

## Deep-sea Benthopelagic Calanoid Copepods and their Colonization of the Near-bottom Environment

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(Accepted January 26, 2004)

**Janet M. Bradford-Grieve (2004)** Deep-sea benthopelagic calanoid copepods and their colonization of the near-bottom environment. *Zoological Studies* 43(2): 276-291. We are still in a discovery phase with respect to the deep-sea benthopelagic fauna and its ecology. New species are being described every year, and our knowledge of the physical and sedimentary environments of the benthic boundary layer is currently being extensively researched by a number of groups. Deep-sea, strictly benthopelagic copepod populations (composed mainly of Calanoida) differ in species composition from those in shallow and shelf waters and probably all represent reinvasions of the benthopelagic environment from the water column. The reasons for this difference are explored, including the possible evolutionary paths of organisms that live in this environment, and the physical conditions in which they live. Oxygen availability was probably a limiting environmental factor in geological time for benthopelagic calanoids. The low oxygen requirements and low weight-specific respiration rates of benthopelagic copepods are suggestive of a Permian reinvasion of the deep benthopelagic environment. That is, they were selected for low oxygen demand by the timing of their reinvasion of the deep benthopelagic environment. It is possible that these hypotheses may be testable using genetic information in the near future. <http://www.sinica.edu.tw/zool/zoolstud/43.2/276.pdf>

**Key words:** Arietelloidea, Clausocalanoidea, Paleoenvironment, Evolution, Colonization.

The low abundance and high diversity of strictly benthopelagic calanoid copepods of the benthic boundary layer (BBL), coupled with difficulties in sampling them in their slope or ocean basin environments (e.g., Bradford and Wells 1983, Hulsemann 1985, Angel 1990 and references therein, Ohtsuka et al. 1998, Nishida et al. 1999), have contributed to the slow rate of accumulation of knowledge of this fauna and its ecology. The deep-sea benthopelagic calanoid fauna contains plesiomorphic as well as more-derived forms which point to a complicated evolutionary history.

Over the last 20 years, a number of studies have increased our knowledge of this fauna in a broad sense, as well as its environment and ecology. In this paper, I assess the deep-sea benthopelagic fauna in its widest sense, what we know of the BBL, what new insights can be gained from analyzing the routes by which this habitat has been populated, and the factors influencing this

invasion over geological time.

### Benthic boundary layer (BBL)

The BBL is a zone of relatively intense biological activity within the deep sea, and is distinguished from the remainder of the water column by its concentrations of particulate matter and biologically active chemical substances, species composition, elevated biomasses of organisms (from bacteria to fish), and elevated metabolic rates (Wishner and Gowing 1987).

The mesopelagic and bathypelagic deep sea harbors a near-bottom mesozooplankton biomass that generally decreases with increasing depth (Rudiyakov 1992). Nevertheless, there is evidence for an increase in planktonic biomass within about 100 m of the seafloor (Wishner and Gowing 1987, Angel 1990), although this phenomenon is not always evident (Angel 1990, Rudiyakov 1992). Copepods, by far, dominate these communities

(Angel 1990 and references therein) when small, fine-meshed nets are used; when nets with larger mouth openings are used, gelatinous species dominate as in Southern California basins (Childress et al. 1989).

The nature of the food supply to the benthic zone was summarized by Angel (1990 and references therein). The benthic boundary layer may receive a more or less predictable quantity of organic carbon from surface layers as directly sedimented phytoplankton, aggregates, dead organisms, and fecal pellets. This detrital material may be repackaged as it sinks through the water column. The fluxes of fine particulate material vary seasonally, but the full range of variability has yet to be defined for this environment.

Thus the benthic interface acts as a sediment trap, accumulating all the material that sinks to the bottom. This organic material influences the characteristics of the benthopelagic fauna. They can exploit it as it sinks onto the seabed, at the interface between the water and sediment, or when it is resuspended from the interface in either particulate or dissolved form (Angel 1990). Resuspension of sediments caused by currents, tidal oscillations, and benthic storms (caused by intense eddy activity), may inject nepheloid layers high into the water column. These events are of considerable importance to the ecology of the benthopelagic environment, as are larger food falls that occur unpredictably. These latter events are probably the reason why there can be large populations of scavengers in the benthopelagic zone.

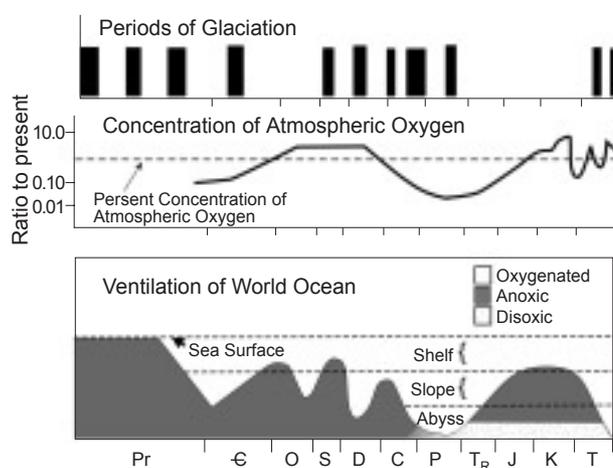
Oxygen concentrations near the sea floor in the deep ocean at depths > 1000 m are usually high (> 4 ml L<sup>-1</sup> or μmol kg<sup>-1</sup>). There are minimum concentrations (< 2 ml L<sup>-1</sup>) above 1000 m in the mid-Pacific (particularly in the eastern part), tropical Indian Ocean, and western tropical Atlantic although oxygen concentrations here are not quite so low (Pickard and Emery 1990). In certain regions (e.g., the Black Sea, the Cariaco Trench in the Caribbean, and in some fjords), there is no oxygen at all, and there are no reports of copepods living in such environments. Therefore, the oxygen concentrations that the benthopelagic fauna experiences greatly depends on the geographic region and where the sea floor intersects the oxygen profile.

### Benthopelagic paleoenvironments

One of the largest barriers to colonization of deep benthopelagic environments has been the

periodic deoxygenation of the world's oceans. Marcotte (1999) summarizes current thinking on the extent of oxygenation of the oceans (Fig. 1). Extensive areas across continental shelves were covered by apparently anoxic waters during non-glacial intervals when sea levels were high. The oceans became progressively ventilated with oxygen over time, from an initial anoxic state after the appearance of oxygen in the atmosphere. It is thought that Lower Paleozoic oceans were ventilated by wind mixing to a relatively shallow depth. The oxygen demand created by the sedimentation of surface-produced decaying organic matter ensured that the inferred anoxic layer was relatively near the surface. The major mechanism by which the deep ocean was ventilated was the formation of sea ice at high latitudes.

