

SOME OF THE DEEP-SEA FAUNA IS ANCIENT

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ABSTRACT

Decreasing deep-sea floor temperatures during the mid Cainozoic, and a presumed widespread disoxia in the deep sea prior to this era has lead many authors to suggest that the deep-sea fauna has accumulated during the last 30-40 mybp only. This hypothesis argues for extinction and replacement of earlier faunas. Some taxa, such as the Ostracoda, show extensive taxonomic replacement during the Miocene that is correlated with declining sea floor temperatures. A recent evaluation of the deep Atlantic distribution of major isopod clades, however, demonstrated that two different historical patterns are present. One pattern ("Flabellifera") conforms to a relatively recent Cainozoic and ongoing colonization of the deep sea, with relative impoverishment of species with depth. The other pattern (Asellota) is one that is rich in deep-sea species, and has a high level of endemic morphological diversity, suggesting a long period of evolution in isolation. Glaciation during the late Palaeozoic and an early phylogenetic origination of the Asellota support the hypothesis that these isopods colonized the deep sea prior to the disoxia events during the Mesozoic and the early Cainozoic. The Mesozoic deep sea is unlikely to have become completely anoxic globally owing to vertical halothermal circulation at low latitudes, allowing the possibility of oxygenated refuges in deep water. Elements of the Palaeozoic fauna, therefore, may have persisted through the Mesozoic without representation in marine shallow waters. Within the isopods, these Palaeozoic relicts have taken two adaptive directions. In freshwater, the Phreatoicidea show morphological stasis, with modern taxa resembling fossils from Carboniferous and Triassic eras. The Asellota, on the other hand, have evolved into a many different morphological types and a huge number of species globally.

RÉSUMÉ

La diminution de la température dans l'océan profond pendant le Cénozoïque ainsi qu'un présumé appauvrissement en oxygène apparu avant cette ère a conduit beaucoup d'auteurs à suggérer que la faune profonde ne s'est accumulée que pendant les derniers 30-40 mybp seulement. Cette hypothèse plaide pour l'extinction et le remplacement des faunes antérieures. Quelques taxa, tels les Ostracoda, montrent un remplacement taxonomique important pendant le Miocène qui est corrélé avec les températures en baisse de l'océan profond. Une évaluation récente de la distribution atlantique profonde des clades principaux d'Isopodes montre cependant que deux configurations historiques différentes sont présentes. Une configuration ("Flabellifera") se conforme à une colonisation Cénozoïque récente et continue de la mer profonde, avec un appauvrissement relatif des espèces avec la profondeurs. L'autre configuration (Asellota) traduit une grande richesse

des espèces profondes, et un niveau élevé de diversité morphologique endémique, suggérant une longue période d'évolution en isolement. Les Glaciations à la fin du Paléozoïque et une origine phylogénétique plus ancienne des Asellota supportent l'hypothèse que ces Isopodes ont colonisés la mer profonde avant les événements d'appauvrissement en oxygène pendant le Mésozoïque et le Cénozoïque ancien. La mer profonde du Mésozoïque est peu susceptible d'être devenue complètement anoxique en raison, globalement, de la circulation verticale halothermique sous les basses latitudes, ce qui avait permis la possibilité de refuges oxygénés dans l'eau profonde. Les éléments de la faune du Paléozoïque ont pu donc persister lors du Mésozoïque sans représentants dans les eaux peu profondes marines. Chez les Isopodes, ces relictés du Paléozoïque ont pris deux directions adaptatives. Dans les eaux douces, les Phreatoicidea montrent une stase morphologique avec des taxa modernes ressemblant à des fossiles du Carbonifère et/ou du Trias. Les Asellota d'autre part, ont évolué en beaucoup de types morphologiques différents et, globalement, en un nombre énorme d'espèces.

Two hypotheses about the age of the deep-sea fauna have been proposed.

The **entire** deep-sea fauna died out prior to the mid Cainozoic Era, and was replaced by immigrants from shallow water.

**Some** deep-sea fauna survived from ancient Palaeozoic and Mesozoic Eras, and co-exist with recent immigrants from shallow water.

