptilus oxycephalus* Park, 1988:9–14, figs. 5–6.
- Heterorhabdus austrinus* Giesbrecht, 1902: Ant-sAnt  
*Heterorhabdus austrinus* Giesbrecht, 1902:28, pl. 6, figs. 1–9; Park, 2000:132–133, figs. 104–105.
- Heterorhabdus lobatus* Bradford, 1971: sAnt-Ntemp  
*Heterorhabdus lobatus* Bradford, 1971:131, figs. 9, 10a–c; Park, 2000:105–106, fig. 74.
- Heterorhabdus paraspinosus* Park, 2000: sAnt-Stemp  
*Heterorhabdus paraspinosus* Park, 2000:131–132, figs. 102–103.
- Heterorhabdus pustulifer* Farran, 1929: Ant-sAnt  
*Heterorhabdus pustulifer* Farran, 1929:266, fig. 27; Park, 2000:124–125, figs. 92–93.
- Heterorhabdus spinosus* Bradford, 1971: sAnt-Stemp  
*Heterorhabdus spinosus* Bradford, 1971:121, figs.1, 2g–k, 3c, 4c; Park, 2000:130–131, figs. 100–101.
- Heterostylites nigrotinctus* Brady, 1918: Ant-sAnt  
*Heterostylites nigrotinctus* Brady, 1918:27, pl. 6, figs. 1–8; Park, 2000:44–45, figs. 22–23.
- Landrumius antarcticus* Park, 1983a: Ant  
*Landrumius antarcticus* Park, 1983a:192–195, figs. 15–16.
- Landrumius gigas* (Scott, 1909): sAnt-Trop  
*Brachycalanus gigas* Scott, 1909:81–82, pl. 35, figs. 10–18.  
*Lophothrix gigas* Grice and Hulsemann, 1968:332–334, figs. 63–74.  
*Landrumius gigas* Park, 1983:195–197, figs. 17–18.
- Lophothrix frontalis* Giesbrecht, 1895: sAnt-Ntemp  
*Lophothrix frontalis* Giesbrecht, 1895:254–255, pl. 2, figs. 1–5, 9–12; Park, 1983a:178–184, figs. 7–10.
- Lophothrix humilifrons* Sars, 1905: Ant-Ntemp  
*Lophothrix humilifrons* Sars, 1905a:22; 1925:166–167, pl. 46, figs. 15–22; Park, 1983a:184–188, figs. 11–12.
- Lucicutia bradyana* Cleve, 1904: Ant-Trop  
*Lucicutia bradyana* Cleve, 1904:204–206, pl. 6, figs. 33, 34; Markhaseva and Ferrari, 2005:1084–1091, figs. 3–7.
- Lucicutia curta* Farran, 1905: Ant-sArc  
*Lucicutia curta* Farran, 1905:44, pl. 12, figs. 1–7; Vervoort, 1957:128–129, figs. 114–117.
- Lucicutia macrocera* Sars, 1920: Ant-sArc  
*Lucicutia macrocera* Sars, 1920:10; 1925:213, pl. 57, figs. 12–15; Vervoort, 1957:130, figs. 118, 119.
- Lucicutia magna* Wolfenden, 1903: Ant-sArc  
*Lucicutia magna* Wolfenden, 1903:124; Wolfenden, 1911:316–317, text fig. 59; Hulsemann, 1966:727, fig. 119.
- Lucicutia ovalis* (Giesbrecht, 1889): Ant-sArc  
*Isochaeta ovalis* Giesbrecht, 1889a:812.  
*Lucicutia frigida* Wolfenden, 1911:320, text fig. 62; Vervoort, 1957:126–128, figs. 111–114.
- Lucicutia wolfendeni* Sewell, 1932: Ant-sArc  
*Lucicutia wolfendeni* Sewell, 1932:289; Markhaseva and Ferrari, 2005:1091–1094, figs. 8–9.
- Megacalanus princeps* Wolfenden, 1904: Ant-sArc  
*Megacalanus princeps* Wolfenden, 1904:49, fig. 4; Vervoort, 1957:32, fig. 7.
- Metridia brevicauda* Giesbrecht, 1889: sAnt-sArc  
*Metridia brevicauda* Giesbrecht, 1889b:24; 1893:340, pl. 33, figs. 5, 10–11, 14, 21, 32; Vervoort, 1957:122.
