6. Zoologische Systematik
Zoological systematics

Systematische Untersuchungen an Tieren polarer Regionen
Zoosystematic research in animals of polar regions

Benthic ecology in the Southern Ocean and the biology and evolution of Antarctic Isopoda (Crustacea: Peracarida)
Benthosökologie im Südpolarmeer und die Lebensweise und Evolution antarktischer Isopoda (Crustacea: Peracarida)

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Summary

The peculiarities of Antarctic benthic invertebrates are a result of the geological, climatic history and the long period (about 20 m. y.) of existence of the polar environment. Results of research about the biology and ecology of benthic invertebrates and especially of the Crustacea Isopoda are briefly summarized. Combining biogeographical data with results of a phylogenetic analysis show that the radiation of Antarctic taxa can be correlated with the successive fragmentation of Gondwana. Present day Serolidae have 3 centres of radiation (Antarctica, South America, Australia), they evolved after the separation of Africa. The suspension-feeding Arcturinae probably evolved in the same period.

Introduction

James Eights, «the first qualified naturalist to set foot on land south of the Antarctic Convergence» (Hedgpeth 1971), described in 1833 the first Antarctic isopod *(Brongniartia trilobitoides)*. Since then several faunistic surveys of restricted areas have been published, but until now only few taxa have been revised comprehensively (e. g. Newman and Ross 1971: Cirripedia; Cairns 1982: Scleractinia; Gibson 1985: Heteronemertini). It can be gathered from these studies that the Antarctic marine benthos differs distinctly in composition and biology from the fauna of other oceans. Comparing the biology, phylogenetic relationships and biogeography of benthic invertebrates with climatic history and plate tectonics some aspects of the evolution of Antarctic taxa can be deduced. An important prerequisite is the reconstruction of phylogenetic relationships, which have been proposed only for few Antarctic groups (e. g. Nototheniidae (Perciformes): Andersen 1984; Iphimediidae (Amphipoda): Watling and Thurston 1989; Isopoda: Wägele 1989, in press; Brandt 1991).

In the following account some peculiarities of the Antarctic benthos are explained (see also

Dayton 1990). The contribution of systematics to the reconstruction of the historical development of the Antarctic fauna is described using examples from the isopod taxa Serolidae and Arcturinae.

Climatic history and the fragmentation of Gondwana

The cooling of the Southern Ocean increased markedly with the formation of the circumpolar current (westwind drift) about 30 to 25 m. y. b. p., which isolated Antarctica thermically after the opening of the Drake Passage and the northward movement of Australia (Kennett 1977; Barker et al 1988). In the following period glaciation of Antarctica increased until the polar ice-cap was fully developed (about 20 m. y. b. p.: Hayes and Frakes 1977; Birkenmajer 1985). The fossil record does not allow a detailed reconstruction of the history of marine benthic invertebrates, but it is evident that several species became extinct after the Eocene/Oligocene temperature reduction, for example, nearly all decapod crustaceans (cf. summary in Brandt 1991). During the course of oscillation in the maximal extension of the shelf-ice, large areas of the continental shelf were covered with grounded ice about 5 m. y. b. p. and again about 2.4 m. y. b. p. (Kennett 1977; Barker et al 1988). An exctinction of all shelf species as a result of these events seems to be unlikely because of the high number of extant endemic species that are neither descendants of deep-sea ancestors nor immigrants from South America (see below).

Peculiarities of the Antarctic benthos

Species diversity: In comparison with other oceans the number of species is high in many taxa. The shelf fauna of the Arctic Ocean is distinctly less rich than that of the South Polar Ocean (see Knox and Lowry 1977). Each year new species are discovered in Antarctica, an actual review of species numbers does not exist (recent taxonomic reviews: Cairns 1990: Scleractinia; Zdzitowiecki 1991: Acanthocephala; Wägele 1991: Isopoda Valvifera). The reason for the high diversity discussed in literature are the age of the southern polar ecosystem, the regular seasonality (predictability), and the diversity of bottom morphology and sediment types (e. g. Lipps and Hickman 1982). Furthermore speciation might be favoured by the reduced gene exchange between populations, caused by the low mobility of individuals and the absence of pelagic stages (e. g. Picken 1980; Wägele 1986). The rich adaptive radiation during the Cenozoic obviously originates from a reduced number of species that survived the cooling of the Southern Ocean. Watling and Thurston (1989) call Antarctica an «evolutionary incubator».

