HISTORICAL INFLUENCES ON DEEP-SEA ISOPOD DIVERSITY IN THE ATLANTIC OCEAN

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Abstract -- Most isopod crustaceans in the North Atlantic deep sea belong to the suborder Asellota. In contrast, South Atlantic isopod faunas have a significant component of flabelliferan isopods, a phylogenetic clade that contains suborders derived evolutionarily later than the Asellota. The flabelliferans decrease in diversity from shallow water to deep water and on a south-to-north latitudinal gradient. Although many asellote families are endemic to the deep sea, none of the flabelliferan families appear to have evolved in the abyss. Recent colonisations of the deep sea, which may have been limited to the southern hemisphere by oceanographic conditions, have significant consequences for observed regional diversities of some taxa. Instability in oceanographic conditions owing to glaciation and benthic storms may have further limited benthic species richness of the North Atlantic deep-sea benthos.

INTRODUCTION

Renewed interest in deep-sea species richness has stimulated new contributions on global diversity (e.g. Gage and Tyler, 1991; Grassle, 1991; Grassle and Maciolek, 1992; May, 1992; Poore & Wilson, 1993; see Gage, 1996 for a recent review) and latitudinal trends (Rex et al., 1993, in press). Questions about how such diverse assemblages can exist on an ecological time scale (Gage, 1996) may overlook the source of the diversity. Many invertebrate assemblages may show few effects of competition or predation, and may be more strongly influenced by regional influences (Ricklefs and Schluter, 1993; Stuart and Rex, 1994). Historical factors, such as colonisation events or length of geological/evolutionary time in a habitat, can have strong influences on the regional diversity, and thereby affect the composition of the local assemblage. Distinguishing between the influences of ongoing processes and of historical events is not straightforward (cf. Rex et al., 1993), because specific events are not easily associated with observed diversity patterns. The association of evolutionary events with the distribution of diversity in the isopod crustaceans is presented here as one example of the role of evolutionary history in deep-sea diversity.

Isopods have been useful for the evaluation of deep-sea biodiversity in the Atlantic Ocean, especially in works on geographic trends of species richness (Hessler and Wilson, 1983; Poore and Wilson, 1993; Rex et al., 1993). These papers used data from an important series of benthic ecology transects conducted in various basins of the Atlantic Ocean by the Woods Hole Oceanographic Institution (WHOI), directed by Howard L. Sanders, Robert R. Hessler, and J.Frederick Grassle. The laboratory of Robert R. Hessler at the Scripps Institution of Oceanography (SIO) has made ground-breaking additions to the systematics of these isopods (e.g., Hessler, 1970a and references in Appendix) and has provided new insights into the biogeography (Hessler and Thistle, 1975; Hessler et al., 1979; Hessler and Wilson, 1983) and speciation (Wilson and Hessler, 1987) of both general faunas, and isopods in particular.

The astonishing range of morphological adaptations exhibited by deep-sea isopods (e.g. the Munnopsididae in Wilson, 1989) has prompted much of this research, which was directed toward discovering the evolutionary patterns behind their diversity. While we cannot claim to have specific answers, recent advances in isopod phylogeny (Brusca and Wilson, 1991) have illuminated the situation considerably. Isopods are a monophyletic order of the crustacean superorder Peracarida. Grouping all isopods together in ecological analyses presumes that they consist of phylogenetic elements of similar history and tendencies, i.e. a suitable taxocene.

Although strictly true in a broad sense, this order nevertheless subsumes important historical heterogeneity, with consequences for understanding of their overall diversity and ecology.

The Isopoda may be classified into up to 10 distinct suborders with significant differences in their geographic distributions. The suborder Asellota contributes markedly to deep-sea diversity, owing to 22 families in the superfamily Janiroidea, 14 of which are found in the deep sea almost exclusively (Wolff, 1962; Hessler et al., 1979; Harrison, 1987; Svavarsson, 1987; Wilson, 1997). No other isopod taxon has deep-sea endemicity at such high taxonomic levels. The suborders Phreatoicidea and Oniscidea are fresh water and terrestrial groups that have no extant representatives in the deep sea. The remaining suborders may be monophyletic, i.e., descended from a single ancestor. The suborder "Flabellifera" *sensu stricto*, which contains a wide diversity of marine and fresh water taxa, is not monophyletic (Brusca & Wilson, 1991). The taxa of the Flabellifera, however, appear to be part of a larger monophyletic clade (fig. 1) including the suborders Valvifera, Anthuridea, Gnathiidea and Epicaridea. All of these taxa have representatives in the deep sea, although their highest diversities are in shallow water. The internal structure and classification of this clade is still under dispute (Wägele, 1989; Brusca & Wilson, 1991), but cladograms obtained by radically different methods (Wilson, 1996) have agreed on the existence of this clade (fig. 1). For the purposes of this paper, this larger clade ("Flabellifera" + Anthuridea + Gnathiidea + Epicaridea + Valvifera) is called the "Flabellifera *sensu lato*" or simply flabelliferans. This terminology is not meant to correspond to any existing hierarchical classification of the Isopoda. These two taxa, the Asellota and the Flabellifera *sensu lato*, are evaluated for their diversity in the deep sea separately. This paper shows how these two groups have different distributions of diversity in the Atlantic Ocean and discusses how their histories may have influenced their present day distribution.

METHODS

Data Sources

This study uses isopod taxonomic data from 66 epibenthic sled samples (Hessler and Wilson, 1983) collected in most of the major basins of the Atlantic Ocean (Table 1, fig. 2). All samples were processed with methods similar to those described in Sanders et al. (1965) and Hessler and Sanders (1967). The Woods Hole Oceanographic Institution sampling programs of Sanders and colleagues provided a total of 63 samples ("WHOI" samples). One sample was obtained by the Institute of Oceanography, Dalhousie, Canada ("IODal" samples collected by E. Mills and party) from the South Shetland Islands, and 2 samples were obtained from the Bay of

Biscay by the Millport Marine Biological Laboratories, United Kingdom ("Allen" samples collected by J. A. Allen and party). One sample from the Mediterranean Sea (WHOI 211) is included because it provides a longitude datum not represented in the North Atlantic. All samples were sorted to major taxa. The specimens were forwarded to SIO, where they were identified to presumptive genera and species. Not all genera in the database corresponded to existing named taxa, but the number of species for each station was as accurate as the material allowed, owing to the considerable taxonomic attention that these collections have received (see Appendix). Isopods are good subjects for diversity research because individuals can be identified to species from fragments, such as a head or a pleotelson. The identification data were entered into a computer database. Although the Atlantic isopod database contains many more than 66 samples, a sample size cut off of 200 individuals was used to provide a higher probability of obtaining the rarer flabelliferans in the samples.

Historical Evaluation

To obtain an historical phylogenetic understanding of asellotan and the flabelliferan diversity, two sources were used: the branching order of isopod phylogenies and the fossil record. The cladograms of Brusca and Wilson (1991), which are similar to trees obtained by other methods (Wilson, 1996), provided an objective description of cladogensis in the isopods. These published cladograms are somewhat different than those produced by my unpublished research on isopod phylogeny, but the overall pattern of early derivation of the Asellota compared to the flabelliferans is supported. Information on the fossil record was derived from Hessler (1969), Schram (1970, 1974, 1980), and Weider and Feldmann (1992), but also including Chilton (1918), Karasawa (1995), Karasawa et al. (1992), and Obata and Omori (1993).