- Metridia curticauda* Giesbrecht, 1889: Ant-sArc  
*Metridia curticauda* Giesbrecht, 1889b:24; 1893:340, pl. 33, figs. 4, 15, 33; Vervoort, 1951:121, figs. 65–67; 1957:122.
- Metridia ferrarii* Markhaseva, 2001: Ant-Ntemp  
*Metridia ferrarii* Markhaseva, 2001:44–46, figs. 1–59.
- Metridia gerlachei* Giesbrecht, 1902: Ant  
*Metridia gerlachei* Giesbrecht, 1902:27, pl. 5, figs. 6–14; Vervoort, 1951:120; 1957:120–121, figs. 109, 110.

- Metridia lucens* Boeck, 1864: sAnt-Ntemp  
*Metridia lucens* Boeck, 1864:238; Vervoort, 1957:119.  
*Metridia hibernica* Giesbrecht, 1893:345, pl. 32, fig. 11; pl. 35, figs. 2, 12, 16, 22, 28, 36, 39.
- Metridia ornata* Brodsky, 1950: Ant-sArc  
*Metridia ornata* Brodsky, 1950:303–305, fig. 210; Markhaseva, 2001:48–49, figs. 184–243.
- Metridia princeps* Giesbrecht, 1889: Ant-sArc  
*Metridia princeps* Giesbrecht, 1889b:24; Markhaseva, 2001:47–48, figs. 148–183.
- Metridia pseudoasymmetrica* Markhaseva, 2001: Ant-sAnt  
*Metridia pseudoasymmetrica* Markhaseva, 2001:46–47, figs. 60–110.
- Metridia venusta* Giesbrecht, 1889: sAnt-Ntemp  
*Metridia venusta* Giesbrecht, 1889b:24; 1893:340, pl. 33, figs. 7, 17, 29; Vervoort, 1957:121–122.
- Microcalanus pygmaeus* (Sars, 1900): Ant-Arc  
*Pseudocalanus pygmaeus* Sars, 1900:73, pl. 21.  
*Microcalanus pygmaeus* Vervoort, 1957:36–37, fig. 9; Bradford-Grieve, 1994:130, fig. 75.
- Mimocalanus cultrifer* Farran, 1908: Ant-sArc  
*Mimocalanus cultrifer* Farran, 1908:23, pl. 1, figs. 5–9; Damkaer, 1975:68–69, figs. 164–168.
- Neocalanus tonsus* (Brady, 1883): sAnt-Stemp  
*Calanus tonsus* Brady, 1883:34, pl. 4, figs. 8, 9; Vervoort, 1957:27, figs. 3–6.  
*Neocalanus tonsus* Bradford-Grieve, 1994:42, figs. 17, 82.
- Nullisetigera bidentatus* (Brady, 1883): Ant-sArc  
*Phyllopus bidentatus* Brady, 1883:78, pl. 5, figs. 7–16; Vervoort, 1957:141.
- Onchocalanus cristatus* (Wolfenden, 1904): Ant-Ntemp  
*Xanthocalanus cristatus* Wolfenden, 1904:119, pl. 9, figs. 18–19.  
*Onchocalanus cristatus* Park, 1983b:335–343, figs. 13–15.
- Onchocalanus hirtipes* Sars, 1905: Ant-Ntemp  
*Onchocalanus hirtipes* Sars, 1905a:20–21; 1925:148–149, pl. 41, figs. 6–11; Park, 1983b:351, fig. 22.
- Onchocalanus magnus* (Wolfenden, 1906): Ant  
*Xanthocalanus magnus* Wolfenden, 1906:32–33, pl. 10, figs. 7–9.  
*Onchocalanus magnus* Park, 1983b:343–347, figs. 16–19.
- Onchocalanus paratrigoniceps* Park, 1983b: Ant-Stemp  
*Onchocalanus paratrigoniceps* Park, 1983b:333–335, figs. 10–12.
- Onchocalanus subcristatus* (Wolfenden, 1906): Ant  
*Xanthocalanus subcristatus* Wolfenden, 1906:31–32, pl. 10, figs. 4–6.  
*Onchocalanus subcristatus* Wolfenden, 1911:278, pl. 31, figs. 6–8.
- Onchocalanus trigoniceps* Sars, 1905: Ant-Ntemp  
*Onchocalanus trigoniceps* Sars, 1905a:20; 1925:144–147, pl. 40, figs. 1–15; Park, 1983b:329–333, figs. 7–9.
