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Origin of Antarctic Isopoda (Crustacea, Malacostraca)

Angelika Brandt

Institute of Polar Ecology, University of Kiel, Olshausenstraße 40–60, D-2300 Kiel, Germany

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Abstract. An analysis of the horizontal and the vertical zonation of the Antarctic Isopoda, combined with knowledge of the geological history of Antarctica and isopod phylogeny, revealed that the isopod family Serolidae and subfamily Arcturinae are likely to have evolved from ancestors that inhabited a cold-temperate Gondwanian province. Antarctic species of other families, such as the Munnopsidae, Nannoniscidae, Desmosomatidae and Ischnomesidae, are likely to have evolved from deep-sea ancestors. It is deduced that emigration of South Patagonian species into the Southern Ocean, although possible, probably did not occur very often. Evolutionary phenomena such as continental-drift vicariance, radiation of species on the continental shelf of Antarctica, and active migration, including submergence and emergence mechanisms are discussed.

Introduction

The isolation of Antarctica was initiated with the separation of Africa [ca. 90 million years before the present time (my bp)], followed by Australia (ca. 55 my bp), and was completed with the final opening of the Drake Passage and the development of the circumpolar current during the Oligocene/Miocene (ca. 30 to 22 my bp) (Dietz and Holden 1970). Subsequent cooling of the Southern Ocean caused the extinction of a large proportion of the marine Gondwanian fauna which had colonized the antiboreal region during the early Tertiary (Feldmann and Zinsmeister 1984a, b; Zinsmeister 1984). Some taxa (e.g. Isopoda, Amphipoda, Cumacea, Tanaidacea, Ascidiacea, Actiniaria, Holothuroidea, Polychaeta, Porifera, notothenioid fishes) radiated into many new, "modern" endemic species (Andriashev 1965, 1987; Koltun 1969, 1970; Dell 1972; Knox 1977; Know and Lowry 1977; Sicinski 1986; Gallardo 1987; Gutt 1988, 1990a, b; Eastman and Grande 1989). Therefore Antarctica has been described as an "evolutionary incubator" (Watling and Thurston 1989).

Biological expeditions to Antarctica started more than a century ago with many new species being described with each successful expedition. Isopods were found to be one of the most numerous and diverse macrobenthic crustacean groups in the Southern Ocean. Although attention has focussed on large, distinctive isopods in the past, available illustrations are often poor or incomplete. The asellote isopods, often smaller than 1 to 2 mm, have not attracted much attention. So far only Kussakin (1967, 1973) has tried to summarize the biogeographic knowledge about the Antarctic and deep-sea isopods. His study was based on 180 species. Since then the number of known species has doubled and the biogeographical regions of Isopoda proposed by Kussakin were reevaluated (Brandt 1991a).

Sieg (1988) investigated the phylogenetic relationship of the Antarctic Tanaidacea and concluded that they became extinct during the Tertiary climatic deterioration. In his opinion, the continental shelf of West Antarctica was recolonized by tanaids from South America in the Pliocene, whereas East Antarctica was resettled by species derived from deep-sea fauna. Sieg (1988), pointing to similar patterns in other crustacean taxa (e.g. Amphipoda, Cumacea, Isopoda, Ostracoda), postulated that the Antarctic crustacean fauna was "young". This statement is scrutinized here, using the zoogeographical distribution of the Isopoda near Antarctica. Data from other disciplines, such as data on the geological history of Antarctica (continental drift), on the hydrography of the Southern Ocean, on the isopods' phylogeny, and on fossil records in Antarctica were used in order to reveal the reasons for the horizontal and vertical distribution of the Isopoda. A comparative analysis of the generic phylogenetic relationship and the present distribution of the isopods allows hypotheses to be formulated on the probable area of origin of some Antarctic taxa. This analysis will show that Sieg's statement cannot be accepted for the isopod family Serolidae (suborder Sphaeromatidea) and the subfamily Arcturinae (suborder Valvifera), which are both very characteristic Antarctic isopod groups and common in the Southern Ocean. On the contrary, fewer species of Arcturinae occur in the North Polar Sea, and Serolidae have not yet been found in the Arctic. Species of the families Idoteidae (Valvifera) and Sphaeromatidae (Sphaeromatidea) mainly occur in the Subantarctic, whereas species of the suborder Asellota are very numerous in the Antarctic. Because of their small size insufficient effort has been put into the study of asellote species in the past and many still have to be described orre-described. Other taxa, such as the Anthuridea, Cirolanidae, and Aegidae occur less frequently in the Antarctic (Brandt 1991 a).

Materials and methods

During expeditions of the R.V. "Polarstern" and R.V. "Walter Herwig" between 1983 and 1989, samples containing isopods were collected by means of an Agassiz trawl or a box corer. The material was sorted out on deck or later with a Wild M5 dissecting microscope from subsamples, fixed in formalin (4%) and later transferred into ethanol (70 to 80%). Isopods were also collected during the second Brazilian-German diving expedition to King George Island in the Antarctic summer of 1989/1990.