Diversity Measures

Because the Asellota and the Flabellifera *sensu lato* were identified as a single taxocene (Isopoda), their diversity was considered as a single unit, with diversity partitions of the two taxa calculated from their species abundances. Diversity was measured using Hurlbert's (1971) modification of Sanders' (1968) rarefaction method, the expected number of species $\mathbf{E(S_n)}$, which is based upon hypergeometric probabilities. The nominated minimum sample size (n) was 200 individuals, so all samples were compared using $\mathbf{E(S_{200})}$. A partitioning of the expected number of species between the asellotans and the flabelliferans was obtained by converting individual species abundances to sampling probabilities at n=200, using the program COMPAH95 (Gallagher, 1995). The probabilities for each species were then grouped into

4

asellotan and flabelliferan components, and summed separately. These expected number of species partitions are designated $E(S_{200})^{Asel}$ for the asellotans and $E(S_{200})^{Flab}$ for the flabelliferans, where $E(S_{200})^{Asel} + E(S_{200})^{Flab} = E(S_{200})^{Isopoda}$. These values are given in Table 1.

Criticisms of the use of $E(S_n)$ in evaluating trends in diversity require some comment. May (1975) showed that the expected number of species, $E(S_n)$, is strongly affected by species evenness at small sample sizes, so the correlation between a measure of evenness, J', and $E(S_n)$ increases for decreasing n. $E(S_n)$ at a particular n may differ considerably between two sites, even though the total site species numbers may be identical. $E(S_n)$ is sensitive to the sampling distribution of the species (evenness), but so are most other diversity measures (Magurran, 1988). Although May (1975) and others (e.g., Gage and Tyler, 1991; Gage and May, 1993) have characterised this property as a disadvantage of $E(S_n)$ compared to S, the number of species, evenness will affect any measurement of species diversity that might be made. In the current case, possible correlations between J' and $E(S_n)$ are minimised owing to the large sample size chosen, n=200. S also has the disadvantage that it is highly correlated with sample size, and will give spurious results for differing sample sizes. The epibenthic sled samples used here showed a range of sample sizes of 203-9272 individuals, so sample size must be normalised in some manner. $E(S_n)$ is preferred over other diversity indices because of its real relationship to the samples collected: it is in the same units as S but is more comparable than S across samples that differ greatly in numbers of individuals. Moreover, the species abundance relationships are part of what is being measured whenever one takes a sample of a species assemblage, so one should not use measures that ignore this component of the diversity. Therefore, $E(S_n)$ is a useful measure of species richness.

Hypothesis Test

Standard multivariate least squares regression analyses were done on $E(S_{200})^{Asel}$ and $E(S_{200})^{Flab}$ against the independent variables depth and latitude. Although a line was fitted to the data in some instances, the intent was not to model the variation, but to indicate a trend in the data. The impact of the phylogenetic groups was tested using Monte Carlo calculation of null model probabilities, asking the question "Does the phylogenetic grouping of flabelliferans show a significantly better correlation with depth and latitude than similar sized random groupings of taxa?" Specifically the multiple regression coefficients between flabelliferan numbers and depth and latitude were tested to determine whether they were more negative than what one could expect by chance alone. This test was done by randomly ordering the hypergeometric sampling

probabilities of the species in each sample and then summing a new randomised group of the same size as the flabelliferans but with no phylogenetic context. The multiple regression was recalculated and the correlation coefficients of $E(S_{200})^{random}$ with depth and latitude were saved. This procedure was iterated more than 1000 times. The number of times that the randomised data correlation coefficient was within 1 standard error of the actual correlation coefficients, R, was recorded. Based on randomisation test methods (Sokal and Rohlf, 1969), the one-tailed probability, that the phylogenetic grouping is no better than random groupings, is R divided by the total number of iterated regressions.

RESULTS

Historical Origins of isopod clades

The fossil record (Hessler, 1979) shows that recognisable marine isopods (Phreatoicidea) were present in the middle Carboniferous (Schram, 1970, 1974; 1980, 1981). The phreatoicideans had colonised the fresh waters of Gondwanaland by the Triassic (Chilton, 1918), and at this time flabelliferan fossils appeared that are presumed to be related to Sphaeromatidae or Serolidae. Evidence of the Epicaridea appeared in the Jurassic, by way of swollen branchial cavities of some fossil decapods. Recognisable Cirolanidae did not appear until the Cretaceous (Wieder & Feldman, 1992), and neither Valvifera nor Oniscidea were seen until the Tertiary. Anthuridea and Gnathiidea, and Asellota do not appear to have a fossil record.

Despite lacking a fossil record, the Asellota may have had an early origin in the evolution of the Isopoda because it appears immediately after the Phreatoicidea in cladograms of the Isopoda (Brusca & Wilson, 1991; Fig. 1) or it is the sister group of the Phreatoicidea (research in progress). The position of the Asellota in figure 1 suggests that the minimum age of the Asellota must be that of the flabelliferans, early Mesozoic (Triassic), because the Oniscidea do not have a Palaeozoic or Mesozoic fossil record. Recent analyses of the Isopoda performed on a revised data set with new flabelliferan taxa described since 1991 places the Asellota as the sister group of the Phreatoicidea, a relationship corroborated by their sharing a unique tagmosis of the body and a lack of an female oostegite on the sixth thoracosomite. This results in a much stronger statement about the age of the Asellota, one which asserts that its minimum age is that of the Phreatoicidea, or Carboniferous.

The distribution of asellotan taxa, particularly the early derived families, corroborates at least an early Mesozoic origin for the Asellota. The early derived families Asellidae,

Stenasellidae and Protojaniridae (Wilson, 1987; in prep.) are found only in fresh water (Banarescu, 1990), similar to the Phreatoicidea. The Asellidae and Stenasellidae have a Northern Hemisphere distribution and the Protojaniridae is restricted to the southern hemisphere or to Gondwanaland fragments in the northern hemisphere (Sri Lanka). This pattern is consistent with independent colonisation events of freshwater during or after the break up of Pangea in the Mesozoic, but before the separation of the Gondwanan elements. These observations suggest that a diversified asellote fauna existed in the early Mesozoic, similar to the Phreatoicidea, although a lack of a fossil record and the isopod cladogram of Brusca and Wilson (1991) forces this time to be the minimum age of the Asellota.

Evolutionary Partitions of Regional Diversity

Unlike the distribution of total isopod diversity in Atlantic (Rex et al., 1993; Poore & Wilson, 1993), the partitioned diversity of the two groups (asellotans and flabelliferans) shows divergent trends. $E(S_{200})$ for all isopods was partitioned into two monophyletic groups, the Asellota, $E(S_{200})^{Asel}$, and the Flabellifera *sensu lato*, $E(S_{200})^{Flab}$, by summing their hypergeometric probabilities separately (Table 1). To show Atlantic-wide trends, latitude was not separated by hemisphere (as in Rex et al., 1993). Other factors, such as sample size or longitude, did not provide significant correlations with $E(S_{200})$. $E(S_{200})^{Asel}$ shows no relationship with latitude over the whole Atlantic Ocean, but $E(S_{200})^{Flab}$ shows a strong decline from South to North (fig. 3). With depth, $E(S_{200})^{Asel}$ and $E(S_{200})^{Flab}$ show opposing trends, with Asellotes increasing and flabelliferans decreasing (fig. 4) with depth.

Multiple regressions were performed on $E(S_{200})^{Asel}$ and $E(S_{200})^{Flab}$ evolutionary partitions separately, using depth and latitude as independent variables. The residuals for each variable were extracted to determine the independent effect of each factor. These results (Table 2; figs. 5-6) parallel those of the univariate regressions. $E(S_{200})^{Asel}$ shows a significantly positive correlation with depth but not with latitude. $E(S_{200})^{Flab}$, however, had significantly negative correlations with both latitude and depth. In all cases, the variance was high (low r values), although sufficient signal was present in each variable to establish its impact on the diversity measure. The hypothesis that these correlations in the flabelliferans were no better than those that would appear in random groupings can be rejected ($p_{depth} < 0.0001$; $p_{latitude} = 0.0225$; fig. 7). Therefore, the flabelliferan data appear to be biased toward the southern hemisphere and shallower depths, in strong contrast to the Asellota.