The first hypothesis is exclusive but the second is not. In this paper, I argue that data on deep-sea isopods are most consistent with the second hypothesis. Because these data come from the isopods, their evolutionary properties in comparison to other isopod clades are discussed.

Stock (1986: 106) argued that "A deep-sea origin of certain animals in salty caves . . . is not likely, since the anoxia stages of the Middle Tertiary would have wiped out the Tethyan bathyal/abyssal fauna." Although Stock's discussion is somewhat peripheral to this paper, it shows the tenacity of ideas relating to the extinction of ancient deep-sea faunas. Proponents of a recent origin of the current deep-sea fauna include Dahl (1954), Wolff (1960), Kussakin (1973), Menzies, George & Rowe (1973), and Stock (1986). Data on the deep-sea Foraminifera (cf. Douglas & Woodruff, 1981) and Ostracoda (cf. Benson et al., 1984, 1985; Van Harten, 1999, this issue) support a period of great faunal change during the middle part of the Cainozoic, with many species being recently derived from shallow water taxa. Most of these works, however, associate substantial declines in bottom water temperature with the faunal change, although a few (e.g., Stock, 1986) mention the influence of oxygen depletion: anoxia or disoxyxia, which was undoubtedly influential at least in the end Palaeocene deep-sea extinctions (Kennett & Stott, 1991, 1995). Many of these papers argue for an ongoing colonization of the deep sea from Antarctic shallow waters where cold conditions provide an isothermal conduit for migration to the deep sea (Wolff, 1960).

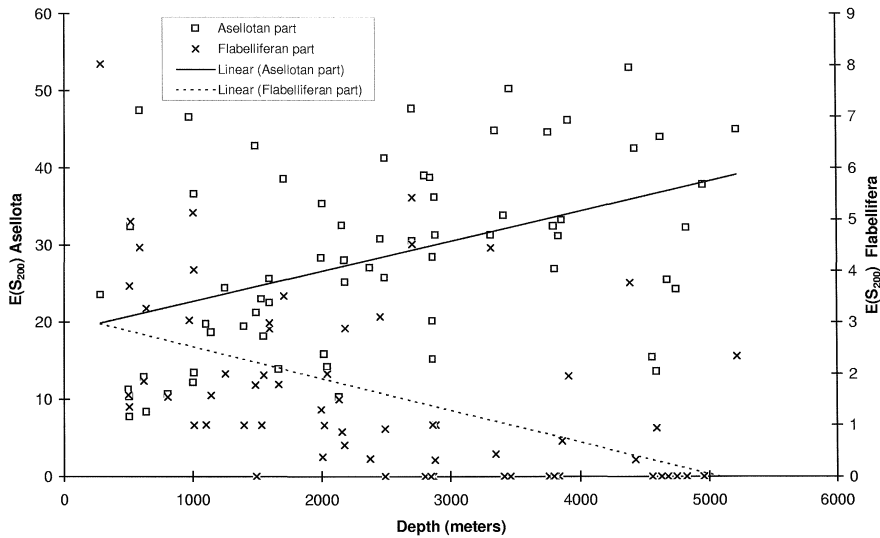
The temperature's magnitude, however, may not be important in influencing deep-sea faunas (Hessler & Wilson, 1983). As seen in isopod crustaceans and other taxa, deep-sea emergents (Hessler, 1970; Hessler & Thistle, 1975; Hessler et al., 1979; Vacelet et al., 1994) are observed in areas where the water column is isothermal, regardless of the water temperature. Deep-sea isopods live where the temperature is relatively stable, regardless of whether the temperature is 13°C at 30 m in the Mediterranean (Desmosomatidae: Schiecke & Fresi, 1969), or -1°C in 20 m at New Harbor, McMurdo Sound, Antarctica (Munnopsididae: Hessler & Strömberg, 1989). For this reason, the Cainozoic rise in deep-sea temperatures is unlikely to have caused the extinction of entire faunas.

The relative isolation of the deep sea from events at the surface has been neglected. Deeper living urchins were more likely to survive the K-T boundary (Smith & Jeffery, 1998). Deep-sea faunas of the late Permian may have had a higher probability of surviving the end Permian event, with new data now suggesting an extraterrestrial impact cause (Bowring, 1998). Deep-sea taxa of great antiquity, such as monoplacophorans (Rokop, 1972) or polychelid decapod crustaceans, have high taxonomic distinctiveness when compared with related shallow water taxa (Hessler & Wilson, 1983).