Taxonomic and phylogenetic work had been done in order to establish monophyletic units, which are necessary for the investigation of colonization and distribution of taxa (Brandt 1988, 1990 a, 1990 b, 1991 a, 1991 b, 1992 a, 1992 b, 1992 c; Brandt and Wägele 1988, 1990).

All information on the distribution of the isopods in the Southern Ocean was collected, and maps of the horizontal and vertical distribution of Antarctic Isopods were prepared (Brandt 1991 a). A taxonomic card-index was used as well as the original publications. This index was set up and kindly made available by Dr. Wägele. It contained all illustrations of the species, site localities, distribution, synonyms and length measurements of the isopods.

Results

The zoogeographical investigation of Antarctic isopods revealed a total of 346 Subantartic and High Antarctic species (394 species including the Magellan Region) representing 121 genera (for definitions of Subantartic and High Antarctic see Brandt 1991 a). Of these, 302 species (= 87%) are endemic to the Antarctic and Subantarctic, and 25 genera (= 21%) only occur in the Southern Ocean. The degree of endemism of the isopod fauna varies in the different geographic regions of Antarctica (Table 1). A high proportion of Antarctic isopod families are restricted to the shelf areas (Fig. 1). Most of the families contain shelf species (I), whereas the number of families with deep-sea species is smaller (III). On the shelf, 226 species (65%) of isopods, representing 70 genera (58%) occur (Brandt 1991 a). The high percentage of endemic Antarctic isopod species indicates an intense speciation process. This was probably initiated by the opening of the Drake Passage and the development of the circum-antarctic current (i.e., ca. 30 to 22 my bp in the Oligocene/Miocene), which isolated Antarctica from the other continents. The Oligocene and Miocene climatic deterioration caused the extinction of many benthic taxa (Zinsmeister 1976, 1984; Feldmann and Zinsmeister 1984 a, b; Birkenmajer 1985; Feldmann and Tshudy 1989), and many ecological niches became available for well- or pre-adapted organisms, such as peracarids, which thrive in Antarctica as they do in the deep sea. Since Mid-Tertiary times the exchange of Antarctic species with species of neighbouring continents has been severely restricted by distance and strong currents south of the Antarctic Convergence (e.g. the east- and west-wind drift). Only ten species are common to Antarctica and South Africa. Australia has 11 species in common with Antarctica, and the highest number of species (34) is shared with South America (Fig. 2). The number of species shared between Antarctica and the neighbouring continents (Africa, Australia, and South America) correlates positively with the time of separation and isolation of these continents from Antarctica, as indicated by the distance between these continents and Antarctica.

Table 1. Endemic species (end. sp.) of the Magellan and some Subantarctic and High Antarctic regions (changed after Brandt 1991 a). Column 3 shows regional percentages. Column 4 shows the percentages of endemic species in each of the different regions with reference to the total number of endemic species (302) in Antarctica. –: no endemic species

Region	Σ species	No. of end. sp.	End. sp. (%) (regional)	End. sp. (Antarctica %)
Magellan region				
Magellan region	87	26	29.9	8.6
Falkland Islands	70	22	31.4	7.3
Subantarctic				
South Georgia	49	9	18.3	3.0
South Sandwich Islands	16	5	31.2	1.7
South Orkney Islands[a]	67	19	28.4	6.3
South Shetland Islands	91	23	25.3	7.6
Crozet Islands	31	5	16	1.7
Kerguelen Islands	80	28	35	9.3
Macquarie Islands	10	1	10	0.3
Auckland Islands	13	1	7.7	0.1
Campbell Islands	9	–	–	–
High Antarctic				
Bellingshausen Sea	40	2	5	0.7
Weddell Sea	68	13	19	4.3
Ross Sea	39	3	7.7	1.0
East Antarctica	111	34	30.6	11.2

[a] (after White 1984, p. 437)

The horizontal and vertical distribution of the Antarctic Isopoda has been interpreted (Brandt 1991 a) using recent phylogenetic investigations of the isopods (Wägele 1989, Brandt 1991 a) in order to discover their probable place of origin. These comparisons revealed a similar zoogeographic history for the isopod family Serolidae and subfamily Arcturinae. Fig. 3 shows simplified dendrograms of the families of the Sphaeromatidea (A) and the subfamilies of the Arcturidae (B) (for further details see Wägele 1989). In the zoogeographical analysis, it becomes obvious that phylogenetically primitive, "old Gondwanian relicts" [species of the Holidotheinae, the Pseudidotheinae, the Xenarcturinae (Arcturidae) and the Plakathriidae (Sphaeromatidea)] still survive in a southern temperate area. The disjunct relict distribution of some primitive species is probably caused by continental-