DISCUSSION

The different patterns with latitude and depth among the asellotans and the flabelliferans may be related to their time of divergence from isopod ancestors. The minimum age of the Asellota appears to be between the Carboniferous and the Triassic, based on its cladogram and the fossil record. In accord with this great age, asellotan taxa show a pattern of long habitation of the deep sea, with 14 cosmopolitan deep-sea families (Hessler and Thistle, 1975; Wilson, 1997). Seven families are completely endemic to the deep sea (Wilson, 1997). The 7 non-endemic families have representatives in shallow water only where conditions allow deep-water stenotherms to persist near the surface, such as high-latitude boreal and Antarctic seas (Sars, 1899; Wolff, 1962; Hessler, 1970b; Hessler and Thistle, 1975; Hessler and Wilson, 1983).

Flabelliferans have a low diversity in the deep sea, and have no endemic deep-sea families. A more recent invasion of the abyss may explain this flabelliferan pattern. The main diversification of the flabelliferans may have taken place during the late Mesozoic. Despite a few early fossils in the Triassic, modern flabelliferan families do not appear in the fossil record until the Cretaceous or later (Hessler, 1969; Weider and Feldmann, 1992).

Although not as old as the Asellota, a mid to late Mesozoic age for the flabelliferans seems adequate time to develop a substantial deep-sea presence. Many flabelliferans (e.g. the cirolanid genus *Natatolana*; Keable, 1996, in prep.) are speciose and appear to be rapidly evolving, with many species on the outer shelf and bathyal zone, but with few abyssal representatives. Why flabelliferans have such low deep-sea diversities, compared to the Asellota, may involve several factors, such as biological adaptations of most flabelliferans and influences of palaeoceanographic events.

Many flabelliferans, especially Cirolanidae, have a high proportion of scavengers or predators that may be disadvantaged in the abyss owing to the rarity of prey (Hessler and Wilson, 1983; Gage and Tyler, 1991). Other taxa are parasitic during some stages of their life cycle and may be similarly disadvantaged. A predominance of these life styles among the flabelliferans (e.g. Anthuridea, some Cirolanidae, Epicaridea, Aegidae, Gnathiidea) might explain some their decline with depth, but only partially. Some highly active swimmers among the Cirolanidae seek out food falls (Wong and Moore, 1995, 1996) and may be well adapted to deep-sea conditions owing to their ability to find food over long distances. Dependence on carnivory or parasitism does not explain reduced diversity in other abundant taxa among the flabelliferans that are detritivorous (e.g. the families Sphaeromatidae, Serolidae and the suborder Valvifera).

A more general explanation may be sought in the historical patterns of ocean environments. Taylor and Forester (1979), mostly summarising early synopses of isopods, noted a high resemblance among cold-water isopod faunas between shallow water and the deep sea. The current pattern of isopod distributions was linked to a late Paleozoic cold isothermal water conduit between the deep sea and shallow water. This connection between the present day distribution and Palaeozoic oceanography is confounded by vertical transmigration occurring today (cf. Hessler, 1970b), but it suggests a general process: the diminution of vertical stratification may reduce the barriers to colonisation of the deep sea. Hessler and Wilson (1983) suggested that crustacean transmigration in the Mesozoic period between deep sea and shallow water may have been enhanced by vertical thermohaline circulation at low latitudes, although little evidence supports for this model other than the emergence of a few deep water taxa in the Mediterranean Sea (Hessler and Wilson, 1983; Vacelet et al., 1994). Wide spread anoxia or disoxia during the Mesozoic (Fischer, 1984; Roth, 1989) may have created strong mid depth oxygen minimum zones that limited deep-sea colonisation at all latitudes . Rapid extinction events in the southern high-latitude deep-sea regions are associated with warm temperatures as late as the Palaeocene (Kennett and Stott, 1991, 1995), suggesting that the warmer eras were not good times for deep-sea faunas. Therefore, the cold-water periods, with polar generation of deep bottom water, may be the primary times that species enter the deep sea. Current information suggests that, in addition to the mid Tertiary to present "psychrospheric" cold, deep waters (Benson et al., 1984; Flower and Kennett, 1994), the late Palaeozoic and early Triassic polar glaciation should have been times of the generation of deep cold bottom water (Taylor and Forester, 1979; Fischer, 1984). These times are too early for modern flabelliferans, but early asellotan taxa may have been present to use this deep-water conduit. The flabelliferans may have been able to enter the deep sea only after mid Tertiary times when thermal stratification ended at the onset of polar bottom water generation (Flower and Kennett, 1994; 1995). The Asellota thus could have entered the deep sea much earlier than the Flabellifera, which is consistent with the observed patterns of isopod diversity.

An enhancement of flabelliferan diversity in the southern hemisphere of the deep sea compared to the North Atlantic suggests that ongoing vertical transmigration may have a strong influence on the regional diversity patterns. That the Asellota do not demonstrate a similar pattern reflects a distribution that was established prior to the current oceanographic conditions. Time of origin and colonisation, and subsequent dispersal to other ocean basins provide a single explanation for the observed patterns of isopod diversity.

The phylogenetic details of specific flabelliferan groups show the larger patterns. The Gnathiidea, for which a cladogram is available (Cohen and Poore, 1994), has a small radiation of deep-sea taxa (*Bythognathia* and *Bathygnathia*) that diverged early in the evolution of the suborder. The earliest derived gnathiids, however, are shallow-water (*Thaumastognathia*), and the later derived genera contain mixtures of both shallow-water and deep-sea taxa within genera, indicating ongoing adaptation to deep-sea conditions. This pattern is consistent with recent dispersal of gnathiids into the deep sea. Any historical dispersal pattern for the endemic deep-sea asellotans appears to have been obliterated because most higher-level clades are cosmopolitan (Wolff, 1962; Hessler et al., 1979; Hessler and Wilson, 1983; Wilson, 1997). Where asellotan taxa may have entered the deep sea is therefore less clear.

Alternative explanations might suggest that the flabelliferan pattern may be part of a more general trend seen across higher taxa. The North Atlantic has been identified as an area of reduced diversity compared to the South Atlantic (Poore and Wilson, 1993; Rex et al., 1993). If the decline toward the north were part of a general trend, random groupings of the data should have shown a similar decline. Although the mean randomised multiple correlation coefficient for latitude was approximately -0.006, few of the randomly selected values showed a correlation as large as that of the flabelliferan grouping.

The small but significant increase in asellotan species with depth conflicts with the observation that overall species diversity declines with depth after a bathyal peak (Rex, 1983; Gage and Tyler, 1991; Grassle, 1991; Etter and Grassle, 1992). This pattern appears in the asellote data despite a slight and insignificant ($R^2 = 0.033$, p=0.142) decline in sample sizes with depth. If the Asellota have been in the deep sea since the early Mesozoic, this increase in their diversity with depth is consistent with a long history of specialisation to the deep sea. The morphological diversity of asellotans parallels their species diversity wherein many novel adaptations are found, such as posterior swimming (Hessler, 1993; Hessler and Strömberg, 1989; Wilson, 1989) or foraminivory (Wilson and Thistle, 1985; Svavarsson et al., 1993). The specialised reproductive system of Asellota (Wilson, 1991), which does not occur amongst the flabelliferans, may also be a factor in their ability to maintain themselves at low population densities in the deep sea. As a result of an apparently long history of adaptation, asellotan species may not be greatly disadvantaged by conditions at abyssal depths.

A final query concerns why the North Atlantic seems to be depauperate in its isopod species diversity, compared to the South Atlantic or other southern hemisphere sites (Poore and Wilson, 1993). As we have already seen, the North Atlantic samples contain almost entirely

Asellota, with few flabelliferans. Subtracting the flabelliferans from the data still leaves the higher latitudes of the North Atlantic (i.e., above 25° N) depleted in species compared to the South. Although the different factors are difficult to dissect, two possibly co-acting historical processes need consideration: contributions of diversity from adjacent regions and possible North Atlantic extinction events.