- Onchocalanus wolfendeni* Vervoort, 1950: Ant  
*Onchocalanus wolfendeni* Vervoort, 1950:22–26, figs. 9–11; Park, 1983b:347–351, figs. 20–21.
- Pachyptilus eurygnathus* Sars, 1920: Ant-sArc  
*Pachyptilus eurygnathus* Sars, 1920:18; 1925:321, pl. 114; Vervoort, 1957:140.
- Paraeuchaeta abbreviata* (Park, 1978): Ant-Trop  
*Euchaeta abbreviata* Park, 1978:240–244, figs. 92, 93.  
*Paraeuchaeta abbreviata* Park, 1995:63–64, figs. 58–59.
- Paraeuchaeta antarctica* (Giesbrecht, 1902): Ant-sAnt  
*Euchaeta antarctica* Giesbrecht, 1902:21, pl. 3, figs. 1–8; Fontaine, 1988:32–38, figs. 3–8.  
*Paraeuchaeta antarctica* Park, 1995:88–89, figs. 84–85.
- Paraeuchaeta austrina* (Giesbrecht, 1902): Ant  
*Euchaeta austrina* Giesbrecht, 1902:22, pl. 3, figs. 9–16; Fontaine, 1988:46–49, figs. 6, 13, 16, 17.
- Paraeuchaeta barbata* (Brady, 1883): Ant-Arc  
*Euchaeta barbata* Brady, 1883:66, pl. 22, figs. 6–12.  
*Paraeuchaeta barbata* Park, 1995:37–38, fig. 23.
- Paraeuchaeta biloba* Farran, 1929: Ant-sAnt  
*Paraeuchaeta biloba* Farran, 1929:242, fig. 11.  
*Euchaeta biloba* Park, 1978:217–220, figs. 74–76.
- Paraeuchaeta comosa* Tanaka, 1958: sAnt-Ntemp  
*Paraeuchaeta comosa* Tanaka, 1958:363, fig. 79a–g; Park, 1995:56–57, fig. 50.
- Paraeuchaeta dactylifera* (Park, 1978) Ant-sAnt  
*Euchaeta dactylifera* Park, 1978:240, fig. 91.  
*Paraeuchaeta dactylifera* Park, 1995:70, fig. 67.
- Paraeuchaeta eltaninae* (Park, 1978): Ant  
*Euchaeta eltaninae* Park, 1978:280–283, figs. 118–120.  
*Paraeuchaeta eltaninae* Park, 1995:39, fig. 25.
- Paraeuchaeta erebi* Farran, 1929: Ant  
*Paraeuchaeta erebi* Farran, 1929:239, fig. 9.  
*Euchaeta erebi* Fontaine, 1988:41–45, figs. 11–13.
- Paraeuchaeta exigua* (Wolfenden, 1911): sAnt-Stemp  
*Euchaeta exigua* Wolfenden, 1911:300, text fig. 52.  
*Paraeuchaeta exigua* Park, 1995:77–78, fig. 74.
- Paraeuchaeta hansenii* (With, 1915): sAnt-sArc  
*Euchaeta hansenii* With, 1915:181, text fig. 52.  
*Paraeuchaeta hansenii* Park, 1995:57–58, fig. 51.
- Paraeuchaeta kurilensis* Heptner, 1971: Ant-sArc  
*Paraeuchaeta kurilensis* Heptner, 1971:83, fig. 4; Park, 1995:62–63, fig. 57.
- Paraeuchaeta parvula* (Park, 1978): Ant-sAnt  
*Euchaeta parvula* Park, 1978:256–259, figs. 102–104.  
*Paraeuchaeta parvula* Park, 1995:38, fig. 24.
- Paraeuchaeta pseudotonsa* (Fontaine, 1967): sAnt-Ntemp  
*Euchaeta pseudotonsa* Fontaine, 1967:204, figs. 1B, 2B, 3B, 3E, 6B, 6E, 7B, 8B, E, 9A, 9C, 10, 12.  
*Paraeuchaeta pseudotonsa* Park, 1995:74–75, fig. 71.
- Paraeuchaeta rasa* Farran, 1929: Ant-sAnt  
*Paraeuchaeta rasa* Farran, 1929:240, fig. 10; Park, 1995:46, fig. 35.