Several different lines of evidence suggest that isopods are one of these ancient taxa. Hessler and colleagues (Hessler & Thistle, 1975; Thistle & Hessler, 1976) demonstrated that some deep-sea isopod taxa evolved in situ. Their principal evidence came from deep-sea families that had shallow water representatives, such as species of the genus *Echinozone* (subfamily Ilyarachninae, Munnopsididae). These shallow-living taxa appear to be derived from deep-sea groups, with more generalized taxa occurring in the deepest regions. Moreover, those shallow-living members of deep-sea families lack eyes entirely, as would be expected for deep-sea emergent taxa. The eurycopine genus *Baeonectes* Wilson, 1982 that is found in the shallow Arctic and boreal regions is another example. The cladogram of the Munnopsididae (cf. Wilson, 1989) shows that this genus is derived later than deep-water taxa, demonstrating that *Baeonectes* is a deep-water emergent taxon.

A re-interpretation of isopod species diversity data from the Atlantic Ocean (Hessler & Wilson, 1983; Rex et al., 1993) provides additional evidence for the antiquity of the deep-sea isopods. Their distribution shows two different historical patterns (Wilson, 1998). Isopods found in deep waters may be divided into two phylogenetic groups: the suborder Asellota and a broad assemblage of higher level taxa, informally called the Flabellifera sensu lato, or simply flabelliferans. This latter grouping contains several different suborders, although an analysis of isopod phylogeny (Brusca & Wilson, 1991) suggests that it is monophyletic, derived from a single ancestor. The remaining isopods, the Phreatoicidea and

A



B

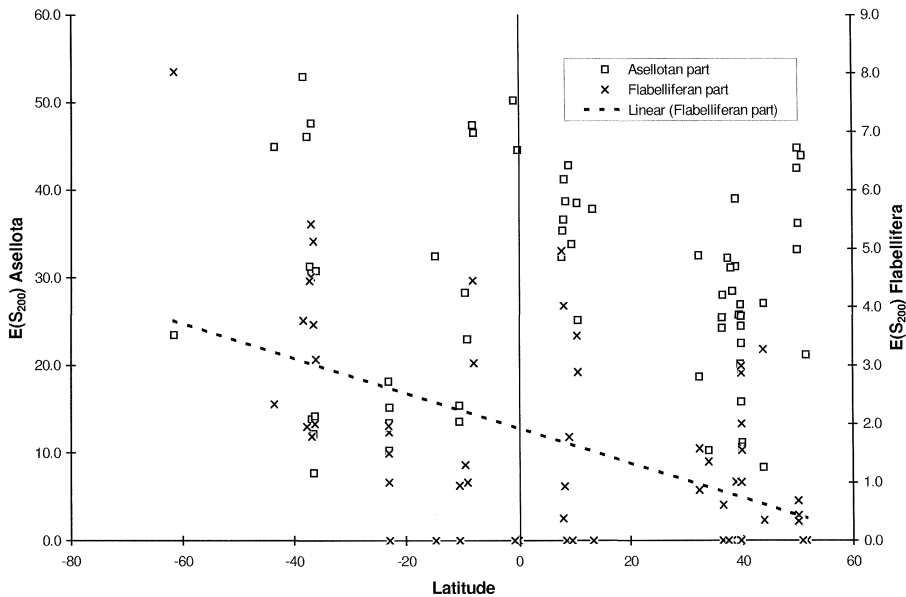


Fig. 1. Isopod diversity in the Atlantic Ocean. Diversity of the Asellota is shown on the left axis and that of the Flabellifera sensu lato is on the right axis. Diversity or species expected in 200 individuals ( $E(S_{200})$ ) is measured as an idealized subsample of a larger sample rarefied to 200 individuals using Hurlbert's (1971) method. The diversity was calculated for all isopods and then the data were partitioned into the two distinct clades afterwards. Lines on the graphs only indicate significant trends in the data. A, Relationship between depth and diversity; B, relationship between latitude and diversity. Asellota diversity has no significant relationship with latitude when both the North and the South Atlantic Ocean are considered. (Fig. after Wilson, 1998.)

the Oniscidea, are terrestrial or fresh water taxa that no longer have a marine representation. A study of isopods in the deep Atlantic Ocean found that the Asellota are diverse and ubiquitous, while the flabelliferans have few species in most areas and are poorly represented at greater depths (fig. 1A). Asellotan diversity, conversely, increases with depth. The flabelliferans also show a distinct decline in species from south to north in the Atlantic Ocean (fig. 1B).