The importance of regional diversity in its influence on local diversity cannot be ignored in faunal assessments (Ricklefs, 1989; Ricklefs and Schluter, 1993; Stuart and Rex, 1994). Consequently, the diversity of ocean basins may be depend at least partially on adjacent basins. South Atlantic basins are adjacent to the Pacific, Indian and Antarctic Oceans and may have many taxa with shared distributions. The North Atlantic, however, is adjacent only to the Equatorial Atlantic and several low diversity Basins, the Mediterranean (WHOI 211 in this paper; Cartes and Sorbe, 1993) and the Arctic (Svavarsson et al., 1990). This suggests that the North Atlantic has a much smaller effective area (cf. Abele & Walters, 1979a,b) to share species. Although the area of the South Atlantic is approximately equivalent to the North Atlantic, its effective area is much higher, owing to adjacent species rich oceans. Taken in aggregate, the basins of the entire Atlantic Ocean form a "peninsula" (M. Rex, pers. comm.), in the existing configuration of the continental margins. The increasing isolation of basins from South to North would suggest a decrease in immigration relative to extinction. Whether the relative isolation of the North Atlantic might affect speciation is unclear.

Hydrodynamic events and rapid changes in glaciation in the North Atlantic Ocean may have reduced its overall diversity in the late Tertiary and Quaternary. Ongoing erosive events, known as benthic storms (Thistle et al., 1985), substantially reduce the number of isopod families that are present at a site (Thistle and Wilson, 1987, 1996). Other evidence for recent environmental instability in the North Atlantic also exists. Warm-cold oscillations (called Dansgaard-Oeschger events) punctuated the last glaciation which culminated in enormous discharges of icebergs into the North Atlantic (called Heinrich events) during the last 100kyr (Bond et al., 1993; Maslin, 1995; Bond and Lotti, 1995). These events appear to affect oceanographic conditions widely in the northern hemisphere with changes also noted in the North Pacific (Kennett and Ingram, 1995; Behl and Kennett, 1996). Rapid shifts in oceanographic conditions (Keigwin and Jones, 1994; Maslin, 1995) may have resulted in the decimation of stenotopic benthic faunas, possibly to great depths. Glaciation in the southern hemisphere has been stable for at least the last 4 million years (Flower and Kennett, 1994, 1995; Kennett and Hodell, 1993, 1995) and possibly longer (Kennett and Barker, 1990). This greater stability in the southern hemisphere may have had fewer impacts on the benthic fauna there. As a result, historical and current instability of benthic conditions in

the North Atlantic may have had a negative effect on its species diversity, compared to that observed in the southern hemisphere.

The combined impact of effective area for sharing species and glaciation-induced extinction events may be the causal factors in lowering diversity in the North Atlantic compared to the South Atlantic. The flabelliferans also may have only a small diversity in the North Atlantic owing to the overall time available for adaptation to deep-sea conditions and dispersal in the deep sea. Further research on diversity of the deep-sea benthos must address these historical factors in a rigorous fashion. At the moment, we can only offer reasonable hypotheses for further testing.

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*Table 1. Atlantic isopod species diversity: expected species in 200 individuals **E(S₂₀₀)**, total and partitioned between Asellota and Flabellifera sensu lato. Station identifiers: "Sarsia", J.A. Allen, "IODal", E.Mills; "WHOI", Woods Hole Oceanographic Institution.*

Station	$E(S_{200})$ Total	$E(S_{200})$ Flabellifera	$E(S_{200})$ Asellota	Total Species	Total Individuals	Midpoint Latitude	Midpoint Longitude	Midpoint Depth
Sarsia 50	27.39	0.35	27.05	37	579	43.78	-3.63	2379
Sarsia 56	11.65	3.27	8.38	21	778	43.72	-3.80	641
IODal 13	31.53	8.02	23.51	39	425	-61.50	-58.00	282
WHOI 62	25.77	0.00	25.77	29	262	39.43	-70.55	2496
WHOI 64	32.29	1.00	31.29	50	1213	38.77	-70.63	2886
WHOI 66	39.02	0.00	39.02	43	267	38.78	-70.15	2802
WHOI 70	25.48	0.00	25.48	34	702	36.38	-67.97	4680
WHOI 72	28.47	0.00	28.47	36	397	38.27	-71.78	2864
WHOI 73	20.47	1.00	19.47	29	1537	39.78	-70.72	1400
WHOI 76	21.13	1.00	20.13	27	955	39.63	-67.97	2862
WHOI 84	24.28	0.00	24.28	42	853	36.40	-67.93	4749
WHOI 85	31.11	0.00	31.11	39	320	37.98	-69.43	3834
WHOI 87	20.79	1.00	19.79	27	2588	39.82	-70.68	1102
WHOI 96	12.80	1.58	11.22	14	343	39.92	-70.67	498
WHOI 103	16.84	1.00	15.85	18	280	39.73	-70.62	2022
WHOI 118a	20.28	1.58	18.70	32	1513	32.32	-64.58	1144
WHOI 119	33.41	0.86	32.55	35	230	32.27	-64.53	2159
WHOI 125	32.25	0.00	32.25	34	254	37.42	-65.87	4825
WHOI 126	26.90	0.00	26.90	39	916	39.62	-66.76	3806
WHOI 128	26.46	2.00	24.46	31	348	39.78	-70.75	1254
WHOI 131	28.63	0.61	28.02	39	656	36.48	-67.97	2178
WHOI 142	42.04	3.51	38.53	58	747	10.50	-17.87	1710
WHOI 145	28.04	2.88	25.15	29	226	10.60	-17.82	2185
WHOI 155	44.59	0.00	44.59	53	446	-0.05	-27.80	3757
WHOI 156	50.25	0.00	50.25	90	2008	-0.77	-29.43	3459
WHOI 167	49.61	3.04	46.57	76	1258	-7.90	-34.28	975
WHOI 169a	51.89	4.45	47.44	85	1397	-8.05	-34.40	587
WHOI 188	14.73	1.85	12.88	23	2043	-23.00	12.97	620
WHOI 189	14.46	1.00	13.47	21	612	-23.00	12.75	1011
WHOI 191	20.12	1.97	18.16	25	709	-23.08	12.53	1553
WHOI 192	11.81	1.50	10.32	22	1028	-23.03	12.32	2136
WHOI 194	15.21	0.00	15.21	16	234	-22.90	11.92	2864
WHOI 195	32.46	0.00	32.46	36	335	-14.74	9.92	3797
WHOI 197	14.54	0.94	13.60	15	212	-10.48	9.07	4596
WHOI 198	15.44	0.00	15.44	16	236	-10.44	9.11	4563
WHOI 201	29.65	1.30	28.35	39	517	-9.45	11.59	1998
WHOI 202b	24.00	1.00	23.00	27	275	-9.01	12.27	1535
WHOI 207	12.23	1.55	10.68	16	852	39.85	-70.92	808
WHOI 209a	25.38	2.87	22.51	36	802	39.78	-70.83	1597
WHOI 209b	28.60	2.98	25.62	32	269	39.78	-70.83	1597
WHOI 211	11.69	1.35	10.34	15	565	33.95	15.13	505
WHOI 236a	11.43	3.70	7.73	16	1877	-36.46	-53.53	508
WHOI 237a	17.34	5.13	12.21	29	5285	-36.55	-53.38	1002
WHOI 239a	15.67	1.79	13.88	31	9272	-36.82	-53.25	1670
WHOI 242	56.75	3.77	52.98	70	435	-38.28	-51.93	4392
WHOI 245a	53.08	5.42	47.66	109	2521	-36.93	-53.02	2707
WHOI 245b	35.07	4.52	30.55	74	1938	-36.93	-53.02	2707
WHOI 247a	47.30	2.34	44.97	73	1316	-43.55	-48.97	5216
WHOI 256	48.09	1.95	46.13	87	1593	-37.68	-52.32	3912
WHOI 259a	35.74	4.45	31.30	60	1551	-37.22	-52.75	3311
WHOI 262a	33.92	3.11	30.81	49	665	-36.08	-52.30	2460
WHOI 264a	16.21	2.00	14.21	18	293	-36.22	-52.72	2045
WHOI 287	37.85	0.00	37.85	54	653	13.27	-54.88	4957
WHOI 293	44.62	1.78	42.84	76	1125	8.97	-54.07	1487
WHOI 295	40.66	4.02	36.65	58	1248	8.07	-54.35	1011
WHOI 297	37.36	4.96	32.41	55	979	7.75	-54.40	516
WHOI 299	35.75	0.38	35.37	61	1358	7.92	-55.70	2009
WHOI 301	42.19	0.93	41.26	61	899	8.20	-55.83	2494
WHOI 303	38.74	0.00	38.74	44	312	8.48	-56.08	2848
WHOI 306	33.82	0.00	33.82	34	203	9.52	-56.35	3411
WHOI 313	21.21	0.00	21.21	27	791	51.53	-12.60	1495
WHOI 321	36.54	0.32	36.22	67	2716	50.20	-13.60	2879
WHOI 323	45.25	0.43	44.82	60	808	50.13	-13.87	3347
WHOI 326	33.91	0.69	33.22	60	1282	50.09	-14.44	3859