- Paraeuchaeta regalis* (Grice and Hulsemann, 1968): Ant-Stemp  
*Euchaeta regalis* Grice and Hulsemann, 1968:329, figs. 34–40.  
*Paraeuchaeta regalis* Park, 1995:50, fig. 41.
- Paraeuchaeta sarsi* (Farran, 1908): sAnt-Ntemp  
*Euchaeta sarsi* Farran, 1908:41, pl. 3, figs. 15–16.  
*Paraeuchaeta sarsi* Park, 1995:47–48, figs. 37–38.
- Paraeuchaeta scotti* (Farran, 1908): sAnt-Ntemp  
*Euchaeta scotti* Farran, 1908:42, pl. 3, figs. 11–12.  
*Paraeuchaeta scotti* Park, 1995:40–41, fig. 27.
- Paraeuchaeta similis* (Wolfenden, 1908): Ant  
*Euchaeta similis* Wolfenden, 1908:19, pl. 4, figs. 1–4; Park, 1978:227–229, fig. 82; Fontaine, 1988:38–41, figs. 6, 9, 10.
- Paraeuchaeta tumidula* (Sars, 1905): Ant-sArc  
*Euchaeta tumidula* Sars, 1905a:15.  
*Paraeuchaeta tumidula* Park, 1995:82–83, fig. 79.  
*Euchaeta biconvexa* Park, 1978:264–267, figs. 108, 109.
- Paraeuchaeta tycodesma* (Park, 1978): Ant  
*Euchaeta tycodesma* Park, 1978:229–231, fig. 83; Fontaine, 1988:45–46, figs. 13–15.
- Paraheterorhabdus compactus* (Sars, 1900): sAnt-Arc  
*Heterorhabdus compactus* Sars, 1900:83, pls. 24, 25.  
*Paraheterorhabdus compactus* Park, 2000:85–88, figs. 56–58.
- Paraheterorhabdus farrani* (Brady, 1918): Ant-sAnt  
*Heterorhabdus farrani* Brady, 1918:27, pl. 4, figs. 10–18.  
*Paraheterorhabdus farrani* Park, 2000:78–80, figs. 48, 49.
- Paralabidocera antarctica* (Thompson, 1898): Ant  
*Paracartia antarctica* Thompson, 1898:295, pl. 18, figs. 1–12.

- Paralabidocera hodgsoni* Wolfenden, 1908:26, pl. 6, figs. 1–13.  
*Paralabidocera antarctica* Farran, 1929:280; Vervoort, 1951:148.  
*Paralabidocera grandispina* Waghorn, 1979: Ant  
*Paralabidocera grandispina* Waghorn, 1979:465, figs. 5–8.  
*Paralabidocera separabilis* Brodsky and Zvereva, 1976: Ant  
*Paralabidocera separabilis* Brodsky and Zvereva, 1976:234, figs. 1–4.  
*Pleuromamma abdominalis* (Lubbock, 1856): sAnt-Ntemp  
*Diaptomus abdominalis* Lubbock, 1856:22, pl. 10.  
*Pleuromamma abdominalis* Steuer, 1932:9–17, kartes 3–7; Vervoort, 1957:123–124.  
*Pleuromamma antarctica* Steuer, 1931: Ant-sAnt  
*Pleuromamma robusta* forma *antarctica* Steuer, 1932:24–25, karte 10; Vervoort, 1951:123–126, figs. 68, 69; Vervoort, 1957:125.  
*Pleuromamma antarctica* Ferrari and Saltzman, 1998:217–220, fig. 8.  
*Pleuromamma peseki* Farran, 1929: sAnt-Ntemp  
*Pleuromamma gracilis* forma *peseki* Steuer, 1932:34–36.  
*Pleuromamma peseki* Farran, 1929:260, figs. 23, 24; Vervoort, 1957:124.  
*Pleuromamma quadrungulata* (Dahl, 1893): sAnt-Ntemp  
*Pleuromamma quadrungulata* Dahl, 1893:105.  
*Pleuromamma quadrungulata* Steuer, 1932:26–30, karte 12–13; Vervoort, 1957:124.  
*Pleuromamma xiphias* (Giesbrecht, 1889): sAnt-Ntemp  
*Pleuromamma xiphias* Giesbrecht, 1889b:25; 1893:347, pl. 32, fig. 14; pl. 33, figs. 42, 45, 50.  
*Pleuromamma xiphias* Steuer, 1932:1–9, karte 1–2; Vervoort, 1957:124.  