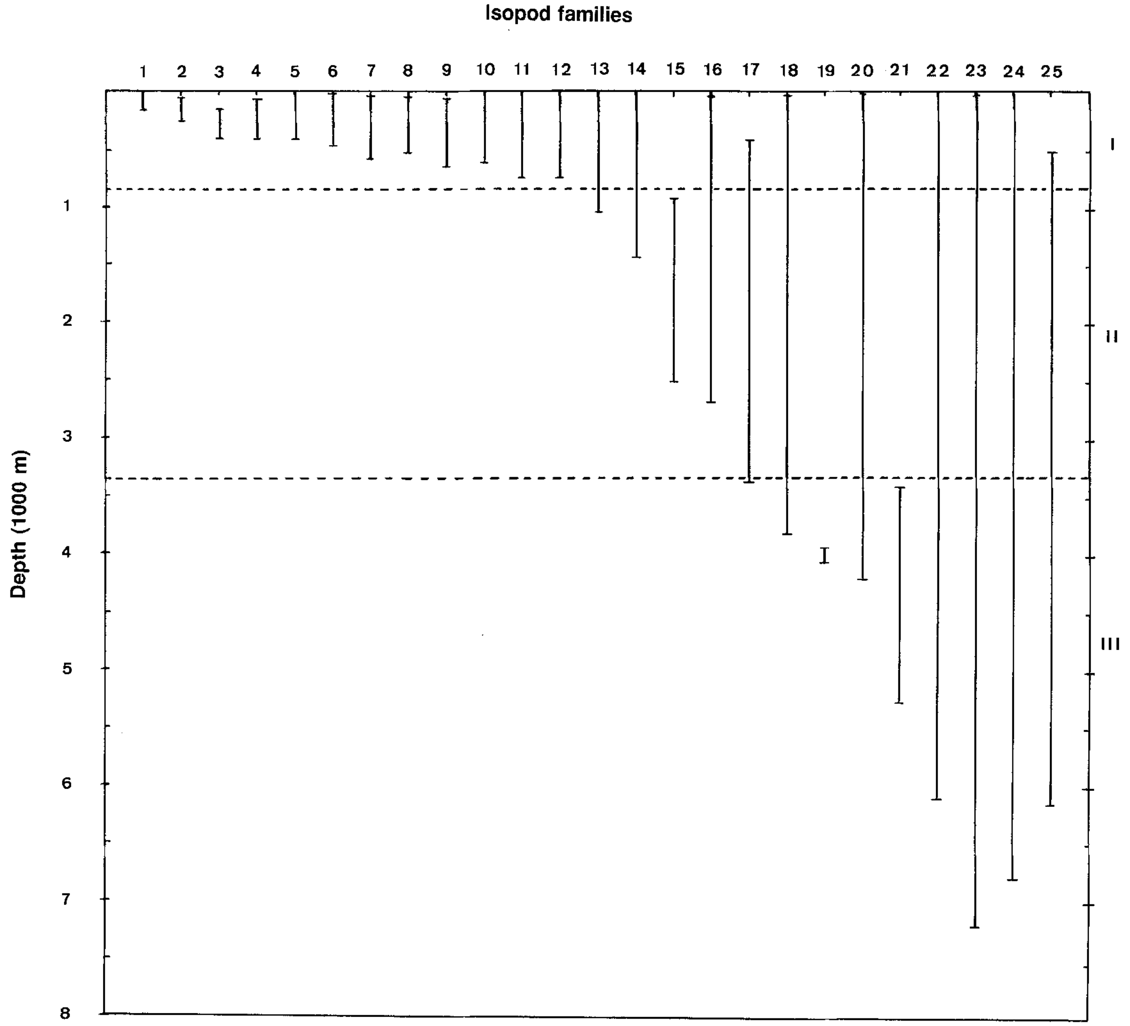

Fig. 1. Vertical distribution of Subantarctic and High Antarctic Isopoda. The arabic numbers symbolize the following families: (1) Pleurocopidae (0 to 95 m); (2) Desmosomatidae (16 to 250 m); (3) Dendrotionidae (196 to 385 m); (4) Nannoniscidae (70 to 385 m); (5) Hyssuridae (0 to 385 m); (6) Anthuridae (0 to 454 m); (7) Paranthuridae (13 to 655 m); (8) Chaetiliidae (10 to 580 m); (9) Cirolanidae (35 to 670 m); (10) Sphaeromatidae (0 to 610 m); (11) Aegidae (0 to 700 m); (12) Janiridae (0 to 700 m); (13) Idoteidae (0 to 1 180 m); (14) Joeropsidae (0 to 1 408 m); (15) Anuropidae (851 to 2 502 m); (16) Paramunnidae (10 to 2 681 m); (17) Stenetriidae (385 to 3 397 m); (18) Serolidae (6 to 3 813 m); (19) Mesosignidae (3 981 to 4 038 m); (20) Arcturidae (1 to 4 209 m); (21) Haploniscidae (3 300 to 5300 m); (22) Munnidae (0 to 6 110 m); (23) Acanthaspidiidae (3 to 7 720 m); (24) Munnopsidae (0 to 6 730 m); (25) Ischnomesidae (500 to 6 071 m). The roman numbers on the right-hand side of the figure stand for the main distribution of the species within the families in the following regions: (I) continental shelf; (II) continental slope; (III) Antarctic deep sea. Abscissa: families; ordinate: depth in 1 000 m