Thus the possibility that a benthopelagic fauna could exist at slope depths occurred only in the late Ordovician and mid Devonian, and down to abyssal depths in the Permian when the first really deep ventilation of the oceans occurred. After the Permian, there was another expansion of the oxygen minimum zone (OMZ) in the Jurassic and Cretaceous. Nevertheless, it is thought that deoxygenation of bottom waters was not complete at that time (Horne 1999 and references therein). Survival of fine-particle-feeding benthic platycopid ostracods during the Jurassic, Cretaceous, and Paleogene (e.g., Whatley 1995) shows that bottom waters were not anoxic then, but instead were low



**Fig. 1.** Changes in glaciation, atmospheric oxygen, and water-column oxygenation through geologic time (adapted from Horne 1999 and Marcotte 1999). E, Cambrian; C, Carboniferous; K, Cretaceous; J, Jurassic; D, Devonian; O, Ordovician; P, Permian; Pr, Proterozoic; S, Silurian; T, Tertiary; T<sub>R</sub>, Triassic.

in oxygen. The relationship of fine-particle feeders with low-oxygen environments is supported by the observation that benthic platycopid ostracods dominate the OMZ of modern oceans (Dingle et al. 1989). It is likely that this history of ventilation of the world's oceans is intimately connected with the selection and evolution of families and species of benthopelagic calanoid copepods that currently populate the deep sea.

It is noted that the near-bottom fauna in a Norwegian fjord, where  $O_2$  was  $< 1.1 \text{ ml L}^{-1}$ , was dominated by the copepod, *Stephos rustadi* (Strömberg 1969). It is possible that this species evolved when oxygen levels were low (Jurassic and Cretaceous), but this adaptation being specific to a fjord environment cannot be discounted.

The feeding environment of calanoid copepods in anoxic or low-oxygen environments during the Jurassic and Cretaceous and previous periods was not necessarily enhanced in organic carbon near the sea floor (Thunell et al. 2000). Recent work on the ecology of anoxic environments shows that sulfate reduction is as efficient as aerobic respiration in degrading labile organic matter (Thunell et al. 2000). Thus it is probable that detritus was no more available than in seas of recent times adjacent to the seafloor, given the basic productivity of the overlying water. Distinct protistan assemblages are associated with oxic, microaerobic, and anoxic waters (Fenchel et al. 1995), although anaerobic eukaryotes appear to have a low net growth efficiency thus ensuring that the ratio between phagotrophic and prey biomass is lower than in aerobic communities, and that bacterial numbers are controlled by protozoan grazing in some anaerobic environments (Fenchel and Findlay 1990). There are abundant populations of the dinoflagellates, *Gymnodinium* and *Prorocentrum*, in anoxic waters at 50-100 m in the upwelling region off Peru (Sorokin and Kogelschatz 1979). Thus, the availability of microbial food during the Jurassic and Cretaceous probably depended on where in the water column a calanoid copepod was living.

In order for a number of lineages to have survived the Cretaceous-Tertiary (K-T) catastrophe that occurred during the boundary event, primary production would have had to have continued, if only at low levels. The impact of the meteorite at the Chicxulub site, Mexico, (e.g., Grieve and Theriault 2000) caused temporary heating and darkening of the atmosphere and later cooling, with the resulting suppression of photosynthesis and an immediate detrimental effect on the biota.

Initially, there would have been a large pulse of detritus as large metazoans and phytoplankton died and sank to the sea floor. The heterotrophic destruction of this material would have provided niches for scavengers, detrital feeders, and grazers on protists. The ultimate survival of primary producers would have been favored by the possession of resting stages for those organisms with a high light requirement (e.g., Bravo and Anderson 1994, Kuwata and Takahashi 1999), or by possessing an ability to photosynthesize at low light levels and different qualities of light (e.g., Ikeyal et al. 1991, Vila and Abella 2001). Modern oligotrophic environments that are dominated by picophytoplankton are probably a good model. These communities are dominated by microbial processes (e.g., Bradford-Grieve et al. 1999), and calanoid copepods in these systems rely on microzooplankton prey (e.g., Atkinson 1996). Therefore, there would have been opportunities for life to "tick over" immediately after the K-T boundary event as long as species were able to scavenge for food and feed on detritus, or had other mechanisms for surviving conditions for which they were not adapted.

### Benthopelagic calanoid copepod fauna

The deep-sea, strictly benthopelagic copepod fauna comprises species that are found immediately adjacent to the seafloor, are hardly ever found in plankton tows, and have a morphology and build that suggest that these species are not capable of extended swimming in the water column (Bradford 1969, Grice and Hulsemann 1970, Grice 1972). That is, these species have a heavy compact build, they have enlarged outer exopodal spines on the swimming legs, and in some species, the antennules are very short or even asymmetrically developed (Ohtsuka et al. 1993 1994). These might be called "hypobenthopelagic" in the sense of Vereshchaka (1995). Nevertheless, other studies have shown that maximum numbers of copepods, often thought of as meso- or bathypelagic, may occur between 20 and 100 m above the seafloor; these species/genera seem to have a vertical distribution that is related in some way to the BBL (Wishner 1980, Wiebe et al. 1988, Sirenko et al. 1996, Christiansen et al. 1999).

For example, it was noted that members of the Metridinidae have been observed to be associated with the seafloor, although they are generally common constituents of plankton hauls (e.g., Wishner 1980, Christiansen et al. 1999, Bradford-Grieve 2001a). Recent studies of the Metridinidae

in the North Pacific Ocean (Hattori 1989) show that members of this family have a bimodal distribution. As well as feeding in phytoplankton-rich surface waters, the deep-living parts of the populations feed on “intact and damaged diatoms which were frequently packed in faecal pellet-like particles and on radiolarians”. This observation of association with detrital material is further corroborated by Widder et al. (1999), who observed peaks in bioluminescence associated with *Metridia lucens* at density discontinuities where marine snow has been observed to accumulate. These species might be called “epibenthopelagic” in the sense of Vereshchaka (1995). Bradford-Grieve (2002) suggested that this multiple mode of existence probably reflects the path by which ancient benthopelagic antecedents of the Arietelloidea first invaded the pelagic realm and is the reason why they have survived through geological time. Because it is not yet clear how or if families such as the Lucicutiidae, Metridinidae, Aetideidae, and Euchaetidae relate to the BBL, they have been included in Table 1 to indicate which taxa are commonly taken within 100 m of the seafloor.

Those species that do have a very close relationship with the seafloor have some specific adaptations to that environment. *Paramisophria platysoma* has been observed to swim continuously above the bottom on its left side with the longer left antennule extended forwards (Ohtsuka and Mitsuzumi 1990). The oviduct openings are also asymmetrically placed, apparently to ensure that the reproductive products are not mechanically dislodged during foraging. This type of swimming has also been noted in species of *Stephos* (Ohtsuka and Hiromi 1987), and *Metacalanus* also has asymmetrical antennules (Ohtsuka 1984). Their food may vary from living organisms to detritus. *Thompsonopia* feeds mainly on epibenthic pennate diatoms but also includes naked ciliates, tintinnids, cysts, and pollen (Ohtsuka 1992 as *Pseudocyclopia*), and *Stephos pacificus* feeds on hypotrich ciliates and diatoms (Ohtsuka and Hiromi 1987). Matthews (1964) mentioned the scavenging habit of the Aetideidae and Phaennidae and that their maximum abundance coincided with periods of decline of plankton abundance in upper water layers. Deep benthopelagic copepods ingest detritus and associated bacteria (Gowing and Wishner 1986, Wishner and Gowing 1992). Taxa such as *Tharybis* and the misophrioid, *Benthomisophria*, can distend their guts, thus altering the shape of their bodies, (Boxshall and Roe 1980 and references therein, Bradford-Grieve

1999). This capacity to gorge on food and distend the body is a way of opportunistically surviving in an environment with an irregular food supply.