*Pseudaugaptilus longiremis* Sars, 1907: Ant-Arc  
*Pseudaugaptilus longiremis* Sars, 1907:24; 1925:310, pl. 109; Vervoort, 1951:144–147, fig. 82; 1957:140.  
*Pseudeuchaeta brevicauda* Sars, 1905: Ant-sArc  
*Pseudeuchaeta brevicauda* Sars, 1905a:5, 18; Park, 1978:187–191, figs. 57, 58.  
*Pseudochirella batillipa* Park, 1978: Ant, Ntemp, Arc  
*Pseudochirella batillipa* Park, 1978:176, figs. 50, 51; Markhaseva, 1996:255–256, fig. 203.  
*Pseudochirella dubia* (Sars, 1905): Ant-sArc  
*Undeuchaeta dubia* Sars, 1905a:15.  
*Pseudochirella dubia* Markhaseva, 1996:262, figs. 208–209.  
*Pseudochirella formosa* Markhaseva, 1989: Ant  
*Pseudochirella formosa* Markhaseva, 1989:33, figs. 1, 7; 1996:264, fig. 212.  
*Pseudochirella hirsuta* (Wolfenden, 1905): Ant-Stemp  
*Euchirella hirsuta* Wolfenden, 1905:17, pl. 6, figs. 7–8.  
*Pseudochirella hirsuta* Park, 1978:163–165, figs. 41, 42; Markhaseva, 1996:266, figs. 214–215.  
*Pseudochirella mawsoni* Vervoort, 1957: Ant-sAnt  
*Pseudochirella mawsoni* Vervoort, 1957:64, figs. 44–48; Park, 1978:172–176, figs. 48, 49; Markhaseva, 1996:272–275, figs. 219–220.  
*Pseudochirella notacantha* (Sars, 1905): Ant-sArc  
*Gaidius notacanthus* Sars, 1905a:9.  
*Pseudochirella notacantha* Markhaseva, 1996:275–276, figs. 221–222.  
*Pseudochirella obtusa* (Sars, 1905): Ant-sArc  
*Undeuchaeta obtusa* Sars, 1905a:4, 13.  
*Pseudochirella obtusa* Markhaseva, 1996:278, figs. 225–226.  
*Pseudochirella polyspina* Park, 1978:169–172, figs. 45–47.  
*Pseudochirella pustulifera* (Sars, 1905): Ant-sArc  
*Undeuchaeta pustulifera* Sars, 1905a:14.  
*Pseudochirella pustulifera* Park, 1978:165–169, figs. 43–44.  
*Pseudochirella spectabilis* (Sars, 1900): Ant, Arc  
*Undeuchaeta spectabilis* Sars, 1900:59, pls. 15, 16.  
*Pseudochirella spectabilis* Markhaseva, 1996:289–290, figs. 233–235.  
*Euchirella elongata* Wolfenden, 1905:19, pl. 6, figs. 12–13.  
*Pseudochirella elongata* Park, 1978:159–163, figs. 37–40.  
*Racovitzanus antarcticus* Giesbrecht, 1902: Ant, sAnt, sArc  
*Racovitzanus antarcticus* Giesbrecht, 1902:26–27, pl. 4, figs. 8–13; pl. 5, figs. 1–5; Park, 1983:172–177, figs. 4–6.  
*Rhincalanus gigas* Brady, 1883: Ant  
*Rhincalanus gigas* Brady, 1883:42, pl. 8, figs. 1–11; Vervoort, 1951:57; 1957:34.  
*Rhincalanus nasutus* Giesbrecht, 1888: sAnt-Ntemp  
*Rhincalanus nasutus* Giesbrecht, 1888:334; 1893:152–154, 761, pl. 3, fig. 6; pl. 9, figs. 6, 14; pl. 12, figs. 9–12, 14, 16, 17; pl. 35, figs. 46, 47, 49; Vervoort 1957:33.  
*Scaphocalanus antarcticus* Park, 1982: Ant  
*Scaphocalanus antarcticus* Park, 1982:83–89, figs. 3–7.  
*Scaphocalanus cristatus* (Giesbrecht, 1895): sAnt-Ntemp  
*Scolecithrix cristata* Giesbrecht, 1895:252–253, pl. 2, figs. 6–8; pl. 3, figs. 1–5.  
*Scaphocalanus cristatus* Park, 1982:92–95, fig. 10.  