drift vicariance of the Tertiary Gondwanian fauna. The relict species are closely related to the assumed ancestors of derived Antarctic taxa. These "modern" taxa evolved after the Tertiary climatic deterioration during the early Oligocene (ca. 30 my ago). In Fig. 4, the geographical distribution of the Serolidae and Arcturinae (present in all oceans, especially the derived taxa) is presented. The sister-group of the Serolidae, the Bathynataliidae, is distributed in South Africa and Australia; the primitive Plakathriidae (compare Fig. 3) occur in the Magellan Region, at the South Shetland Islands, South Orkney Islands and at Australia and New Zealand. Serolidae and Bathynataliidae species are probably derived from an ancestor of the Tertiary antiboreal fauna of Gondwanaland (Fig. 4 – region within dashed line with present areas of distribution indicated). From this region, taxa evolved and radiated in Antarctica, where primitive species related to the South Gondwanian fauna were isolated by continental drift vicariance. Some species are circumantarctic, and only some derived and phylogenetically modern serolids species submerged into the Atlantic deep sea (genera *Atlantoserolis* and *Glabroserolis*) (Fig. 4). Few species have colonized the Pacific Ocean, and those probably did so before the Panama land bridge closed (Woodring 1966). In South Africa, the Serolidae are absent, except for a single deep-water species (*Serolis brinki* Kensley, 1987), which was probably derived from Atlantic deep-water relatives. The phylogenetic-biogeographic analysis revealed that the Serolidae have three centers of speciation with endemic genera and species, namely, in South and Southeast America, in South and Southeast Australia, and in Antarctica (for further details of distribution and phylogenetic relationship compare Brandt 1991 a).

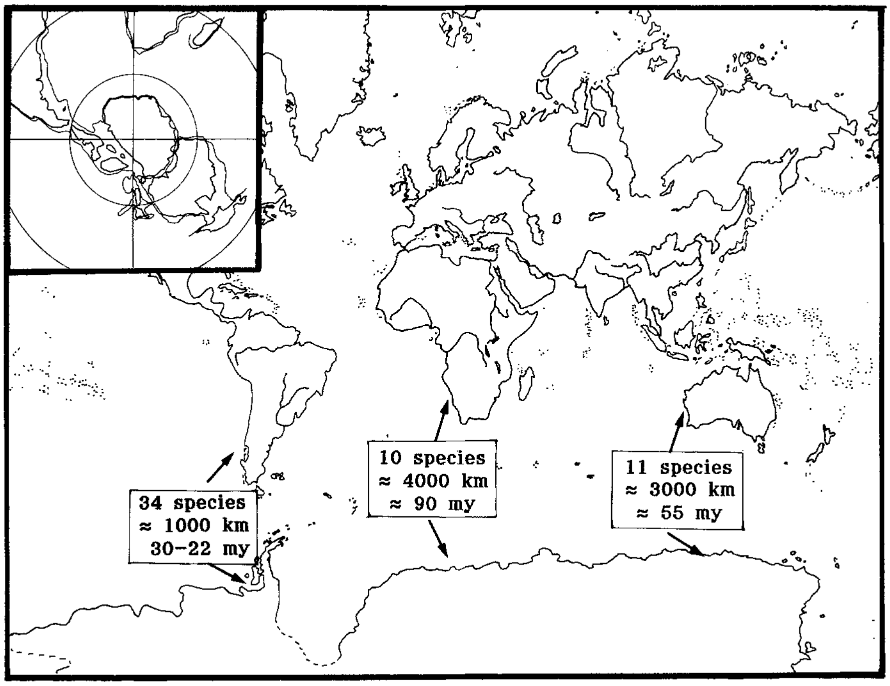

Fig. 2. Number of species shared between Antarctica and South America, South Africa, and South Australia. Information in boxes: number of species, approximate distance between these continents and Antarctica, estimated time of separation of these continents from Gondwana or Antarctica. Inset: reconstruction of the south polar Eocene palaeogeographic evolution (after Tarling 1978). my: millions of years