The deep-sea, near-bottom (including strictly benthopelagic) copepod fauna of the world's oceans (Table 1) is still not well known, and new species are currently being regularly described (e.g., Alvarez 1985, Schulz 1990, Heinrich et al. 1993, Markhaseva and Ferrari 1996, Ohtsuka et al. 1998, Ferrari and Markhaseva 2000a b, Schulz and Markhaseva 2000, Markhaseva and Kosobokova 2001). Some collections of deep-living biota have a good definition of the distance they were caught above the seafloor. Those collections that are dominated by Copepoda (e.g., Wishner 1980, Smith et al. 1986, Wiebe et al. 1988, Christiansen et al. 1999) have apparently not all yet been identified to species and the records published.

In addition to the strictly deep-sea benthopelagic calanoids, there are other species that have consistently been taken in near-bottom samples (Table 1). These include at least members of the Metridinidae, Lucicutiidae, Bathypontiidae, Aetideidae, Euchaetidae, Scolecitrichidae, and Phaennidae. Compared with the benthopelagic fauna at shelf depths, strictly benthopelagic deep-sea faunas greatly differ (Table 2).

The most primitive benthopelagic calanoid families are found only at shallow to shelf depths (Huys and Boxshall 1991). The Pseudocyclopoidea and Epacteriscioidea are found only at shelf depths as well as are some genera of the Arietelloidea (Table 2). There are also other taxa represented on the continental shelf in the Diaptomoidea and Clausocalanoidea. The deep-sea fauna is composed mainly of the Arietelloidea, Ryocalanoidea, Bathypontiidea, and Clausocalanoidea. Setting aside the Pseudocyclopoidea and Epacteriscioidea, that have probably always been benthic, there are two thirds as many families known from continental shelf depths as are known from slope and deeper depths. The Arietellidae, Aetideidae, and Tharybidae all have a greater diversity in the deep sea, whereas the Diaixidae and Phaennidae are more diverse in shallower waters. The Pontellidae, Pseudodiaptomidae, Mesiokeraidae, Pseudocyclopiidae, and Stephidae are represented only in the shallow-water fauna, while the Hyperbionychidae, Bathypontiidae, Ryocalanidae, and Parkiidae are known only from the deep sea. On balance, it appears that there has been a more intense diversification in the benthopelagic environment in the

deep sea.

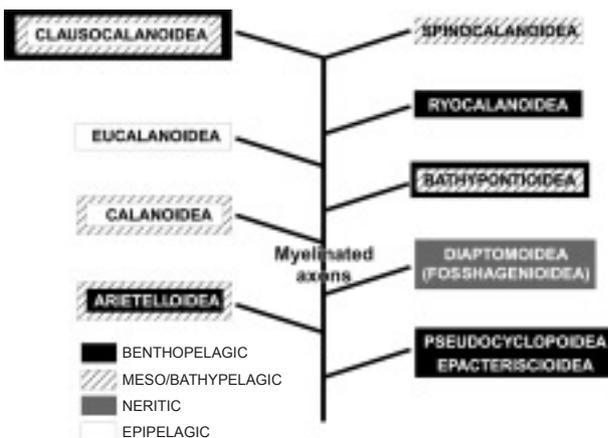
### Evolution of deep-living benthopelagic species

For purposes of this paper, I have accepted the analysis of the evolutionary history of calanoid copepods summarized in the works of Bowman and Abele (1982) and Park (1986), with nomenclature updated by Andronov (1991) (Fig. 2). These relationships are largely supported by preliminary results from an analysis using the methods of phylogenetic systematics (Prof. Geoff Boxshall, The Natural History Museum, London, pers. comm.). It is clear that members of the Pseudocyclopoidea and Epacteriscoidea, all shallow-water benthopelagic forms, are the oldest, most ancestral forms, and that the benthopelagic habit is the more ancient. The ancestors of these superfamilies could have existed prior to the Devonian, at a time when the first pelagic calanoids are postulated to have evolved (Bradford-Grieve 2002). Copepod-like maxillopodan crustaceans (e.g., *Dala peilertae* Müller, 1983) have been taken, with preserved soft parts, from the Upper Cambrian of Sweden (e.g., Walossek and Müller, 1998).

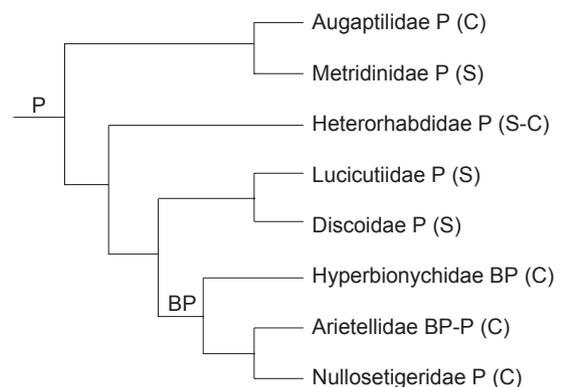
It is postulated that the arietelloidean and diaptomoidean lineages radiated into the water column from the Devonian onwards (Bradford-Grieve 2002). Soh (1998), from a cladistic analysis

of the Arietelloidea, deduced that the history of habitat exploitation was from surface waters followed by descent into the bathypelagic or benthopelagic habitats (Fig. 3). The first branch is the Augaptilidae-Metridinidae clade and appears to have colonized the deep-sea realm earlier than other clades. This clade along with the next two clades (Heterorhabdidae and Lucicutiidae-Discoidea) contains only pelagic taxa. The final offshoot, the Hyperbionychidae-Arietellidae-Nullosetigeridae clade, may have adapted as carnivores to the deep-sea benthopelagic environment. Soh (1998) notes that the asymmetry of the antennules, found exclusively in benthopelagic taxa, is evident in the Hyperbionychidae and Arietellidae, and that the right antenna of the Nullosetigeridae is longer than the left (Soh et al. 1999) implying that the ancestor of this family might have been benthopelagic. The conclusions that can be drawn from Soh's (1998) analysis is that it was later in the evolution of the Arietelloidea that members of this superfamily returned to a benthopelagic habitat, and that some of these then again reentered the pelagic environment.