Endemisms: Brandt (1991) summarized published data, according to which more than 70% of the species of the following groups are endemic: Porifera, Actiniaria, Amphipoda, Cumacea, Tanaidacea, Isopoda, Holothuroidea, Echinoidea, Ophiuroidea, Ascidiacea, fishes. The lowest value (38%) is recorded for polychaetes.

Guilds: In shelf communities of many localities sessile suspension feeders are dominant in terms of biomass (e. g. Bullivant 1967; Dayton et al 1974; Gutt 1988; Voß 1988). Voß (1988) for example obtained in the western Weddell Sea trawl samples with up to 90% sponges (wet weight). Among predators such as amphipods a number of unusual specialists were discovered, which feed on suspension feeders (Coleman 1989, 1991; Klages and Gutt 1990). These prey species are also the diet of several nudibranchs (Wägele 1989, 1990). It is remarkable that 5 out of 6 frequent occurring asteroids of the McMurdo Sound feed exclusively on sponges (e. g. McClintock 1987). This specialization of predators indicates the abundance of suspension feeders. Another frequent mode of nutrition is necrophagy (Arnaud 1974a; Pressler 1986). Detritus originating from sedimentation or horizontal transportation must be an important energy source in areas permanently covered with ice and in deeper water.

Reduction of planktotrophic stages: Broodcare, the reduction of pelagic stages in connection

with the production of relatively few and large eggs are common features of Antarctic invertebrates (e. g. Arnaud 1974b; Clarke 1982b; Wägele 1987a). Many Antarctic asteroids probably do have pelagic larvae, but most of these are lecitotrophic (e. g. Bosch and Pearse 1990). While among malacostracan crustaceans nearly all decapod taxa are absent, the breeding peracarids are found with high abundances and species numbers (e. g. Jazdzewski et al 1991). These phenomena are usually considered to be adaptations to the short plankton blooms at low, growth-delaying temperatures (e. g. Picken 1980).

Cold adaptations: While fishes are able to produce glycoproteins as anti-freeze substances (e. g. Eastman and DeVries 1987), the hitherto studied invertebrates tolerate few degrees below the freezing point of sea water by hyperosmotic regulation (e. g. Rakusa-Suszczewski and McWhinnie 1976). Respiration measurements indicate the absence of a metabolic cold adaptation in most species (e. g. Ralph and Maxwell 1977a, b; Rakusa-Suszczewski and Lach 1991). The low metabolic rate is in accordance with observations of slow growth and low reproductive rates (Clarke 1980), though low temperatures must not *per se* induce a retardation of all biological processes. Species with relatively fast growth, which probably compensate the effect of low temperatures to some degree are e. g. the isopod *Glyptonotus antarcticus* (see Belman 1975) and the bivalves *Laternula elliptica* and *Adamussium colbecki* (Ralph and Maxwell 1977a).

K-selection: Many species have the typical features of K-selected organisms: longevity, large body size and low reproductive rates. Slowness as a physiological effect of low temperatures can not easily be discerned experimentally from evolutionary adaptations to a stable, predictable ecosystem. Slow growth and longevity have frequently been observed (e. g. Pearse 1969; Richardson 1979; Ekau 1988; Wägele 1990; Arntz and Gorny 1991). Several sponge species of the McMurdo Sound did not visibly grow during the course of 10 years (Dayton 1979). Embryonic development has shown to be unusually slow in many species and contributes to the retardation of life cycles (e. g. Pearse 1969; Wägele 1987, 1988, 1990). It is therefore not surprising that the commercial exploitation of Antarctic fish species in the Atlantic Sector of the Southern Ocean led within a short time to a considerable reduction of the standing stock (e. g. Kock and Köster 1989).