This distribution is significant because the Asellota are derived early in isopod evolution, while the flabelliferans originate after the appearance of the terrestrial isopods, Oniscidea (Brusca & Wilson, 1991; Wilson, 1998). Combination of the flabelliferans into one clade and removing the oniscideans provides the simplified cladogram (fig. 2) that shows the historical patterns of origination of these clades, relative to the earliest derived isopods, the Phreatoicoidea. The fossil record of

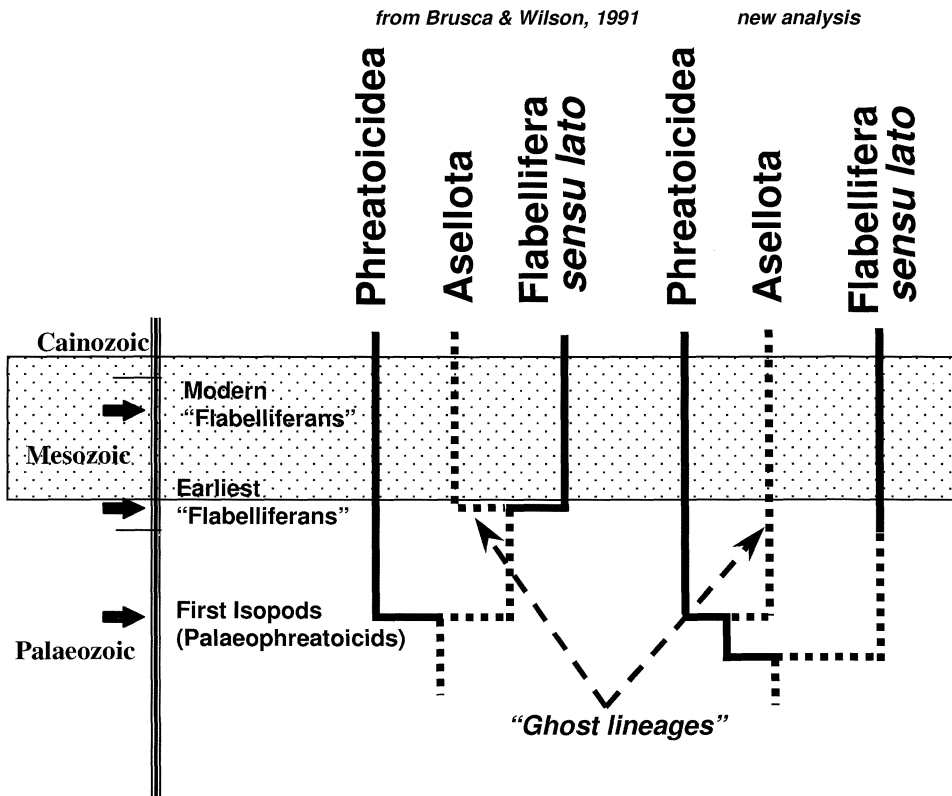


Fig. 2. Trimmed clades of the Isopoda, omitting the Oniscidea and merging all taxa in the informal taxon Flabellifera sensu lato, to show the relative origination of this taxon relative to the Phreatoicoidea and the Asellota. An approximate geological time scale is shown on the right with first appearances of fossil taxa. Ghost lineages are shown for the Asellota and earliest flabelliferans owing to an absence of a fossil record. The shaded rectangle marks the approximate periods of the highest frequency of anoxic events.