In the Permian, a reduction in turbidity also occurred with the deep ventilation of the oceans. Bradford-Grieve (2002) suggests that the Permian was a very important time in calanoid evolution. The Arietelloidea probably radiated into many environments, both pelagic and benthopelagic. This period may also have been responsible for the evolution of myelinated sheaths surrounding nerve axons in the Calanoidea, Eucalanoidea, and Clausocalanoidea, a relatively rare occurrence among invertebrates (Weatherby et al. 2000). The appearance of myelinated nerve axons, coupled



**Fig. 2.** Calanoid classification, phylogeny, and habitat type (after Bowman and Abele 1982, Park 1986, Andronov 1991) (adapted from the Pacific Biomedical Research Centre, University of Hawaii at Manoa website: [www.pbrc.hawaii.edu/~lucifer/gifs/copepod-taxo-evol.gif](http://www.pbrc.hawaii.edu/~lucifer/gifs/copepod-taxo-evol.gif)). The Fosshageniidae are here placed in the Diaptomoidea. Suárez-Morales and Iliffe (1996) created a separate superfamily for this family, but because in a number of characteristics, *Fosshagenia* overlaps with genera in the Diaptomoidea, it is placed here pending a more-objective analysis.



**Fig. 3.** Habitat and feeding cladogram of arietelloidean families (adapted from Soh 1998). BP, benthopelagic; C, carnivore; P, pelagic; S, suspension feeder.

with the doubling of aesthetacs and loss of the geniculation on the male antennule (Ohtsuka and Huys 2001), appears to be significant evolutionary steps which would have made pelagic members of the superfamilies involved better equipped to withstand the impacts of sighted predators, compared with the Arietelloidea and Diaptomoidea. The escape reaction of a species such as *Pleuromomma xiphias* is 6.6 ms in duration compared with that of *Undinula vulgaris* which is 1.5 ms (Lenz et al. 2000). The period of copulation of *Calanus* (without a geniculated male antennule) is very short compared with that of the Diaptomoidea (Tsuda and Miller 1998).

For the lineages that existed in the Permian to show continuity through to the modern fauna, they would have had to have survived the expansion of the OMZ in the Jurassic and Cretaceous as well as the K-T boundary event. In the case of the Jurassic-Cretaceous expansion of the OMZ, some taxa that survived must have been epipelagic to escape the anoxic conditions, while other taxa may have adapted to the low-oxygen conditions (Saltzman and Wishner, 1997) either in the water column or near the sea floor. During the K-T boundary event, taxa would have survived if they were not obligate herbivores and fed on micro-heterotrophs or detritus, or were carnivores, had dormant periods in their life cycle, or already lived benthopelagically, feeding on detritus or carnivorously.

### Colonization routes of the deep-sea benthopelagic Calanoida

There are two possible routes by which the ancestors of the Arietelloidea and Clausocalanoidea could have invaded the deep-sea benthopelagic environment from the Permian onwards (Fig. 5). First, they could have remained in surface waters during the Jurassic to Cretaceous expansion of the OMZ, then invaded shallow benthopelagic habitats, and only in the Tertiary migrated into deeper waters. Second, as carnivores, detritivores, or omnivores, they could have adapted to the low-oxygen waters near the deep seafloor and then to deep benthopelagic habitats during the Jurassic to Cretaceous expansion of the OMZ and were thus well equipped to survive the K-T boundary event. It is possible that both of these routes were used.

One piece of evidence that may support a Permian/Triassic reinvasion of the deep benthopelagic environment is that Childress et al.

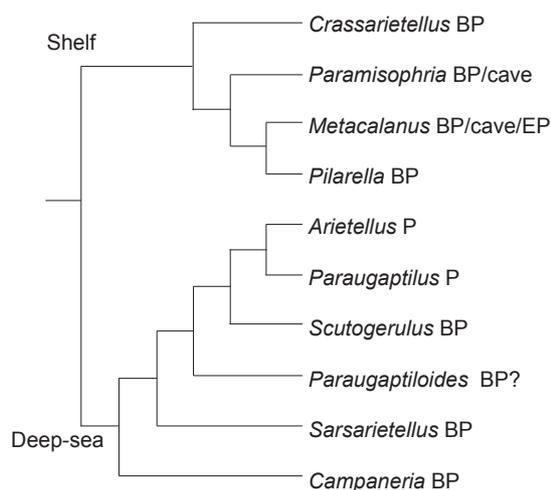
(1989) found that benthopelagic copepods, ranging in wet weight from 0.020 to 0.125 g, consumed on average  $0.067 \mu\text{l O}_2 (\text{mg wet wt})^{-1} \text{h}^{-1}$ . This is low compared with about  $0.2 \mu\text{l O}_2 (\text{mg wet wt})^{-1} \text{h}^{-1}$  for epipelagic copepods (e.g., Drits et al. 1994). Christiansen et al. (2001) also remarked on the low weight-specific respiration rates for the bathyal benthic boundary layer zooplankton community in the NE Atlantic. These data are suggestive of a Permian/Triassic reinvasion of the deep benthopelagic environment. That is, they were selected for low oxygen demand by the timing of their reinvasion of the deep benthic boundary layer.

In the following sections, details, as far as there is evidence, are teased out for the two main superfamilies that currently populate the deep-sea benthopelagic.

### Arietelloidea

Among the Arietelloidea, it is mainly the Arietellidae that are strictly benthopelagic, although other families do seem to have a looser association with the seafloor (Table 1). It is possible that the carnivorous Arietellidae invaded the deep benthopelagic realm in the late Carboniferous and Permian during the first really deep ventilation of the oceans. Soh's (1998) cladistic analysis (see above) (Fig. 3) is consistent with this hypothesis.

Ohtsuka et al.'s (1994) cladistic analysis of the Arietellidae (Fig. 4) fits within the analysis of Soh (1998) and indicates that they are basically



**Fig. 4.** Habitat cladogram of the Arietellidae (adapted from Ohtsuka et al. 1994). BP, benthopelagic; EP, epipelagic; P, pelagic.

benthopelagic with only a few being pelagic. There are two main lineages: one inhabiting shelf depth environments, and the other inhabiting slope and deeper depths. It is suggested here that this radiation occurred in the Permian/Triassic. The more plesiomorphic genera of both the shallow and deepwater lineages are benthopelagic. Nevertheless, Ohtsuka et al. (1991) showed that the most plesiomorphic species of *Paramisophria* are found near the edge of the continental shelf, while the most apomorphic species are found in the lower intertidal and upper subtidal zones. Jaume et al. (2000), in a study of Mediterranean *Paramisophria*, concluded that cave species are derived from the shallow-water fauna, and they suggested that bathyal species have been derived repeatedly from a shallow-water ancestral stem. The survival of benthopelagic Arietelloidea lineages may have been enhanced by the selection of those species with a tolerance to low oxygen concentrations after the Permian. The Arietelloidea is now dominant among those pelagic species that are tolerant of low oxygen concentrations in the tropical eastern Pacific (Saltzman and Wishner, 1997).