| WHOI 328 | 42.84 | 0.33 | 42.52 | 70 | 1113 | 50.09 | -15.75 | 4431 |
| WHOI 330 | 43.95 | 0.00 | 43.95 | 52 | 383 | 50.80 | -17.96 | 4632 |

Table 2. Multiple regression correlation coefficients of evolutionary partitions of $E(S_{200})$, Flabellifera sensu lato ("Flab") and Asellota ("Asel"), on the independent variables depth (metres) and latitude (decimal degrees), with two-tailed T tests of the null hypothesis ($H_0(cc)$) that the correlation is not different from 0 (i.e., no correlation).

Evolutionary partition	r	depth (z) corr. coef.	prob. $H_0(cc_z=0)$	latitude (lat) corr. coef.	prob. $H_0(cc_{lat}=0)$
$E(S_{200})^{Flab}$	0.716	-0.0006	.000003	-0.0282	.00000001
$E(S_{200})^{Asel}$	0.447	0.0039	0.0002	-0.0186	0.6603
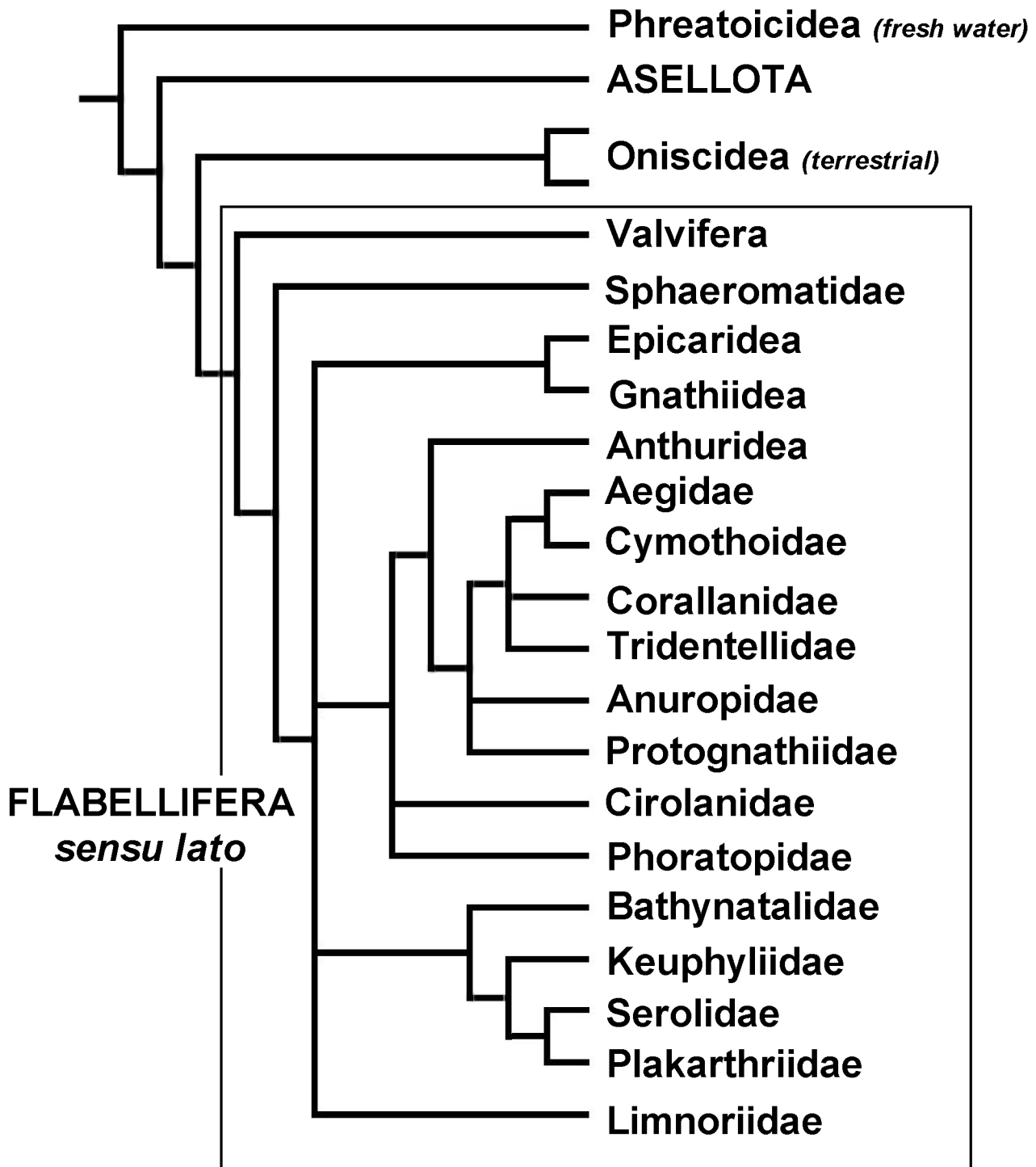
Figure 1. Cladogram of the Isopoda: one of 16 trees found by Brusca and Wilson (1991), minor or reclassified taxa removed. The phylogenetic clade "Flabellifera *sensu lato*" is outlined by a box.
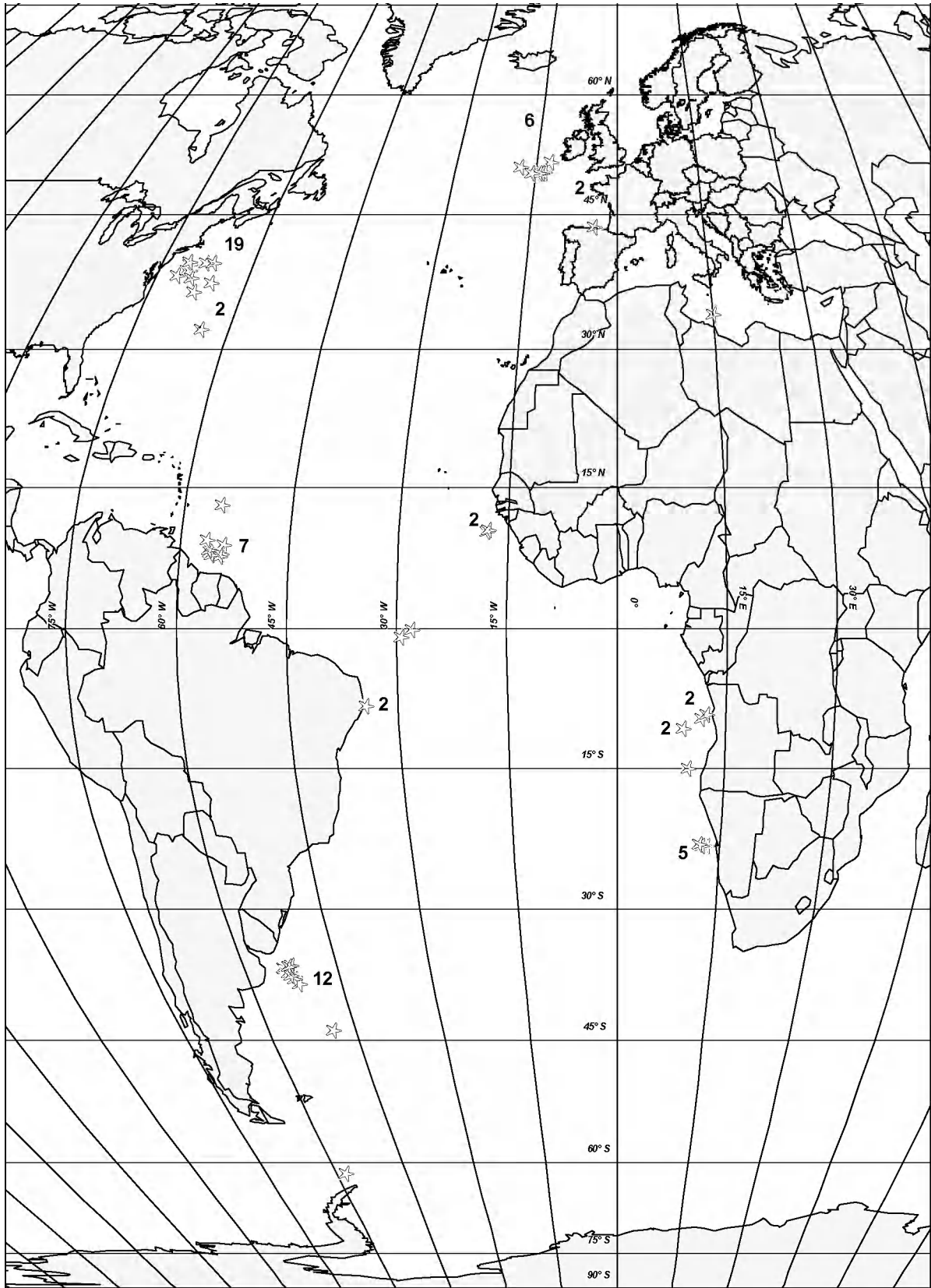
Figure 2. Distribution of deep-sea isopod sites in the Atlantic Ocean and Mediterranean Sea having more than 200 individuals.
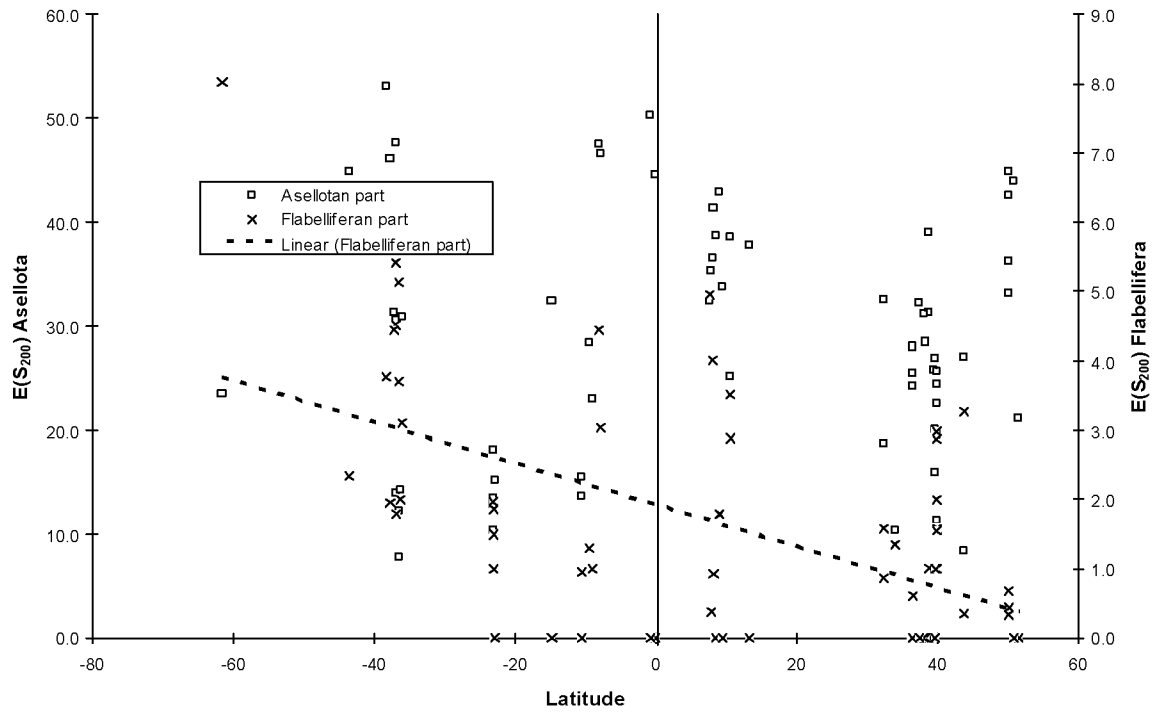