these major groups (Chilton, 1918; Hessler, 1969; Schram, 1970, 1974; Weider & Feldmann, 1992; Obata & Omori, 1993) provides palaeodates for these originations. The Phreatoicoidea have a fossil record from the late Carboniferous, thus providing a minimum age for all isopods. The flabelliferans have a few primitive taxa that appear by the Triassic, while modern flabelliferans (belonging to recognizable genera) appear only by the Cretaceous. Although the Asellota have no fossil record, their minimum age is Triassic, that of the Flabelliferans (see "ghost lineage" in fig. 2). A recent re-analysis of the isopods (unpublished data) finds that the Asellota are the sister group of the Phreatoicoideans, owing to their sharing a pattern of oostegite plates and tagmosis that is distinctly different from the rest of the Isopoda. The distributional pattern of the early derived fresh water Asellota (cf. Wilson, 1998) also supports a late Palaeozoic-early Mesozoic diversification of the Asellota.

If the Asellota were present in the late Palaeozoic, they may have colonized the deep sea prior to the extinctions of many invertebrate taxa at the end of the Palaeozoic. Owing to the ubiquitous but rare presence of some shallow water families, however, shallow water asellotes apparently survived the end Permian event. Nevertheless, the diversification of the Asellota appears to be earlier than that of the flabelliferans.

This early origination of the Asellota, the Palaeozoic (similar to the Phreatoicoideans) or Triassic at the latest, is significant when compared to the palaeoceanographic patterns during these periods. The mid to late Mesozoic periods and the early Cainozoic were times of frequent anoxia events (Fischer, 1984; Hay, 1988; Horne, 1999, this issue), evident as the widespread deposition of black shales. These events were symptomatic of an oceanography different from modern oceans. In the current oceanographic pattern, deep waters are generated by cold thermohaline flows from polar regions. Past seas may have shown "thermospheric" (Benson et al., 1984) patterns, which were caused by low thermal gradients between the poles and, to some extent, the arrangement of the continents. The low vertical transport of water masses caused by globally stratified oceans favoured reducing conditions in the sediments, which led to the deposition of anoxic sediments and black shales. De-oxygenation of deeper water masses also may have resulted. Some deep-sea geological sequences also show distinct extinction events during times of periods of rapid temperature change and suspected disoxia (e.g., the terminal Palaeocene event in the South Atlantic; Kennett & Stott, 1991, 1995).

Complete global anoxia below the surface mixed layers, however, is unlikely because bottom water may be generated anywhere by processes that form high density water at the sea surface, including in the equatorial regions (Hay, 1988;

Horne, 1999, this issue). Although warm saline water carries less oxygen than cold saline water (Weiss, 1970), oxygenation is still likely to be adequate to support deep-sea animals (Diaz & Rosenberg, 1995). Fairly diverse deep-water invertebrate communities still exist in low oxygen levels, such as off southern California (Jumars, 1976), although at a reduced diversity. Overall benthic invertebrate diversity is not greatly influenced by low oxygen levels until the dissolved oxygen concentration drops below  $1.0 \text{ ml} \cdot \text{l}^{-1}$  (Levin & Gage, 1998).

Division of water columns by global midwater anoxic layers seems much more likely. Midwater oxygen minimum zones have a strong impact on the benthic fauna where they intersect the sea floor (Levin & Gage, 1998). Oxygen minimum zones may have important consequences for allopatric speciation by forming barriers against vertical transmigration of propagules or gene flow (White, 1987). Global oxygen minimum zones that persist for millions of years could also prevent shallow water taxa from colonizing the abyssal regions, thereby changing the evolutionary character of the deep-sea faunas, compared to those in shallow water.

The geological period when anoxic events were more frequent (Fischer, 1984) is superimposed on the trimmed cladograms (fig. 2). During warm "thermospheric" periods (Benson et al., 1984), the oceans were likely to have persistent oxygen minimum zones: depleted barriers to transmigration in the global bathyal zones. The flabelliferans appeared during these warm, stratified periods, and although they diversified greatly in shallow water, they may have been prevented from entering the deep sea by the oxygen minimum zone barriers. The Asellota, on the other hand, were present when bottom water generation operated in the polar regions and provided a cold isothermal conduit to the deep sea, much as current oceanographic conditions (Menzies et al., 1973; Taylor & Forester, 1979). As a result, the Asellota could have entered and diversified in the abyss during the late Palaeozoic and early Mesozoic. The evolutionarily younger flabelliferans could have migrated to deep water only after the re-establishment of polar cold water generation in the mid Cainozoic.