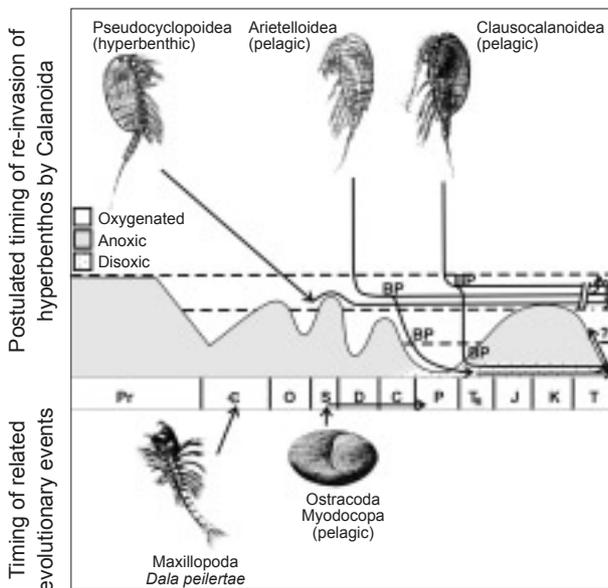
On balance, my working hypothesis is that the deep-sea benthopelagic Arietelloidea apparently reinvaded the benthic environment, at both shallow and deep depths, possibly as early as the Permian/Triassic (Fig. 5). The known number of deep-sea species is relatively small, and most have been taken at slope depths, although *Crassiarietellus huysi* is known from about 4000 m (Table 1).

### Clausocalanoidea

Several clausocalanoidean families dominate deep-sea benthopelagic calanoid copepods faunas: the mostly omnivorous Aetideidae and some of the group of families that have sensory setae on the maxilla are assumed to be detritivores. As mentioned previously, the Clausocalanoidea are distinguished from the more primitive forms by having developed myelinated nerve sheaths and thus have faster reaction times (Lenz et al. 2000). It is possible that the pelagic realm was the primary habitat in which the evolution of the ancestors of the Clausocalanoidea arose, because that is where the lowering of environmental turbidity that occurred in the Permian is hypothesized to have driven the selection of myelinated nerve axons and other characteristics as a response to predator avoidance (Bradford-Grieve 2002). Members of this more apomorphic superfamily have also secondarily reinvaded the benthic realm.

### Aetideidae

Within the Aetideidae, there are a number of characters that can have a more or less plesiomorphic state. For example, the antennal exopod may have all the ancestral segmental setae present (not counting the 3 terminal setae), all the way to the setae on ancestral segments 1-3 or 4 and 9 being absent. Although female, pelagic members of this family have no leg 5, some benthopelagic species have a rudimentary leg 5 present (*Comantenna*, *Parabradyidius*, *Pseudotharybis*, *Sursamucro*, and some species of *Aetideopsis*). Pedigerous somites 4 and 5 may be separate or in various stages of fusion, and male leg 5 may be biramous on both sides, uniramous on both sides, and even absent from one side. A superficial examination shows that these characters are not necessarily correlated, based on existing descriptions, so we await a cladistic analysis of aetideid genera to help with the interpretation of relationships and phylogeny. Nevertheless, it is tempting



**Fig. 5.** Summary of the hypotheses concerning the appearance of benthopelagic Calanoida (e.g., Pseudocyclopoidea) and main periods of re-invasion of the benthopelagic habitat by calanoid copepods of the superfamilies Arietelloidea and Clausocalanoidea; summary of supporting evidence from fossil benthic Maxillopoda (*Dala peilertae*) (sketch made available by Prof. Dieter Waloszek, Univ. of Ulm, Germany), pelagic Ostracoda *Mydocopa* (from Moore 1961) (lower part of diagram). The key to the geological periods is in fig. 1.

Table 1. Species of calanoid Copepoda recorded from near the deep-sea floor at depths &gt; 200 m

Species	Seafloor depth (m)	Height above bottom (m)	Geographic region	Reference	Species	Seafloor depth (m)	Height above bottom (m)	Geographic region	Reference
Arietellidae					<i>Metridia</i> spp.	1895-1930	?	Guaymas basin	Wiebe et al. 1988
Arietellidae	4500	0-100	NE Atlantic	Christiansen et al. 1999	Metridiidae	4500	0-100	NE Atlantic	Christiansen et al. 1999
<i>Campaneria latipes</i>	1234-1260	?	NE NZ slope	Bradford 1969 as <i>S. pelophilus</i> M; Ohtsuka et al. 1994	Bathypontiidae	1238-1690	?	NE NZ slope San Diego Trough	Bradford 1969
<i>Crassaretellus huysi</i>	3976-4060	?	off W Africa	Ohtsuka et al. 1994	<i>Alloiodopus pinguis</i>	1100-1200	10	NE Atlantic	Wishner 1980
<i>Griceus buskeyi</i>	675	30	Hawaii	Ferrari and Markhaseva 2000b	<i>Bathypontia</i> sp.	4500	0-100	NE Atlantic	Christiansen et al. 1999
<i>Paramisophria bathyalis</i>	1258	0.1	Mediterranean	Jaume et al. 2000	Ryocalanidae				
<i>Paramisophria intermedia</i>	400	0.1	Mediterranean	Jaume et al. 2000	<i>Ryocalanus asymmetricus</i>	2973-2992	1-5	E tropical Pacific	Markhaseva and Ferrari 1996
<i>Paraugaptiloides magnus</i>	1060-1070	2	SW Indian Ocean	Heinrich 1993 as <i>Paraugaptilus magnus</i>	<i>Ryocalanus bicornis</i>	1291-1316	1-5	E tropical Pacific	Markhaseva and Ferrari 1996
<i>Paraugaptiloides magnus</i>	1697	?	NE NZ slope	Bradford 1969 as <i>Paraugaptilus magnus</i> ; Ohtsuka et al. 1994	<i>Ryocalanus bowmani</i>	3022-3100	1-5	E tropical Pacific	Markhaseva and Ferrari 1996
<i>Sarsarietellus abyssalis</i>	?	?	?	Sars 1905; Ohtsuka et al. 1994	<i>Ryocalanus spinifrons</i>	1500	100	Sagami Bay, Japan	Shimode et al. 2000
<i>Sarsarietellus natalis</i>	1083-1090	30	SW Indian Ocean	Heinrich et al. 1993	Aetideidae				
<i>Scutogerullus pelophilus</i>	1234-1278	?	NE NZ slope	Bradford 1969	<i>Aetideidae</i>	4500	0-100	NE Atlantic	Christiansen et al. 1999
Hyperbionychidae					<i>Aetideopsis</i> sp. 1	1100-1200	10-100	San Diego Trough	Wishner 1980
<i>Hyperbionyx pluto</i>	3870-4036	20-100, 100-500	NE Atlantic	Ohtsuka et al. 1993	<i>Aetideopsis magna</i>	1750-1820	0.3	south of Woods Hole	Grice & Hulsemann 1970
Lucicutiidae					<i>Aetideopsis minor</i>	1983	1.0-1.3	Wedell Sea	Schulz & Markhaseva 2000
<i>Lucicutia</i> sp. 1	1100-1200	10-100	San Diego Trough	Wishner 1980	<i>Aetideopsis rostrata</i>	2000-3000	?	Laptev Sea	Sirenko et al. 1996
<i>Lucicutia</i> sp. 2	1100-1200	10-100	San Diego Trough	Wishner 1980	<i>Aetideopsis tumorosa</i>	299-452	?	NE NZ upper slope	Bradford-Grieve in press
<i>Lucicutia</i> sp. 7	1100-1200	100	San Diego Trough	Wishner 1980	<i>Azygokeras columbiae</i>	650	400-600	Bute Inlet, British Columbia[?]	Koeller and Littlepage 1976
Lucicutiidae					<i>Bradyetes inermis</i>	991-1500	0.2-0.5	off E US	Grice 1972
	4500	0-100	NE Atlantic	Christiansen et al. 1999	<i>Bradyetes matthei</i>	548-580	?	Fensfjorden, Norway	Johannessen, 1976
Metridiidae					<i>Bradydillus capax</i>	299-452	?	NE NZ upper slope	Bradford-Grieve in press
<i>Metridia</i> sp. 1	1100-1200	10-100	San Diego Trough	Wishner 1980	<i>Bradydillus lulae</i>	1465-1500	0.2-0.5	off E US	Grice 1972
					<i>Bradydillus similis</i>	550-1000	?	Laptev Sea	Sirenko et al. 1996