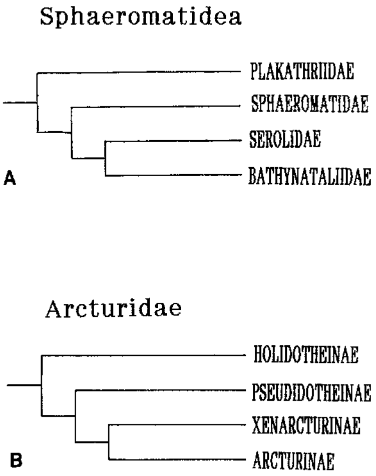

Fig. 3. Simplified dendrograms. (A) families of the primitive Sphaeromatidea, and (B) subfamilies of the Arcturidae (for further details compare Wägele 1989)

The zoogeographic investigation of the Arcturinae shows a very similar pattern (see Fig. 4). Most of the northerly distributed species are more derived than the Antarctic species, which are phylogenetically older. The primitive subfamilies of the Arcturinae, the Pseudidotheinae, Xenarcturinae, and Holidotheinae, only occur where "relict" species of the Serolidae do in the southern hemisphere (dotted region with marked areas in Fig. 4). The most primitive species of the subfamiliy Arcturinae were also most often found in the southern hemisphere. Zoogeographic and phylogenetic considerations indicate that the Arcturinae were derived from ancestors living in South Gondwana (dotted region). The primitive subfamilies Holidotheinae (found in South Africa) and Pseudidotheinae (found in South Patagonia, the Falkland Islands, the South Shetland Islands, and the Crozet and Kerguelen Islands) were derived from these ancestors. The phylogenetically primitive genera *Chaetarcturus* Brandt, 1990, (see Brandt 1990a) and *Neoarcturus* Barnard, 1920 have experienced an adaptative radiation in Antarctica. They now have a circumpolar distribution (small arrows around the Antarctic continent in Fig. 4) and are characterized by many endemic Antarctic species. In contrast, the species of highly derived "modern" genera (e.g. *Astacilla* Cordiner, 1793 and *Neastacilla* Tattersall, 1921 have also colonized the northern hemisphere as well as the deep sea and now have a worldwide distribution. At present it is unknown when and where these migrations occurred, but it is obvious that the most specialized genera, for instance those with elongated fourth pereonites, are absent in the continental Antarctic region.

The phylogenetic system of most of the other Antarctic isopod taxa is not so well known (compare Wägele 1989), and therefore interpretations are not as detailed as for the family Serolidae and subfamily Arcturinae. Nevertheless, in some taxa the phylogenetically primitive species inhabit the continental shelf, while their derived relatives are distributed in the deep sea. This phenomenon of submergence is shown by the isopod genera *Acutiserolis, Ceratoserolis, Cuspidoserolis* (Serolidae) Brandt, 1988 (see Brandt 1988); *Anuropus* (Cymothoida, Anuropidae): *Joeropsis* (Janiroidea, Joeropsidae); *Bathygonium, Neasellus* (Janiroidea, Paramunnidae); *Astrurus* (Janiroidea, Munnidae); *Zenobianopsis* (Valvifera, Holognathidae); *Acantharcturus, Antarcturus, Chaetarcturus, Dolichiscus, Oxyarcturus, Paradolichiscus* (Valvifera, Arcturinae) (Brandt and Wägele 1988, 1990; Brandt 1990a); *Acanthaspidia, Ianthopsis* (Janiroidea, Acanthaspidiiae) (Brandt 1990b); *Stenetrium* (Stenetriidae); *Euneugnathia* (Cymothoida, Gnathiidae) (compare Brandt 1991a). In other genera, the primitive species occur in the deep sea, whereas the more derived ones can be found on the