With the exception of invertebrates that produce calcareous skeletons most taxa contain species that grow to a large size. DeBroyer (1977) calculated that 12% of the Antarctic amphipod species are ‹giants› and more than 30% are larger than the generic median size.

Modes of life of Antarctic Isopoda

A summary of modes of life has been published by Wägele (1991). Antarctic *Asellota* represent about 60% of all hitherto discovered isopod species of the region, but their mode of life is generally not well studied. Many species are probably omnivorous and able to exist by consuming detritus. With the exception of many Munnopsidae (see Fig. 3A), which are able to swim with their paddle-shaped pereopods 5–7, most asellotes are benthic crawling or burrowing organisms (e. g. Hult 1941; Hessler and Strömberg 1989). The taxonomy of the *Valvifera* has recently been revised (Wägele 1991). *Glyptonotus antarcticus* (Chaetiliidae) is a stenothermal ‹gigantic› species (length > 12 cm), which does not survive temperatures above 6 °C (White 1975). Specimens can be found circumpolarly on all types of substrates from 0 to about 800 m depth. The Idoteidae are rare and avoid the colder areas. In contrast the Arcturidae are one of the characteristic groups of the Antarctic benthic fauna. Most of these isopods have a highly specialized morphology (Fig. 4D): pereopods 2 to 4 bear long setae forming a sieving basket. This can be held into the water due to special joints between pereonites 5 to 7 that allow a dorsal bending of the thorax. Animals with this morphology (Arcturinae) are passive filterfeeders that probably depend mainly on phytoplankton and microzooplankton of large size (particles > 50–80 µm) (Wägele 1987c). Of the *Sphaeromatidea* (see Wägele 1989) only the Serolidae are common in Antarctica. These are flattened, discoid animals (see Fig. 3A) with several morphological analogies to trilobites. Many species live on soft bottoms. Serolids
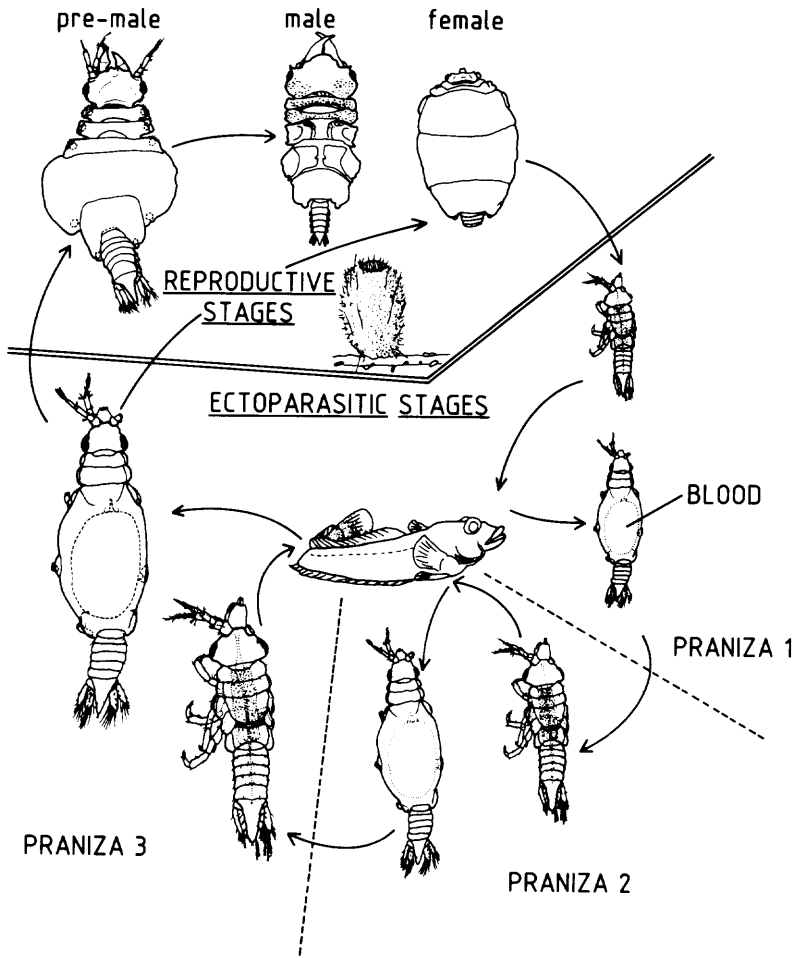
Fig. 1: Life-cycle of the Antarctic fish parasite *Gnathia calva* (after Wägele 1988).