Fig. 3. Relationship between latitude and diversity partitions $E(S_{200})$ Asellota (left axis) and $E(S_{200})$ Flabellifera *sensu lato* (right axis).
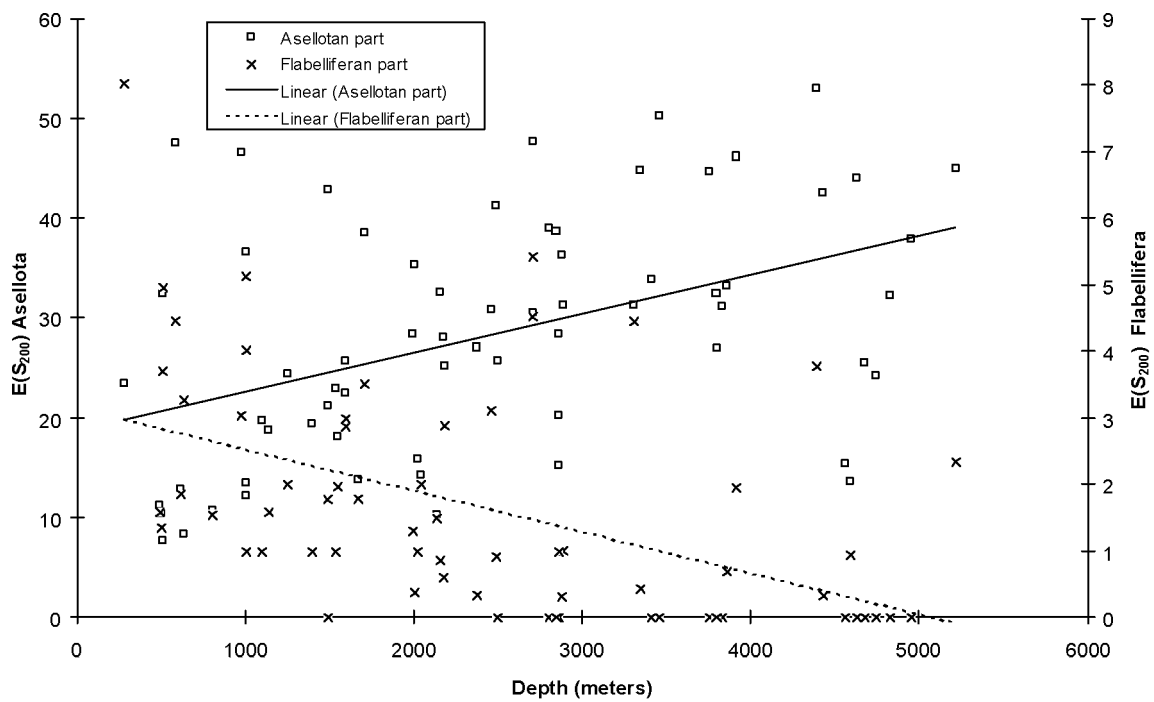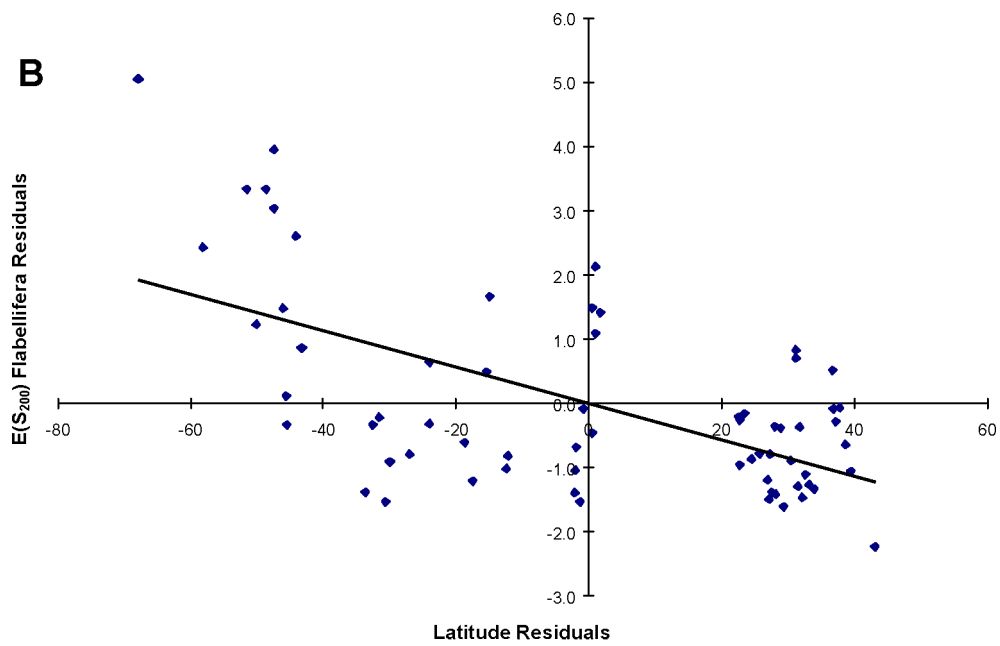
Fig. 4. Relationship between depth (meters) and diversity partitions $E(S_{200})$ Asellota (left axis) and $E(S_{200})$ Flabellifera *sensu lato* (right axis).
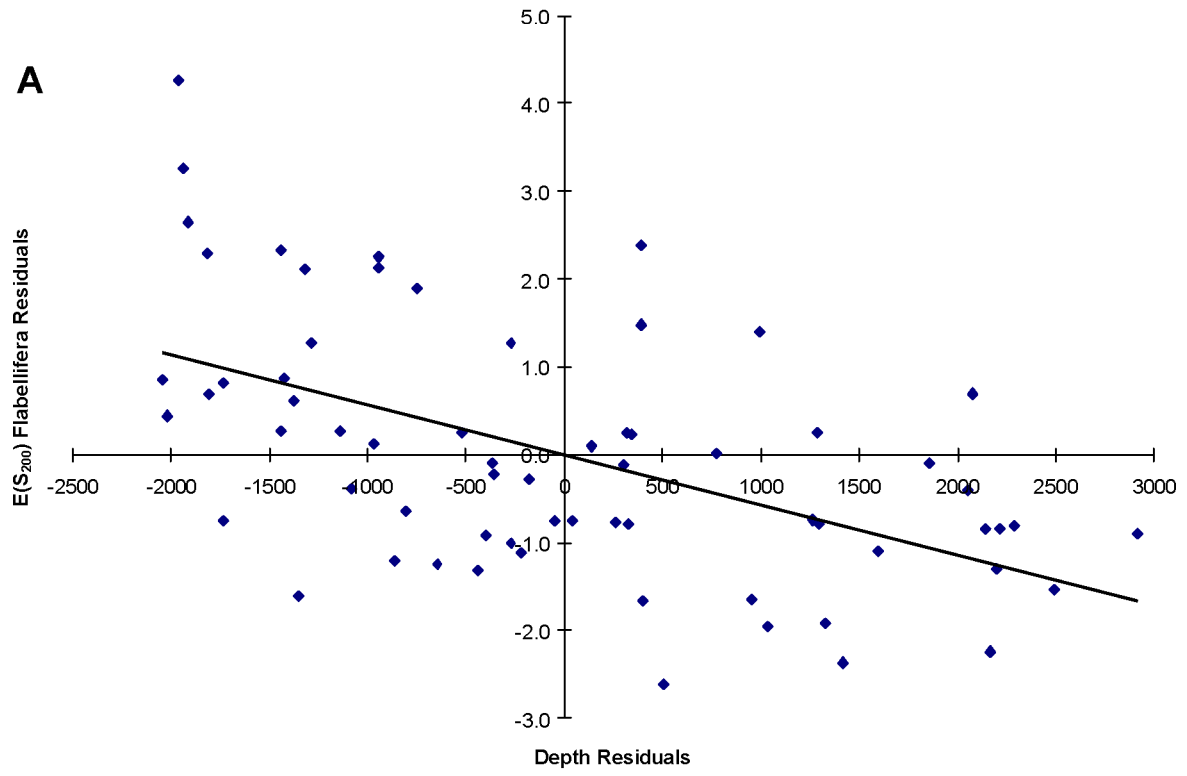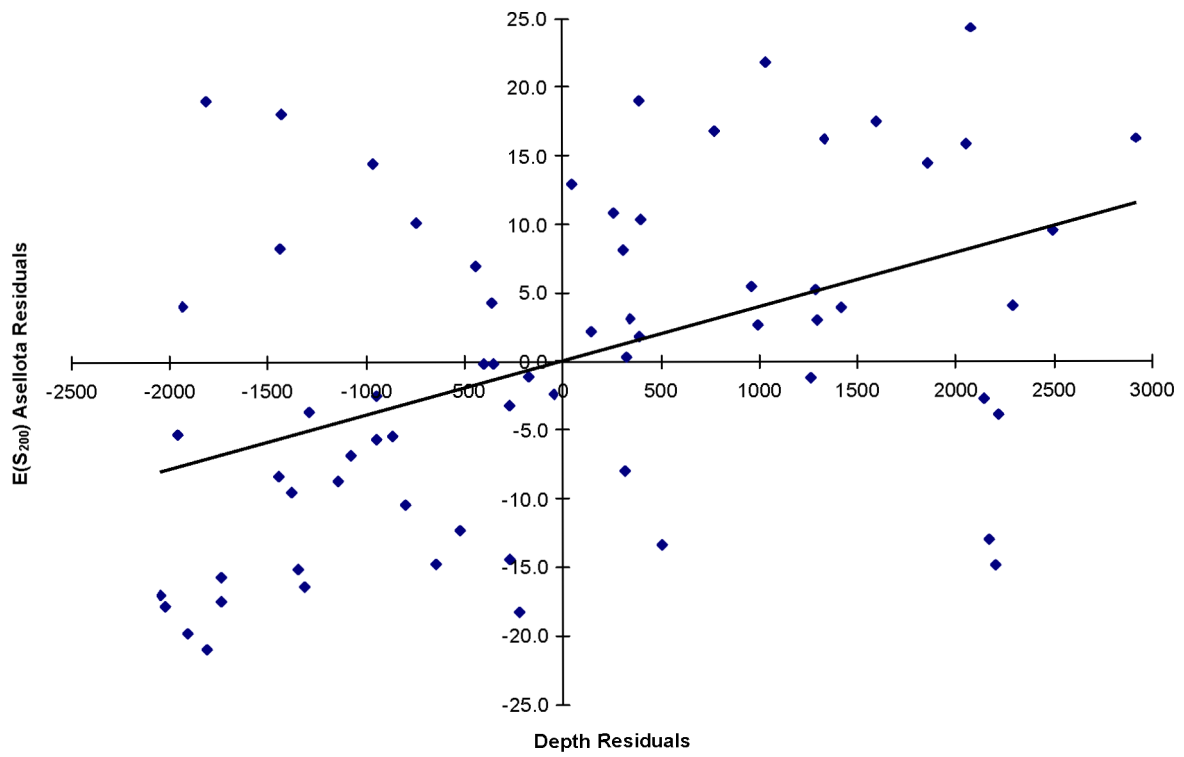
Fig. 5. Depth (A) and Latitude (B) residuals from a multiple regression on diversity partitions $E(S_{200})$ Flabellifera *sensu lato*.
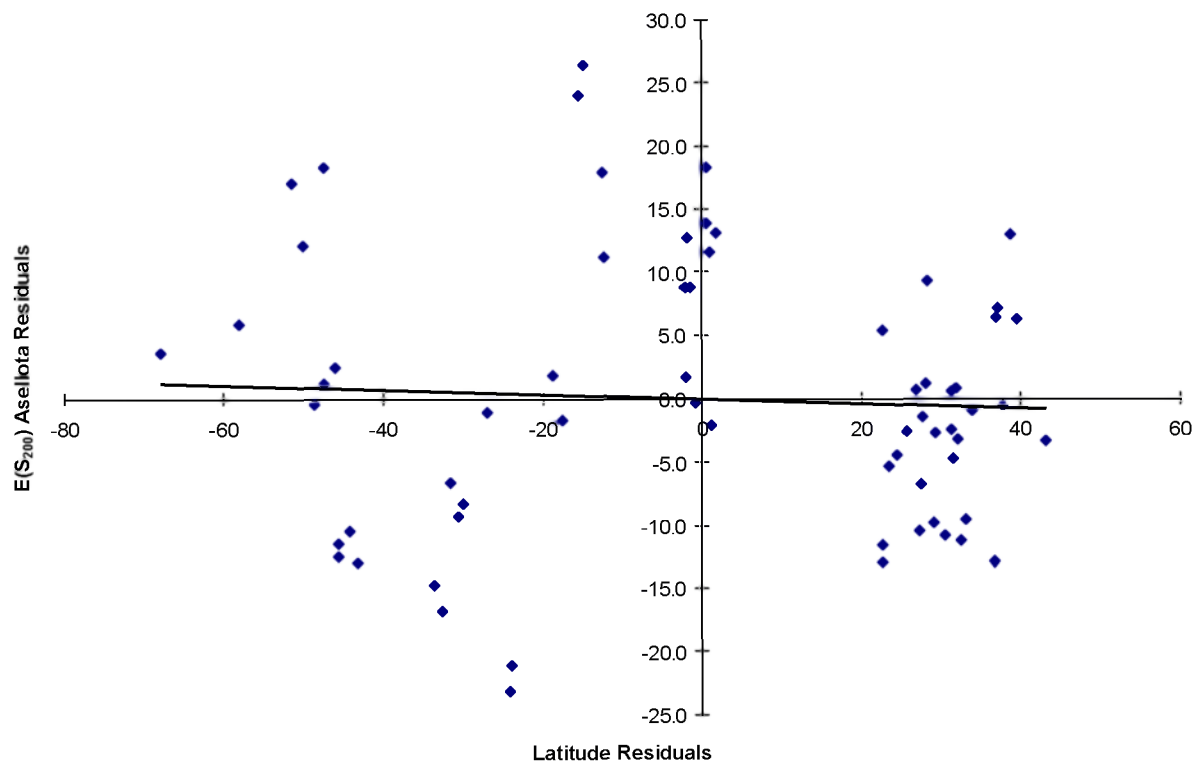
A