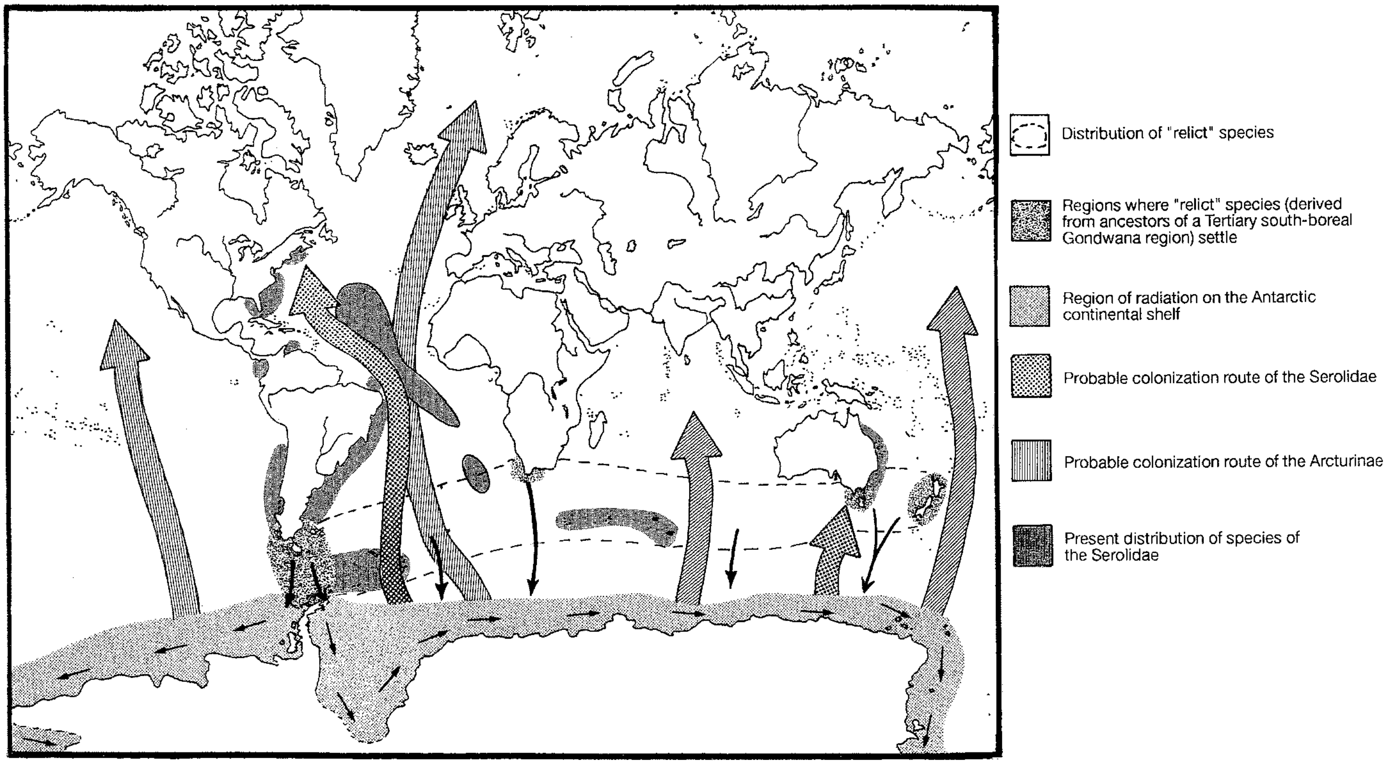

Fig. 4. Schematic illustration of the probable geographic dispersal of the Serolidae (broad dotted arrows) and the Arcturinae (broad hatched arrows). The center of origin of these families lies in a cold-tempertate Gondwana province (area within dashed line). (For further details see description in 'Results')

Antarctic shelf. This mode of derivation, called polar emergence, is very likely for the species of the following genera: *Austroniscus, Nannoniscus* (Janiroidea, Nannoniscidae); *Desmosoma* (Janiroidea, Desmosomatidae) (Brandt 1992a); *Coperonus, Lionectes* (Janiroidea, Munnopsidae, Lipomerinae) (Brandt 1992b); *Echinozone, Ilyarachna* (Janiroidea, Munnopsidae, Ilyarachninae) (Brandt 1990b); *Disconectes, Eurycope* (Janiroidea, Munnopsidae, Eurycopinae); *Munnopsoides, Munnopsurus, Paramunnopsis* (Janiroidea, Munnopsidae, Munnopsinae); *Munneurycope* (Janiroidea, Munnopsidae, incertae sedis); *Baktromesus, Ischnomesus* (Janiroidea, Ischnomesidae) (Brandt 1991a, Brandt 1992c). Some other genera contain either shelf or deep-sea species (for further details see Brandt 1991).

Discussion

Antarctic fauna originates from various sources (Dell 1968). Some of the species are remnants of an "old" Gondwanian fauna, others colonized Antarctica from South America via the Scotia Arc or emerged from deep-sea relatives. The earliest fossil isopods are recorded from the lower Carboniferous (Schram 1982), but no fossil Isopoda are known from the Southern Ocean. Therefore, the probable age of Antarctic isopod fauna, its possible origin, as well as the routes of distribution can only be investigated by means of phylogenetic relationship and plate tectonics (geological history), and the zoogeographic distribution of isopods in Antarctica.

Many biogeographical investigations of benthic Antarctic taxa have been undertaken in the past, but usually the authors did not present any hypotheses concerning the phylogenetic relationship of these groups. Hypotheses about the origin of the Tanaidacea (Sieg 1986, 1988), Ostracoda (Hartmann 1988, 1990), and the Nototheniiformes (Andersen 1984, Iwami 1985, Andriashev 1987, Eastman and Grande 1989) have been formulated. These authors combined data on zoogeographic distribution and phylogenetic relationships to derive possible origins of these taxa. The evolution of the notothenioid fishes appears to follow a pattern similar to that derived here for species of the isopod taxa Serolidae and Arcturinae. Most of the non-notothenioid Cenozoic fish taxa died out as the climate deteriorated. The subsequent radiation of the Nototheniidae is illustrated by the high number of endemic species (88%) (e.g. Dell 1972, Andriashev 1987). In contrast to the isopod taxa Serolidae and Arcturinae, the notothenioid fishes did not colonize more northerly habitats but remained in the Antarctic and in the very south of bordering continents, such as South America, New Zealand and South Australia.