are predators and carrion-feeders. In captivity they prefer polychaetes. *Paraserolis polita* (Pfeffer) is a common species of near-shore soft bottoms in the South Shetlands area, with abundances of 100 to more than 300 ind/m² in dense populations (e. g. Wägele and Brito 1990). The largest species of the worm-like *Anthuridea* is the Antarctic *Accalathura gigantissima* Kussakin (up to 4–5 cm). Specimens suck-out body fluids of amphipods with their acute mouthparts (Wägele 1985). *Eisothistos antarcticus* (Hyssuridae) probably occupies a similar niche as the mediterranean species of the genus (see Wägele 1979), which live within serpulid tubes and feed on the original inhabitants. Species of the *Cymothoida* are predators or carrion-feeders specialized on fishes (Cirolanidae), ectoparasites of fishes (Aegidae, Cymothoidae) or of crustaceans (Bopyridae). Specimens of *Aega antarctica* kept for 2 years in aquaria grew very slowly. According to these data females reach maturity at an age of more than 10 years, the number of eggs is verly low (between 9 and 53), embryonic development takes more than 30 months (Wägele 1990). The *Gnathiidae* also are ectoparasites of fishes, but only in the immature stage, the adults have reduced and modified mouthparts. Wägele (1988) described the life-cycle of *Gnathia calva* Vanhöffen (Fig. 1), a species with harems of up to 43 females or juveniles per male that inhabit small hexactinellid sponges. A special rectal vesicle contains symbiotic bacteria (Juilfs and Wägele 1987). Embryogenesis takes about 12 months, sexual maturity is reached about 3–4 years after hatching.

Conspicuous characteristics of the Antarctic isopod fauna

Gigantism (Fig. 2A): The largest species of the Paranthuridae, Chaetiliidae, Arcturidae, Serolidae and Gnathiidae live in Antarctica. The average maximal length of Antarctic taxa is clearly greater than in related taxa occurring north of the convergence (Fig. 2A). Gigantism is somehow correlated with low temperatures: southern populations of *Ceratoserolis trilobitoides* have fewer and larger eggs than populations from slightly warmer areas (Wägele 1987a)
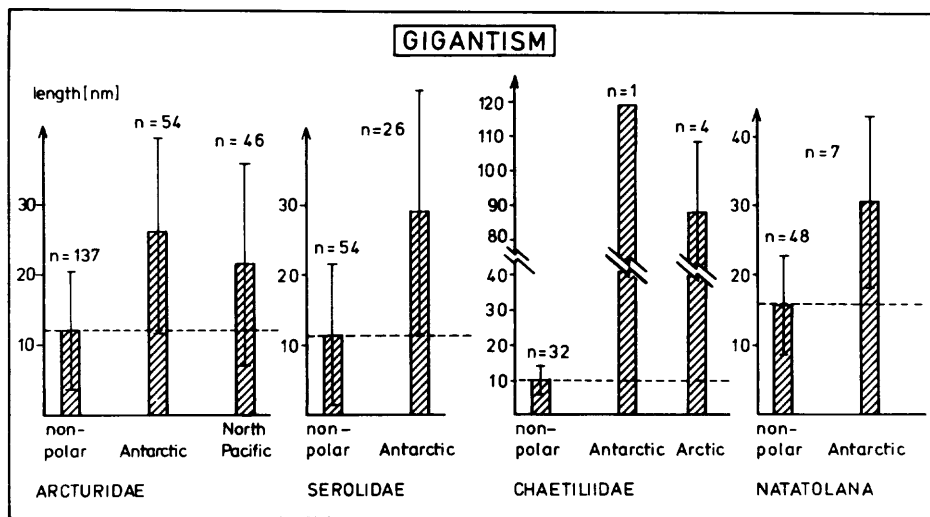
A)
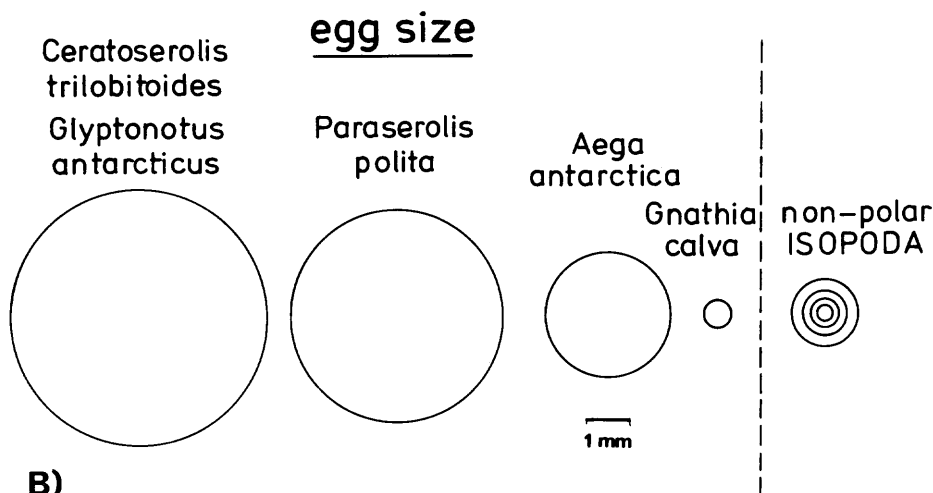
B)