B

Fig. 6. Depth (A) and Latitude (B) residuals from a multiple regression on diversity partitions $E(S_{200})$ Asellota.
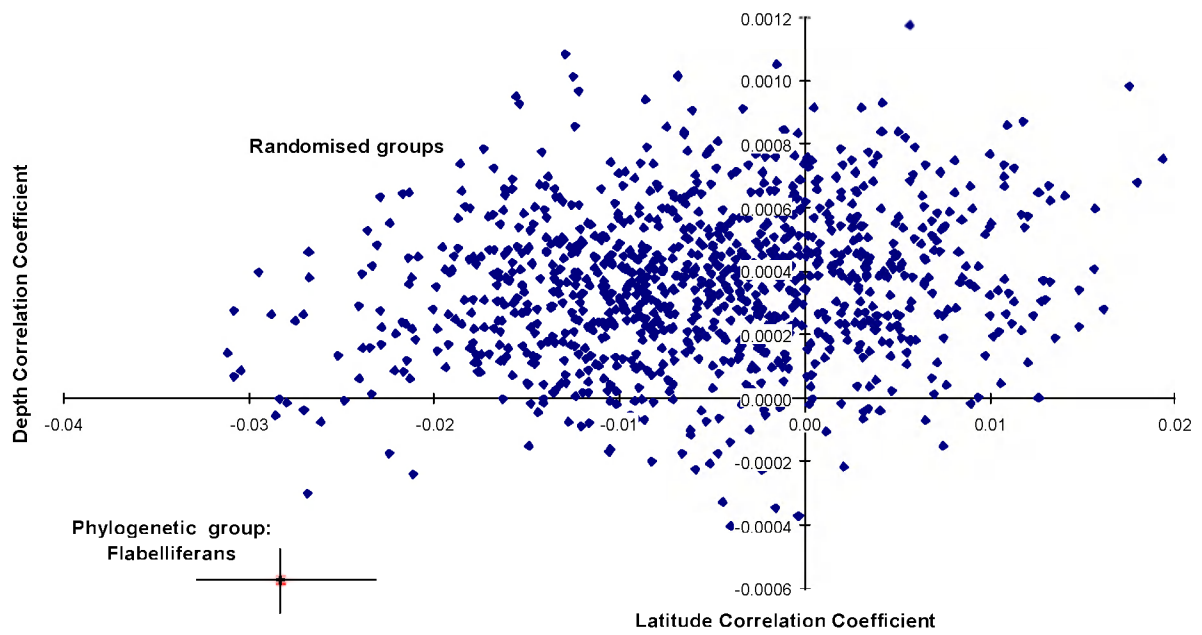
Fig. 7. Null model test of the relationship between correlation coefficients and phylogenetic grouping of the Flabelliferans versus random groups. Flabelliferan point shown with standard error bars.

APPENDIX.

Papers on Isopoda originating from the laboratory of R.R. Hessler and associates.

HAUGSNESS J. A. and R. R. HESSLER (1979) A revision of the subfamily Syneurycopinae (Isopoda: Asellota: Eurycopidae) with a new genus and species (*Bellibos buzwilsoni*). *Transactions of the San Diego Society of Natural History*, **19**, 121-151.

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HESSLER R. R. and H. L. SANDERS (1967) Faunal diversity in the deep sea. *Deep-Sea Research*, **14**, 65-78.

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