Sieg (1988) investigated the zoogeographic distribution of the Tanaidacea and concluded that the Antarctic shelf fauna became extinct during the Miocene ice age and was replaced in the Pliocene by species from the Magellan Region: "... it can be assumed that almost the entire Antarctic tanaidacean fauna was extinguised during the first dramatic drop of temperature. Cold-stenothermic eurybathic species then have colonized the Antarctic shelf. After the phase of maximal glaciation in the Pliocene the fauna of the West Antarctic was finally modified by Magellanic elements, which in some cases have to be accepted as phylogenetically old forms . . . the species composition of the East Antarctic tanaidacean fauna is more like that of the deep-sea“ (Sieg 1988, p. 364). Sieg (1988) pointed out that other available information about Crustacea, especially Cirripedia, Ostracoda, Decapoda, and Isopoda, supports this hypothesis. Furthermore Sieg (1988) stated that the Antarctic crustacean fauna, in general, is comparatively young and was mainly established ca. 38 my ago. Sieg's opinion is open to challenge, because new data on the phylogeny of at least Ostracoda (Hartmann 1986, 1988, 1990) and Isopoda (Wägele 1989, Brandt 1991 a) demonstrate that phylogenetically "primitive" taxa occur in Antarctica, and therefore Sieg's hypothesis cannot be accepted any longer. This hypothesis is also dubious, because Sieg did not consider the possibility that the phylogenetically primitive elements from the Magellan Region are likely to have survived the ice ages on the Antarctic continental shelf in biological refugia.

Kussakin (1973) hypothesized that the most ancient isopod fauna colonized tropical shallow water, that the fauna of Antarctica is more recent, and that in the deep sea the youngest fauna occurs. These assumptions by Kussakin (1973) can only be demonstrated for some isopod taxa, namely the species of the serolid-like Sphaeromatidea, the subfamily Arcturinae, the munnoid Janiroidea (Brandt 1991 a) and the Acanthaspidiidae (Brandt 1991 b) (for different theories on submergence and emergence of isopods see also Brandt 1991 a). Relatives of phylogenetically derived species of the families Munnopsidae, Nannoniscidae, Desmosomatidae and Ischnomesidae, colonizing the continental shelf of Antarctica, live in the deep sea and have done so for a long time (Wolff 1962, Thistle and Hessler 1976, 1977, Hessler et al. 1979, Hessler and Wilson 1983). It is unknown how, in time and space, these taxa colonized the deep sea.

The dispersal of the isopod taxa Serolidae and Arcturinae is essentially equivalent to the scenario reconstructed by Zinsmeister (1976) and Zinsmeister and Feldmann (1984) from the distribution of fossil and recent molluscs, echinoderms, and decapod crustaceans. These authors pointed out that the circumpolar shelf areas had been the centre of origin and dispersal of the former mollusc and echinoderm species. Zinsmeister (1976) characterized a "Weddellian Province", a shallow-water marine province ranging from South America via West Antarctica to Australia. The Serolidae and related families as well as the Arcturinae show a slightly different pattern of distribution in the southern hemisphere (Fig. 4). The archaic, most primitive genera, which are closely related to the Antarctic Serolidae and Arcturinae, also occur in South Africa as well as in Australia and South America. This indicates a minimum evolutionary age of ca. 80 to 90 million years (Brandt 1991 a), shortly after South Africa had separated from Antarctica (Dietz and Holden 1970, Dietz and Sproll 1970). The living species of the Serolidae and Arcturinae evolved from ancestors that colonized a cold-temperate Gondwana province. Species of other families have either colonized Antarctica via the deep sea, or their ancestors have survived the Tertiary climatic deterioration and undergone species radiation on the continental shelf. This also explains the high percentages of endemism.

The climatic deterioration of the Oligocene and Miocene ice ages (Shackleton and Kennett 1975) meant that only those organisms could survive in the Southern Ocean which were pre-adapted or tolerant to these extreme environmental conditions (De Vries 1969, 1970, Clarke 1983, Arnaud 1977, Umminger 1977). Alternatively, the success of the peracarid crustaceans was probably a result of available ecological niches freed by the extinction of most Tertiary decapod species. The success of the peracarids might also be explained by their pre-adaptation to a polar environment (White 1984) by means of brood protection. The marsupium provides shelter against predators and also against passive dispersal by strong currents. Moreover, the fact that the growth of the larvae in the brood pouch restricts dispersal could be regarded as a possible reason for the high percentage of endemic species in the Southern Ocean (White 1977). The high percentages of endemism in other benthic taxa that also practice brood protection support this hypothesis (Dell 1972).