Fig. 2A: Average maximal length of isopod taxa from Antarctica in comparison with other regions. Note that species from colder oceans (Antarctica, North Pacific, Arctic) are larger than other species. B: Egg size of Antarctic isopods in comparison with other species.

(see Thorson's rule: Thorson 1936, 1950). Largest isopod eggs occur in Antarctic species (Fig. 2B).

Low reproductive rates and long life cycles: While isopods of the North Sea usually live for 1 year, summer generations only for few months, the life cycles of Antarctic species take much longer to reach maturity. *Glyptonotus antarcticus* probably can not achieve maturity in less than 5 years, females of *Paraserolis polita* need 28 months, while the larger *Ceratoserolis trilobitoides* needs 3.5 to 4 years, *Gnathia calva* 3 to 4 years, *Aega antarctica* more than 10 years (references in Wägele 1987a, 1990). Embryogenesis contributes to the retardation of life cycles. While European species usually hatch after only 25 to 45 days, in Antarctica embryonic development takes 1 to nearly 3 years (Wägele 1987a, b, 1990) (see Table 1). Lowest reproductive values occur in Antarctic and interestingly also in stygobiontic species. This indicates that not only cold climate but also stable, unproductive environments can trigger the evolution of slow development. The parasite *Gnathia calva* produces more (but very small) eggs in comparison with serolids, but *Aega antarctica*, the other fish parasite, has the lowest value recorded for Antarctic isopods. *Glyptonotus antarcticus*, a relatively fast growing species (precise data are still wanting), reaches a large size and produces a large number of eggs (White 1970; the value in Table 1 assumes a generation time of 5 years plus 20 months embryogenesis). With this exception populations of Antarctic isopods must have a much lower regenerative potential than populations of European species.

Cold adaptations: Metabolic adaptations seem to be absent in most hitherto studied species. Respiration measurements (White 1975; Luxmoore 1984) have shown that Antarctic isopods have a metabolic rate no higher than in European species at winter temperatures.

Vertical distribution: The absence of a pronounced stratification in the water column enables species that are independent of plankton concentration to be eurybathic. These conditions also favour the evolutionary exchange between deepsea and shelf (Fig. 3A). Cases of polar emergence and polar submergence are summarized in Brandt (1991).