From these palaeoceanographic considerations, an explanation for the observed patterns of isopod diversity may be proposed. While the flabelliferans show evidence of robust evolutionary activity in shallow water (highly speciose, cosmopolitan taxa such as the Cirolanidae: cf. Keable, 1996), they have few species that reach into the abyssal zone (fig. 1A). Because bottom water generation is strongest in the Antarctic, the deep water flabelliferans also show highest diversity in the southern hemisphere (fig. 1B), primarily among those taxa that are well represented in the Antarctic shallow water benthos (Wägele, 1992). The Asellota have a huge diversity in the deep sea, unparalleled to that of shallow

water ecosystems. This suborder has 11 families that are endemic to the deep sea, a rare occurrence among other deep-sea peracarid crustaceans. Most non-endemic deep-sea families are present in shallow water only in places where the water column is isothermal and stable. A few asellotan shallow-water families seen in the deep sea, such as the Munnidae and the Paramunnidae, show a pattern of recent deep-sea colonization (Wilson, 1980).

Because deep-sea Asellota are phylogenetically old and may have been present in the deep sea from 200 mybp or longer, comparisons with the equally ancient Phreatoicoidea may illuminate the evolutionary processes involved. Although deep-sea isopods might be considered ancient relicts, they may have survived under a different evolutionary regime. Relicts in fresh ground waters, such as the phreatoicoidan isopods, show morphological stasis where the modern taxa are largely unchanged from their Palaeozoic marine ancestors (Schram, 1970; Wilson & Johnson, in press). This stasis may arise from specific adaptations to a range of ground water environmental conditions (Danielopol et al., 1994). The janiroidean isopods are adapted to the low-energy, stenotopic regime of the deep sea. This latter habitat, however, is the largest and possibly oldest ecosystem on the planet, allowing both time and space for evolutionary novelty. The deep-sea janiroideans do not appear to be morphologically constrained by their habitat.

Morphological stasis in the phreatoicoideans also reflects their diversity. A few more than 50 phreatoicoidan species in total have been described, although this number may increase substantially as more information is gathered on species differentiation in the suborder (Wilson & Keable, in press [isopod conference paper]). Nevertheless, phreatoicoideans are at the low end of the diversity spectrum. A single lake in Tasmania had no more than 6 species (Fulton, 1983), which in itself was exceptional because most phreatoicoidan sites yield only 1 or 2 species (unpubl. data). The deep-sea asellotes, on the other hand, may show as high a diversity as 100 species in a single sample, and random subsamples of 200 individuals can exceed 50 species (fig. 1).

Why do these modern descendents of the Palaeozoic isopods show differing diversities in their preferred habitats: fresh-water hypogean vs. deep sea? At the moment, we can only speculate. Because of their freshwater habitat, phreatoicoideans may have been exposed to a higher probability of extinction. Perhaps phreatoicoidan diversification in fresh water was similar to that of the deep-sea asellotans, but suffered extinctions that did not occur in the abyss. Sometime before, during or after the end Permian event, phreatoicoideans became extinct in the oceans; they have marine fossils from the Carboniferous and Permian, but only fresh water fossils known from the Triassic. The shallow marine Asellota persisted through this event, with many families surviving today. A few early



derived asellotan families live exclusively in fresh water: the Asellidae and Stenaseillidae found North of Wallace's line, and the Protojaniridae found in the southern biogeographic regions — including Sri Lanka (see Bănărescu, 1990). The former two families of Asellota each have a described diversity exceeding that of the entire suborder Phreatoicoidea.

This comparison suggests that the diversity differences between the Asellota and the Phreatoicoidea may not be simply a result of the asellotes living in the vast areas of the deep sea, while the phreatoicoideans live in the much more restricted Gondwanan ground waters. The phreatoicoideans suffered extinctions in several environments, while the Asellota have survived and diversified, albeit in a limited way in shallow marine waters. The phreatoicoideans were lucky to have survived the end Permian event.

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