As mentioned above, Sieg (1988) assumes that the crustacean fauna had colonized Antarctica during Pliocene times via the Scotia Arc. Although such a process might have occurred, for example, passively by transport of benthic organisms on drifting algae, it does not seem likely for the following reasons. First, the circumpolar current is characterized by comparatively high velocities in the Drake Passage (Hellmer and Bersch 1985). Second, the islands of the Scotia Arc are surrounded by a deep-sea barrier restricting active migration of the shallow-water benthos. Third, the dispersion of isopods attached to drifting seaweed from the South Sandwich Islands or the South Orkney Islands to the South Shetland Islands or the Antarctic Peninsula would be directed against the movement of the circumpolar current. Another possible explanation for benthic organisms survival of the Tertiary and Quaternary ice ages is that some taxa had already dispersed northwards to areas free of ice and recolonized the Antarctic shelf areas from their northern habitats when the climate became warmer again.

However, a more likely alternative is that some species survived the ice ages in biological refugia on the continental shelf. The following arguments support this hypothesis. Littlepage and Pearse (1962) were the first to report that benthic communities (Actiniaria, Polychaeta, Copepoda, Amphipoda, Isopoda, Tanaidacea, Echinoidea) exist in the Ross Sea 22 km from the shelf-ice edge under the sea ice. A few years later cryopelagic fishes (*Trematomus brochgrevinki*) were found at a distance of 80 km from the open Ross Sea under an ice cover of 275 m thickness (Andriashev 1987). The most spectacular records were made in 1979 when, at a distance of 475 km from the shelf-ice edge, benthos were found at a depth of 597 m (Azam et al. 1979, Bruchhausen et al. 1979, Lipps et al. 1979). At this drilling hole (J9), the ice was 420 m thick, the height of the water column was only 177 m. Photographs of baited traps showed a high abundance of amphipods (*Orchomene* spp.) around the cages (Lipps et al. 1979, Stockton 1982). Infauna was almost completely absent at this site. Azam et al. (1979) observed very low microbial activity in the sediment in comparison with other deep-sea samples. "This is 10^3 to 10^4 times less activity than in the Ross Sea around McMurdo Sound, and this probably is the slowest rate of turnover of D-glucose pool reported for any oceanic environment" (Azam et al. 1979, p. 452). Therefore one can conclude that even without primary production benthic life under the ice is possible, where food could have only been provided by horizontal currents. For these reasons, I consider it reasonable to assume that during the Tertairy life between ice and shelf was maintained in biological refugia.

In the past, many different hypotheses about the origin of the deep-sea fauna have been proposed. Some authors supported the hypothesis that deep-sea fauna evolved by a process of submergence of taxa from continental shelf areas (e.g. Bruun, 1956, 1957, Menzies and Imbrie 1958, Kussakin 1973, Menzies et al. 1973, Schultz 1979). Kussakin (1973) hypothesized that submergence also occurred in the Southern Ocean, because no limiting thermocline exists. The depression of the continental shelf to depths between 400 and 800 m (Deacon 1964, Denton et al. 1970) might have faciliated a deep-sea colonization via the continental slope (Kussakin 1973). Other authors have argued that the deep-sea fauna must have already existed for a long period of time due to environmental stability (Sanders et al. 1965, Hessler and Sanders 1967, Sanders and Hessler 1969, Hessler and Thistle 1976). According to this hypothesis, the deep-sea fauna evolved and radiated in the deep sea, from which area some species colonized the continental shelves, especially in high latitudes. This theory of polar emergence was supported by Zenkevitch and Birstein (1960), Broch (1961), Belayev (1974), Hessler and Thistle (1975), Thistle and Hessler (1977), Hessler and Wilson (1983) and Wilson and Hessler (1987). It is now generally accepted that the processes of polar emergence and submergence have both occurred several times and independently within different isopod taxa (see list of taxa that show either emergence or submergence in 'Results'). Kussakin (1988) pointed out that primary and secondary deep-sea fauna can be discerned, a view that is at present generally accepted. Within the secondary deep-sea taxa, the number of species decreases with increasing depth, whereas within the primary deep-sea taxa the number of species increases in deeper waters (Kussakin 1988).

Contrary to the hypothesis of an evolutionarily young Antarctic crustacean fauna (Sieg 1988), it is concluded that species of the families Serolidae and Arcturidae could not have been totally eliminated during the Tertiary climatic changes, because many phylogenetically primitive elements still colonize the Antarctic shelf, whereas the derived, phylogenetically advanced species are distributed northwards. Moreover, the colonization of Antarctica did not only occur from South America via the Scotia Arc, but some crustacean elements also invaded Antarctica from the deep sea, and yet others were probably isolated on the Antarctic continental shelf due to Tertiary continental-drift vicariance. Once isolated in Antarctica, some crustaceans exploited free ecological niches, following environmental changes, resulting in species radiation among well-adapted groups.

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