*Scaphocalanus echinatus* (Farran, 1905): sAnt-Ntemp  
*Scolecithrix echinata* Farran, 1905:37–38, pl. 4, figs. 15–18; pl. 5, figs. 12–17.  
*Scaphocalanus echinatus* Park, 1982:101–104, figs. 15–16.  
*Scaphocalanus elongatus* Scott, 1909: Ant-Ntemp  
*Scaphocalanus elongatus* A. Scott, 1909:98, pl. 32, figs. 10–16; Park, 1982:106–108, figs. 18–19.  
*Scaphocalanus farrani* Park, 1982: Ant-sAnt  
*Scaphocalanus farrani* Park, 1982:95–101, figs. 11–14.  
*Scaphocalanus major* (Scott, 1894): Ant-Trop  
*Scolecithrix major* Scott, 1894:52, pl. 3, figs. 24–26; pl. 5, figs. 44–45.  
*Scaphocalanus major* Park, 1982:108–110, fig. 20.  
*Scaphocalanus medius* (Sars, 1907): sAnt-Ntemp  
*Amalophora media* Sars, 1907:16.  
*Scaphocalanus medius* Sars, 1925:173–174, pl. 49, figs. 1–8; Park, 1982:110–112, fig. 21.  
*Scaphocalanus parantarcticus* Park, 1982: Ant-sAnt  
*Scaphocalanus parantarcticus* Park, 1982:89–92, figs. 8–9.  
*Scaphocalanus subbrevicornis* (Wolfenden, 1911): Ant  
*Amalophora subbrevicornis* Wolfenden, 1911:262–263, text fig. 37.  
*Scaphocalanus subbrevicornis* Park, 1982:117–121, fig. 26.  
*Scaphocalanus vervoorti* Park, 1982: Ant  
*Scaphocalanus vervoorti* Park, 1982:112–117, figs. 22–25.  
*Scolecithricella altera* (Farran, 1929): Ant-Ntemp  
*Amalophora altera* Farran, 1929:252, fig. 19.  
*Scolecithricella altera* Park, 1980:70–72, fig. 22.  
*Scolecithricella cenotelis* Park, 1980: Ant  
*Scolecithricella cenotelis* Park, 1980:59–60, fig. 18.  
*Scolecithricella dentata* (Giesbrecht, 1893): sAnt-Ntemp  
*Scolecithrix dentata* Giesbrecht, 1893:266, pl.13, figs. 12, 20, 33, pl. 37, figs. 13–14.  
*Scolecithricella dentata* Park, 1980:42–43, fig. 7.  
*Scolecithricella dentipes* Vervoort, 1951: Ant-sAnt  
*Scolecithricella dentipes* Vervoort, 1951:108, figs. 55–59; Park, 1980:46–50, figs. 10–11.  
*Scolecithricella emarginata* (Farran, 1905): Ant-Ntemp  
*Scolecithrix emarginata* Farran, 1905:36, pl. 7, figs. 6–17.  
*Scolecithricella emarginata* Park, 1980:61–66, fig. 19.  
*Scolecithrix polaris* Wolfenden, 1911:252–253, pl. 30, figs. 1–2, text fig. 31a–e.

- Scolecithricella hadrosoma* Park, 1980: Ant-Stemp  
*Scolecithricella hadrosoma* Park, 1980:66, fig. 20.
- Scolecithricella minor* (Brady, 1883): Ant-sArc  
*Scolecithrix minor* Brady, 1883:58, pl. 16, figs. 15–16.  
*Scolecithricella minor* Park, 1980:31–36, figs. 2–3.  
*Scolecithrix glacialis* Giesbrecht, 1902:25, pl. 4, figs. 1–7.
- Scolecithricella obtusifrons* (Sars, 1905): Ant-Ntemp  
*Amalophora obtusifrons* Sars, 1905a:22.  
*Scolecithricella obtusifrons* Park, 1980:66–70, fig. 21.
- Scolecithricella ovata* (Farran, 1905): Ant-Ntemp  
*Scolecithrix ovata* Farran, 1905:37, pl. 6, figs. 13–18; pl. 7, figs. 1–5.  
*Scolecithricella ovata* Park, 1980:58–59, fig. 17.
- Scolecithricella parafalcifer* Park, 1980: Ant-Stemp  
*Scolecithricella parafalcifer* Park, 1980:50–51, fig. 12.