Table 1: Average number of eggs produced per day of minimum generation time by 1000 females (fat Antarctic species, *italics* stygobionts) (for references see Wägele 1987, 1988, 1990).

| species	eggs, day
Asellus hilgendorffi (25° C)	780
Idotea baltica (Sommer)	666
Idotea baltica	580
Idotea baltica (Winter)	403
Idotea chelipes (Sommer)	400
Asellus hilgendorffi (15 ° C)	310
Asellus aquaticus	290–300
Idotea chelipes (Winter)	282
Idotea chelipes (Sommer)	259
Glyptonotus antarcticus	210
Idotea chelipes (Winter)	177
Sphaeroma hookeri	160
Asellus aquaticus	150–160
Saduria entomon	132
Dynamene bidentata	120–130
Asellus aquaticus	82
Idotea pelagica	80
Excirolana braziliensis (Sommer)	79
Gnathia calva	71
Eurydice pulchra (Winter)	61
Limnoria lignorum	55
Cyathura carinata	55
Excirolana braziliensis (Winter)	52
Gnorimosphaeroma insulare	44
Proasellus cavaticus	*21–30*
Serolis polita	28
Ceratoserolis trilobitoides	11
Aega antarctia	9
Stenasellus virei	7

SEROLIDAE   MUNNOPSIDAE

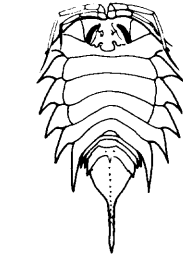*Ceratoserolis pasternaki*
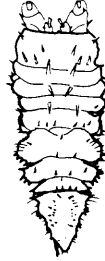(Kussakin, 1967)

Echinozone magnifica
Vanhöffen, 1914
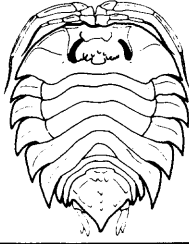
shelf
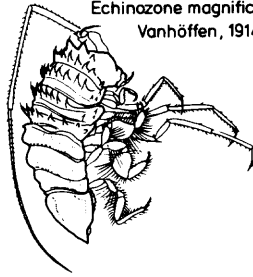
deep sea

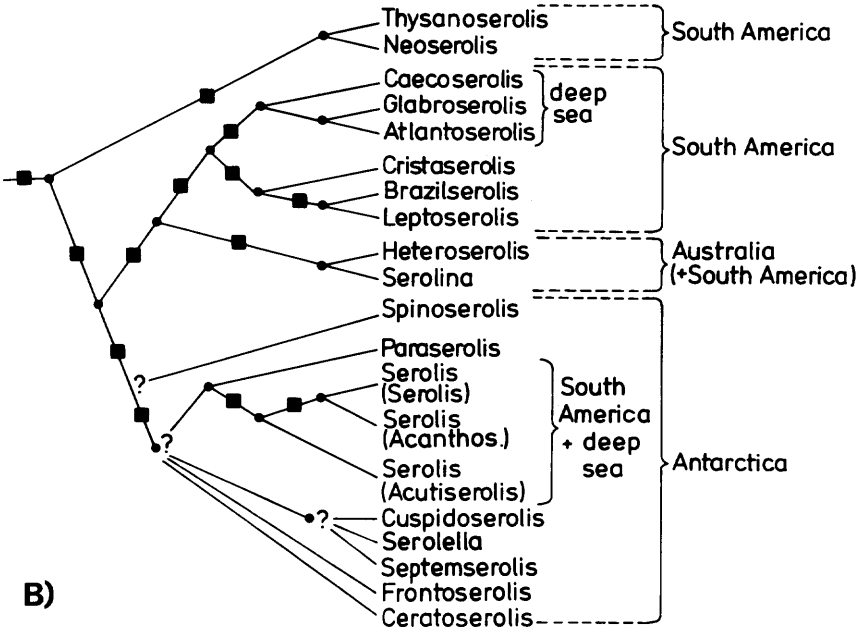*Ceratoserolis meridionalis*
(Hodgson, 1908)

Bathybadistes gurjanovae (Menzies, 1962)
(South Atlantic)

polar submergence   polar emergence

A)

Thysanoserolis
Neoserolis   South America

Caecoserolis
Glabroserolis   deep
Atlantoserolis   sea

South America

Cristaserolis
Brazilserolis
Leptoserolis

Heteroserolis   Australia
Serolina   (+South America)

Spinoserolis

Paraserolis
Serolis
(Serolis)
Serolis
(Acanthos.)   South
America
+ deep
sea   Antarctica
Serolis
(Acutiserolis)

Cuspidoserolis
Serolella
Septemserolis
Frontoserolis
Ceratoserolis

B)

Fig. 3A: Examples for polar submergence and emergence. B: Dendrogram for gener of the Serolidae showing that radiation is correlated with vicariance by continental drift. Squares stand for autapomorphies listed in Wägele (in press).