Table 1. (Cont.)

Species	Seafloor depth (m)	Height above bottom (m)	Geographic region	Reference	Species	Seafloor depth (m)	Height above bottom (m)	Geographic region	Reference
<i>Bradydium spinifer</i>	299-452	?	NE NZ upper slope	Bradford-Grieve 2003	Euchaetidae	1100-1200	10-100	San Diego Trough	Wishner 1980
<i>Chiridius</i> sp. 1	1100-1200	10	San Diego Trough	Wishner 1980	<i>Euchaeta</i> sp. 1	1100-1200	10-100	San Diego Trough	Wishner 1980
<i>Chiridius</i> spp	1100-1200	10	San Diego Trough	Wishner 1980	<i>Euchaeta</i> sp. 2	1100-1200	10	San Diego Trough	Wishner 1980
<i>Chiridius</i> nr. <i>gracilis</i>	1895-1930	?	Guaymas basin	Wiebe et al. 1988	Euchaetidae	4500	0-100	NE Atlantic	Christiansen et al. 1999
<i>Comantenna crassa</i>	1234-1260	?	NE NZ slope	Bradford 1969	Scolecitrichidae	1100-1200	10	San Diego Trough	Wishner 1980
<i>Comantenna recurvata</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970	<i>Amalothrix</i> sp. 1	1100-1200	10	San Diego Trough	Wishner 1980
<i>Crassantenna comosa</i>	1383-1397	?	NE NZ slope	Bradford 1969	<i>Grievella shanki</i>	2788	1	E tropical Pacific	Ferrari and Markhaseva 2000
<i>Crassantenna mimostrata</i>	1234-1697	?	NE NZ slope	Bradford 1969	Phaenidae	4500	0-100	NE Atlantic	Christiansen et al. 1999
<i>Gaidius</i> sp. 1	1100-1200	10	San Diego Trough	Wishner 1980	<i>Scolecitrichidae</i> / <i>Phaenidae</i>	2945-3010	1-5	E tropical Pacific	Ferrari and Markhaseva 2000
<i>Gaidius minutus</i>	1895-1930	?	Guaymas basin	Wiebe et al. 1988	<i>Brachycalanus broodskyi</i>	675	?	Hawaii	Ferrari and Markhaseva 2000
<i>Lutamator hurelyi</i>	1357	?	NE NZ slope	Bradford 1969	<i>Brachycalanus flemingeri</i>	1465-1500	0.2-0.5	off E US	Grice 1972
<i>Lutamator elegans</i>	900	?	Brazilian coast	Alvarez 1984	<i>Brachycalanus minutus</i>	992-1000	0.2-0.5	off E US	Grice 1972 as X. <i>ordinarius</i> ;
<i>Mesocomantenna spinosa</i>	346	?	Brazilian shelf and slope	Alvarez 1986	<i>Brachycalanus ordinarius</i>	1895-1930	?	Guaymas basin	Ferrari and Markhaseva 2000
<i>Parabrydium angelikee</i>	1983	1.0-1.3	Wedell Sea	Schulz and Markhaseva 2000	<i>Xanthocalanus</i> spp.	550-1000	?	Laptev Sea	Wiebe et al. 1988
<i>Parabrydium spinibasis</i>	1690-1697	?	NE NZ slope	Bradford 1969 as <i>Bradydium</i> ; Schulz and Markhaseva 2000	<i>Xanthocalanus alviniae</i>	1750-1822	0.3	south of Woods Hole	Sirenko et al. 1996
<i>Paracomantenna wishnerae</i>	825	1-5	E tropical Pacific	1994/5	<i>Xanthocalanus alviniae</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<i>Paracomantenna minor</i>	800	?	W of Ireland	Farran 1905 as <i>Bryaxis minor</i>	<i>Xanthocalanus distinctus</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<i>Pseudeuchaeta flexuosa</i>	1690-1697	?	NE NZ slope	Bradford 1969	<i>Xanthocalanus elongatus</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<i>Pseudeuchaeta magna</i>	1690-1697	?	NE NZ slope	Bradford 1969	<i>Xanthocalanus elongatus</i>	992-1500	0.2-0.5	off E US	Grice 1972
<i>Pseudochirella vulgaris</i>	2973	1-5	E tropical Pacific	Markhaseva, 1997	<i>Xanthocalanus gracilis</i>	171-659	?	Antarctic	Ohtsuka et al. 1998
<i>Pseudotharyx brevispinus</i>	1194-1278	?	NE NZ slope	Bradford 1969 as <i>Bradydium</i>	<i>Xanthocalanus harpagatus</i>	597	?	under Ross Ice Shelf	Bradford and Wells 1983
<i>Pseudotharyx dentatus</i>	1357-1697	?	NE NZ slope	Bradford 1969 as <i>Bradydium</i>	<i>Xanthocalanus laptevorum</i>	2000	?	Laptev Sea	Markhaseva 1998
<i>Pseudotharyx robustus</i>	1184-1193	?	NE NZ slope	Bradford 1969 as <i>Bradydium</i>	<i>Xanthocalanus macrocephalon</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<i>Pterochirella tuerkayi</i>	1318	0.1	Gulf of Aden	Schulz 1990	<i>Xanthocalanus obtusus</i>	1465-1500	0.2-0.5	off E US	Grice 1972
<i>Sursamuro spinatus</i>	1210-1697	?	NE NZ slope	Bradford 1969					

Table 1. (Cont.)