- Scolecithricella profunda* (Giesbrecht, 1893): sAnt-Ntemp  
*Scolecithrix profunda* Giesbrecht, 1893:266, pl. 13, figs. 5, 26.  
*Scolecithricella profunda* Park, 1980:36–37, fig. 4.
- Scolecithricella pseudopropinqua* Park, 1980: sAnt-Stemp  
*Scolecithrix pseudopropinqua* Park, 1980:51–55, figs. 13–14.
- Scolecithricella schizosoma* Park, 1980: Ant-sAnt  
*Scolecithricella schizosoma* Park, 1980:43–46, figs. 8–9.
- Scolecithricella valida* (Farran, 1908): Ant-sArc  
*Scolecithrix valida* Farran, 1908:55, pl. 5, figs. 14–17; pl. 6, fig. 7.  
*Scolecithricella valida* Park, 1980:55–58, figs. 15–16.
- Scolecithricella verwoorti* Park, 1980: Ant  
*Scolecithricella verwoorti* Park, 1980:72–74, figs. 23–24.
- Scolecithricella vittata* (Giesbrecht, 1893): sAnt-Ntemp  
*Scolecithrix vittata* Giesbrecht, 1893:266, pl. 13, figs. 2, 23, 32, 34; pl. 37, figs. 5, 8.  
*Scolecithricella vittata* Park, 1980:37–42, figs. 5–6.
- Scottocalanus helenae* (Lubbock, 1856): sAnt-Ntemp  
*Undina helenae* Lubbock, 1856:25–26, pl. 4, fig. 4; pl. 7, figs. 1–5.  
*Scottocalanus helenae* Park, 1983:205–208, figs. 23–24.
- Scottocalanus securifrons* (Scott, 1894): sAnt-Ntemp  
*Scolecithrix securifrons* Scott, 1894:47–48, figs. 41, 43–47, 49–52, 54, 56, pl. 5, fig. 1.  
*Scottocalanus securifrons* Park, 1983:200–205, figs. 19–22.
- Scottocalanus thorii* With, 1915: sAnt-sArc  
*Scottocalanus thorii* With, 1915:215–219, pl. 6, figs. 14a–14c; pl. 8, figs. 14a–14b, text figs. 68–70; Park, 1983:208–210, fig. 25.
- Spinocalanus abyssalis* Giesbrecht, 1888: Ant-sArc  
*Spinocalanus abyssalis* Giesbrecht, 1888:355; 1893:209, pl. 13, figs. 42–48; Damkaer, 1975:17–20, figs. 4–10, 148.
- Spinocalanus antarcticus* Wolfenden, 1906: Ant, Arc  
*Spinocalanus antarcticus* Wolfenden, 1906:43, pl. 14, figs. 6–9; Damkaer, 1975:30–35, figs. 43–68, 152; Bradford-Grieve, 1994:101, 103, fig. 57.
- Spinocalanus horridus* Wolfenden, 1911: Ant-Arc  
*Spinocalanus horridus* Wolfenden, 1911:216, text fig. 7, pl. 25, figs. 1–2; Damkaer, 1975:37–41, figs. 69–83, 153.
- Spinocalanus magnus* Wolfenden, 1904: Ant-sArc  
*Spinocalanus magnus* Wolfenden, 1904:118; Damkaer, 1975: 26–30, figs. 35–42, 150.
- Spinocalanus terranova* Damkaer, 1975: Ant  
*Spinocalanus terranova* Damkaer, 1975:60–62, figs. 141–147, 159.
- Stephos longipes* Giesbrecht, 1902: Ant  
*Stephos longipes* Giesbrecht, 1902:20, pl. 2, 6–14; Tanaka, 1960:37, pl. 14, figs. 1–10.
- Stephos antarcticus* Wolfenden, 1908: Ant  
*Stephos antarcticus* Wolfenden, 1908:24, pl. 5, figs. 4–8.
- Subeucalanus longiceps* (Matthews, 1925): sAnt-Stemp  
*Eucalanus longiceps* Matthews, 1925:127, pl. 9; Vervoort, 1957:33, fig. 8.  
*Subeucalanus longiceps* Bradford-Grieve, 1994:88, figs. 40, 41, 91.
- Talacalanus greeni* (Farran, 1905): Ant-Ntemp  
*Xanthocalanus greeni* Farran, 1905:39, pl. 8, figs. 1–13; Park, 1983:325–327, figs. 5–6.  
*Talacalanus calaminus* Wolfenden, 1906, pl. 11, figs. 3–5.  
*Talacalanus greeni* (Farran, 1905); Campaner, 1978:976.
- Temorites brevis* Sars, 1900: Ant-Arc  
*Temorites brevis* Sars, 1900:100, pls. 30, 31; Vervoort, 1957:115–118, figs. 102–108.
- Undeuchaeta incisa* Esterly, 1911: Ant-sArc  
*Undeuchaeta incisa* Esterly, 1911:319, pl. 27, figs. 12, 19; pl. 28, fig. 28; pl. 29, fig. 59; Park, 1978:183–187, figs. 54–56; Markhaseva, 1996:302, figs. 243–244.
- Undeuchaeta major* Giesbrecht, 1888: sAnt-Ntemp  
*Undeuchaeta major* Giesbrecht, 1888, p.336; Markhaseva, 1996:305, figs. 246–247.
- Undeuchaeta plumosa* (Lubbock, 1856): sAnt-Ntemp  
*Undina plumosa* Lubbock, 1856:24, pl. 9, figs. 3–5; Markhaseva, 1996:310, figs. 248–249.
- Undinella brevipes* Farran, 1908: sAnt-sArc  
*Undinella brevipes* Farran, 1908:12, 50, pl. 5, figs. 1–4; Vervoort, 1957:95–96.
- Valdiviella brevicornis* Sars, 1905: Ant-Ntemp  
*Valdiviella brevicornis* Sars, 1905a:17; 1925:101, pl. 28, figs. 11–17; Park, 1978:195–197, fig. 61.
- Valdiviella insignis* Farran, 1908: Ant-Ntemp  
*Valdiviella insignis* Farran, 1908:45, pl. 3, figs. 1–6; Park, 1978:197–199, fig. 62.
- Valdiviella minor* Wolfenden, 1911: sAnt-Ntemp  
*Valdiviella minor* Wolfenden, 1911:249, pl. 29, figs. 8–11; Park, 1978:199, figs. 63, 64.
- Valdiviella oligarthra* Steuer, 1904: Ant-Ntemp  
*Valdiviella oligarthra* Steuer, 1904:593, figs. 1–3; Park, 1978:191–195, figs. 59–60.

## APPENDIX 2

This appendix lists families, alphabetically, and genera within families, alphabetically, with species reported from the Southern Ocean.

- Acartiidae  
*Paralabidocera*
- Aetideidae  
*Aetideopsis*  
*Aetideus*  
*Batheuchaeta*  
*Chiridiella*  
*Chiridius*  
*Chirundina*  
*Gaetanus*  
*Euchirella*  
*Pseudeuchaeta*  
*Pseudochirella*  
*Undeuchaeta*  
*Valdiviella*
- Arietellidae  
*Arietellus*

- Augaptilidae
  - Augaptilus*
  - Centraugaptilus*
  - Euaugaptilus*
  - Haloptilus*
  - Pachyptilus*
  - Pseudaugaptilus*
- Bathypontiidae
  - Temorites*
- Calanidae
  - Calanoides*
  - Calanus*
  - Neocalanus*
- Candaciidae
  - Candacia*
- Clausocalanidae
  - Clausocalanus*
  - Ctenocalanus*
  - Drepanopus*
  - Farrania*
  - Microcalanus*
- Eucalanidae
  - Eucalanus*
  - Rhincalanus*
- Euchaetidae
  - Paraeuchaeta*
- Heterorhabdidae
  - Disseta*
  - Heterorhabdus*
  - Heterostylites*
  - Paraheterorhabdus*
- Lucicutiidae
  - Lucicutia*
- Megacalanidae
  - Bathycalanus*
  - Bradycalanus*
  - Megacalanus*
- Metridinidae
  - Metridia*
  - Pleuromamma*
- Nullosetigeridae
  - Nullosetigera*
- Phaennidae
  - Cornucalanus*
  - Onchocalanus*
  - Talacalanus*
- Scolecitrichidae
  - Cephalophanes*
  - Landrumius*
  - Lophothrix*
  - Racovitzanus*
  - Scaphocalanus*
  - Scolecithricella*
  - Scottocalanus*
- Spinocalanidae
  - Spinocalanus*
- Stephidae
  - Stephos*
- Subeucalanidae
  - Subeucalanus*
- Tharybidae
  - Undinella*