Species	Seafloor depth (m)	Height above bottom (m)	Geographic region	Reference	Species	Seafloor depth (m)	Height above bottom (m)	Geographic region	Reference
<i>Xanthocalanus pinguis</i>	992-1500	0.2-0.5	off E US	Grice 1972	<i>Neoscolecithrix watersae</i>	1465-1500	0.2-0.5	off E US	Grice 1972
<i>Xanthocalanus polaristernae</i>	180-530	?	Laptev Sea	Markhaseva 1998	<i>Parundinella emarginata</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<i>Xanthocalanus polaris</i>	3000	?	Laptev Sea	Sirenko et al. 1996	<i>Parundinella emarginata</i>	1465-1500	0.2-0.5	off E US	Grice 1972
<i>Xanthocalanus spinodenticulatus</i>	2000	?	Laptev Sea	Markhaseva 1998	<i>Rythabis atlantica</i>	2860	100	N Atlantic	Schulz and Beckman 1995
<i>Xanthocalanus</i> sp. 1	1465-1500	0.2-0.5	off E US	Grice 1972	<i>Tharybis angularis</i>	2860	100	N Atlantic	Schulz and Beckman 1995
<i>Xanthocalanus</i> sp. 2	1465-1500	0.2-0.5	off E US	Grice 1972	<i>Tharybis crenata</i>	2860	100	N Atlantic	Schulz and Beckman 1995
<i>Xanthocalanus macilenta</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970	<i>Tharybis inaequalis</i>	299	0.6	NE NZ upper slope	Schulz and Beckman 1995
<i>Xanthocalanus rotunda</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970	<i>Tharybis magna</i>	260-659	?	Antarctica	Bradford-Grieve 2001a
<i>Xanthocalanus rotunda</i>	1465-1500	0.2-0.5	off E US	Grice 1972 as <i>Amalophora</i>				Antarctica	Bradford and Wells 1983; Ohtsuka et al. 1998
<b>Parkiidae</b>					<i>Tharybis minor</i>	540	?	off W Africa	Schulz 1981
<i>Parkius karenwishererae</i>	2945-3010	1-5	E tropical Pacific	Ferrari and Markhaseva 1996	<i>Undinella altera</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<b>Tharybidae</b>					<i>Undinella compacta</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<i>Tharybidae</i>	4500	0-100	NE Atlantic	Christiansen et al. 1999	<i>Undinella compacta</i>	1465-1500	0.2-0.5	off E US	Grice 1972 as <i>Amalophora</i>
<i>Cenognatha antarctica</i>	780-1050	?	Antarctic Sound	Hulsemann 1985 as <i>N. antarctica</i>	<i>Undinella hampsoni</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<i>Cenognatha caetanoi</i>	900	?	Brazilian slope	Alvarez 1985	<i>Xanthanus renatehassae</i>	1050	?	Antarctica	Schulz 1998; Ohtsuka et al. 1998
<i>Cenognatha farrani</i>	550-1000	?	Laptev Sea	Sirenko et al. 1996 as	<i>Tharybidae</i> sp.	1100-1200	10	San Diego Trough	Wishner 1980
<i>Cenognatha farrani</i>	170-255	?	Norwegian coast	<i>Neoscolecithrix</i> Fosshagen 1972					
<i>Cenognatha farrani</i>	530-1016		Laptev Sea	Sirenko et al. 1996	<i>Diaixis asymmetrica</i>	1750-1822	0.3	south of Woods Hole	Grice and Hulsemann 1970
<i>Neoscolecithrix koehlerii</i>	950-1710	?	?	Canu 1996	<i>Diaixis helenae</i>	822-825	?	SW Africa	Andronov 1979
<i>Neoscolecithrix magna</i>	1465-1500	0.2-0.5	off E US	Grice 1972 as <i>Oothrix</i>	<i>Diaixis trunovi</i>	500-800	?	SW Africa	Andronov 1979
<i>Neoscolecithrix</i> cf. <i>magna</i>	452	0.6	NE NZ upper slope	Bradford-Grieve 2001b	<i>Diaixis asymmetrica?</i>	920	?	SW Africa	Andronov 1979
<i>Neoscolecithrix ornata</i>	306	0.6	NE NZ upper slope	Bradford-Grieve 2001b	<b>Spinocalanidae</b>				
					<i>Damkaeria faicifera</i>	1380	?	Norwegian Sea	Fosshagen 1983
					<i>Isaacsicalanus paucisetus</i>	2600	1	East Pacific Rise	Fleminger 1983

to conclude that some deep-sea aetideid genera are older than pelagic genera, as they have several ancestral characters: e.g., pedigerous somites 4 and 5 of *Sursamucro* are separate, the antenna has 9 ancestral setae present on the exopod, and a rudimentary female leg 5 is present (Bradford 1969). In addition, this species has very long, annulate setae on the antennule (the function of which is not known but is probably sensory), which appear to be a characteristic of truly benthopelagic aetideids. Also aetideids are mostly omnivorous feeders (e.g., Arashkevich 1969) and some species can be active predators (Alvarez and Matthews 1975).

It appears that the benthopelagic environment was first invaded by the Aetidae in deep waters as there are many more genera found there, and there is little overlap in genera found in these two environments apart from *Bradyidius*, *Comantenna*, and *Mesocommantenna* (Table 2). Knowledge of the oxygen requirements of various genera might give a clue as to the environment that was originally reinvaded. If a genus has high oxygen requirements, then it may be reasonable to assume that shallow benthic environments were the original habitat with subsequent migration to deeper depths once deep waters became ventilated in the Tertiary. The converse might be true for genera that first evolved in low-oxygen deep water in the Triassic, Jurassic, and Cretaceous and later migrated into shallow waters (Fig. 5).

#### **Diaixidae, Parkiidae, Phaennidae, Tharybidae, and Scolecitrichidae**

Among the deep-sea Clausocalanoidea is a group of families (the Diaixidae, Parkiidae, Phaennidae, Tharybidae, and some Scolecitrichidae) with sensory setae on the maxilla endopod. These sensory setae may be worm-like or brush-like and are inferred, from an ultrastructure study of two scolecitrichid genera, to have properties of the general and specific detection of chemicals in food particles, respectively (Nishida and Ohtsuka 1997). They concluded that these assumed functions are consistent with the food habits of scolecitrichids as detritivores, although much is yet to be learned especially about the high diversity of brush-like setae in the various families. Among these families, there is still much taxonomic confusion (e.g., Ferrari and Markhaseva 2000a). New species, genera, and families are actively being added to the benthopelagic calanoid fauna. Thus a phylogenetic analysis has not yet been

made, and it is very difficult to decide which forms are the more derived.

If these setae have evolved in response to detrital, scavenging, or even carnivorous feeding opportunities (e.g., Arashkevich 1969, Ferrari and Steinberg 1993, Steinberg 1995) in geological time, and only among the Clausocalanoidea, then it might be fruitful to look for the environmental driver that may have brought these adaptations about. Given that the current hypothesis is that the Clausocalanoidean ancestor arose in the Permian (Bradford-Grieve 2002), then the first really big challenges for such pelagic forms would have been the expansion of the OMZ in the Jurassic and Cretaceous as well as the K-T boundary event. Here it is postulated that the shrinking of a well-oxygenated pelagic zone in which these families could live led to new evolutionary opportunities in the benthopelagic zone. Those clausocalanoideans that experienced genetic mutations that resulted in the transformation of endopod setae on the maxillae and some other mouthparts into sensory setae, would have had an advantage in a detrital environment. Those families would also have been the best equipped to survive the K-T boundary event. There is also fossil evidence that other deep-benthic species came through this period (Kennett 1982). The ancestral clausocalanoidean reinvaders of the deep benthopelagic environment may have been like the Tharybidae.

If we consider the Tharybidae to be composed of the genera in Table 1 (a situation not yet generally accepted), then the ancestor of these genera probably had feeding males with well-developed mouthparts, had 3 setae on the second coxal endite of the maxilliped, and had asymmetrical male antennules (*Tharybis*, at least, has slightly asymmetrical male antennules, as ancestral segments XXII and XXIII are fused on the right and separate on the left (Schulz 1981, Bradford-Grieve 2001a)). Thus, the current working hypothesis is that tharybid-like pelagic ancestors of these families adapted to, and reinvaded, the benthopelagic environment in the late Permian/Triassic where they survived the Jurassic and Cretaceous periods. Later, ancestors of the Scolecitrichidae and Phaennidae possibly returned to the water column in the Tertiary (Fig. 5).

The present analysis has not canvassed all the possible options but has concentrated on a story that seems, intuitively, to be the most parsimonious. Nevertheless, with rapid advancements in genetic analysis techniques, it appears likely

**Table 2.** Benthopelagic calanoid copepod taxa from the continental shelf and deep sea. The families marked with an asterisk (\*) have members that live in anchialine caves. The association of some cave-dwelling genera and species with a benthopelagic habit is not obvious, since they were sampled from the water column in such anchialine caves (e.g., Fosshagen et al. 2001). Nevertheless, we may interpret the habitat of species in caves with an indirect connection to the sea as being entirely related to the surfaces of the cave

Superfamily	Shallow water			Deep-sea			
	Family	Genera	Superfamily	Family	Genera	Genera	
Pseudocyclopoidea	Pseudocyclopiidae*	<i>Pseudocyclops</i>	Dixidae	Anawekia	<i>Crassantenna</i>	Mesocomantenna	
		Ridgewayiidae*			<i>Exumella</i>		<i>Gaidius</i>
	Epacteriscioidea	<i>Placocalanus</i>			<i>Mesaiokeras</i>		<i>Lutamator</i>
		<i>Ridgewayia</i>			<i>Macandrewella</i>		<i>Mesocomantenna</i>
		<i>Brattstromia</i>			<i>Brachycalanus</i>		<i>Parabradylidius</i>
		<i>Balinella</i>			<i>Pseudophaenna</i>		<i>Paracomantenna</i>
		<i>Bofuriella</i>			<i>Talacalanus?</i>		<i>Pseudeuchaeta</i>
		<i>Bomburiella</i>			<i>Xanthocalanus</i>		<i>Pseudotharybis</i>
		<i>Bunderia</i>			<i>Brachycalanus</i>		<i>Pterochirella</i>
		<i>Enantiosis</i>			<i>Brachycalanus</i>		<i>Sursamucro</i>
<i>Enantronoides</i>	<i>Brachycalanus</i>	<i>Diaixis</i>					
<i>Epacteriscus</i>	<i>Grievella</i>						
<i>Erebnectes</i>							
<i>Erebnectoides</i>							
<i>Gloinella</i>							
<i>Oinella</i>							
<i>Arietelloidea</i>							
<i>Metacalanus</i>							
Bathypontoidea	Arietellidae*	<i>Campaneria</i>	Pseudocyclopiidae*	Frigocalanus	<i>Parkius</i>	Cenognatha	
		<i>Crassarictellus</i>			<i>Paracyclopia</i>		<i>Cenognatha</i>
		<i>Griceus</i>			<i>Pseudocyclopia</i>		<i>Cenognatha</i>
		<i>Paraugaptiloides</i>			<i>Stygocyclopia</i>		<i>Neoscolecithrix</i>
		<i>Paramisophria</i>			<i>Thompsonopia</i>		<i>Parundinella</i>
		<i>Sarsarietellus</i>			<i>Parastephos</i>		<i>Rythabis</i>
		<i>Scutogerulus</i>			<i>Stephos</i>		<i>Tharybis</i>
		<i>Hyperbionyx</i>			<i>Miostephos</i>		<i>Undinella</i>
		<i>Allolopodus</i>					<i>Xantharus</i>
		<i>Bathypontia</i>					
<i>Ryocalanus</i>							
Ryocalanoidea	Ryocalanidae						
	Pontellidae						
Diptomoidea	Pseudodiptomidae	<i>Calanopia</i>					
		<i>Pseudodiptomus</i>					
Clausocalanoidea	Aetideidae	<i>Aetideopsis</i>					
		<i>Azygokeras</i>					
		<i>Bradyetes</i>					
		<i>Bradyidius</i>					
		<i>Chiridius</i>					
		<i>Comantenna</i>					

that the current hypotheses may be testable using genetic information in the near future.

## CONCLUSIONS

- The deep BBL is a zone of relatively intense biological activity within the deep sea, being distinguished from the remainder of the water column by its concentrations of particulate matter, biologically active chemical substances, species composition, elevated biomasses of organisms (from bacteria to fish), and elevated metabolic rates.
- Oxygen availability was probably a key environmental factor in geological time governing the evolution of deep-living benthopelagic calanoids.
- The deep-benthopelagic calanoid copepod fauna is still not well known.
- The deep-sea calanoid fauna is composed mainly of the Arietelloidea, Ryocalanoidea, Bathypontioidea, and Clausocalanoidea. The most primitive benthopelagic calanoid superfamilies (Pseudocyclopoidea, Epactersicidae, some genera of the Arietelloidea, and a few Diaptomoidea) are found only at shallow depths.
- The Arietellidae, Aetideidae, and Tharybidae all have greater diversity in the deep sea, whereas the Diaixidae and Phaennidae are more diverse in shallow waters. Two-thirds as many families are known from continental shelf depths as are known from slope and deeper depths. Thus there appears to have been more intensive diversification in the deep-sea benthopelagic environment.
- Deep-sea benthopelagic calanoids probably all represent reinvasions of the benthic boundary layer from the water column.
- The Permian onwards is postulated as having been the period when the carnivorous Arietelloidea and the omnivorous and detritivorous Clausocalanoidea invaded the benthopelagic realm as the OMZ expanded and new evolutionary opportunities opened up in the low-oxygen benthopelagic zone. The low oxygen requirements and low weight-specific respiration rates of benthopelagic copepods are suggestive of a Permian/Triassic reinvasion of the deep BBL.

**Acknowledgments:** Support by the New Zealand Foundation of Research Science and Technology (contract CO1X0026) is acknowledged. I acknowledge Prof. Geoff Boxshall's encouragement to

speculate about the origins of calanoids in different environments. Thanks are also due to an anonymous reviewer whose perceptive responses helped to improve the manuscript.

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