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Biogeography and history of the Antarctic isopod fauna

Marine groups with predominantly warm-water species as the *Sphaeromatidae* are poorly represented. In addition also the boreal phytophagous *Idoteidae* did not radiate in Antarctica, despite of the local occurrence of a dense macroalgal vegetation. The species-rich Antarctic Asellota are not well studied, their phylogenetic biogeography cannot be reconstructed in detail at present. The low species number of Antarctic fish parasites (taxa of the Cymothoida) is not surprising in view of the composition of the fish fauna: 88% of the fish species are endemic, more than half are Nototheniodei, a group that radiated in the Southern Ocean (Andriashev 1987). Probably many parasite species do not find an adequate host in Antarctica. Similarly the absence of most decapod taxa is an important cause for the rare occurrence of bopyrids.

An important adaptive radiation in the polar region can be postulated for the Serolidae and Arcturinae. Evolution could be reconstructed in some detail especially for the *Serolidae* (Wägele 1989, in press; Brandt 1991). Related less derived outgroups (Plakarthriidae, Bathynatali-
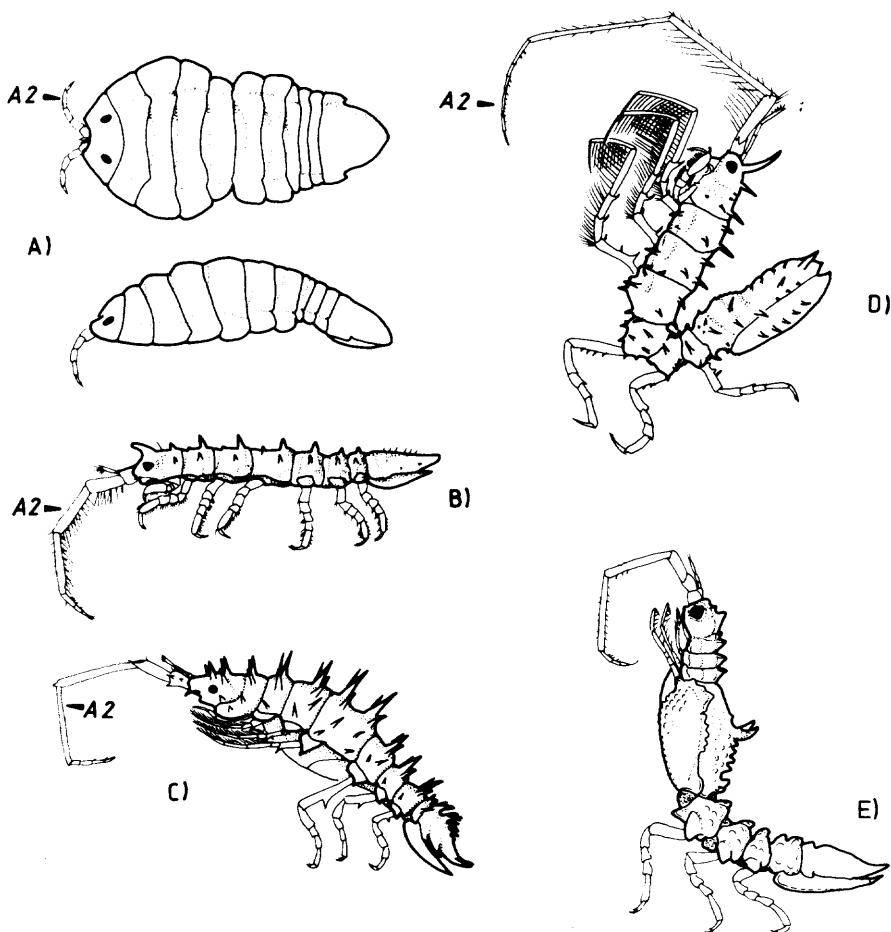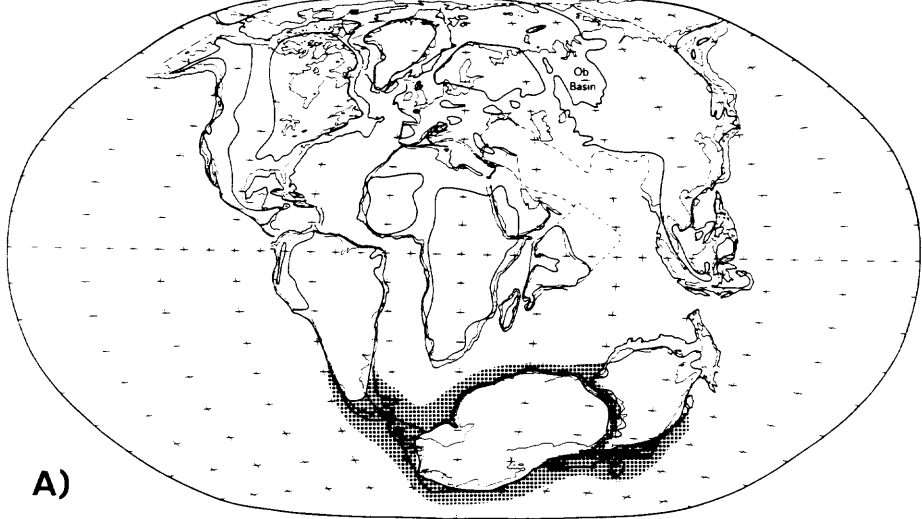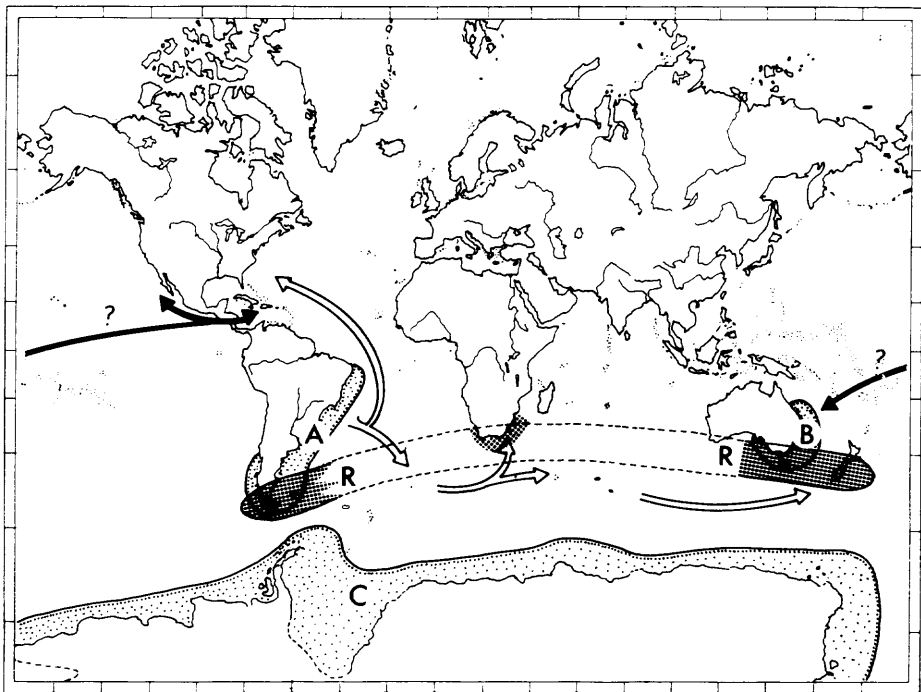

Fig. 4: A–E: Steps in the evolution of arcturids: Elongation of antenna 2 (A 2) and narrowing of body (from A to B), pereopods specialized for suspension-feeding (C), dorsal bending of thorax (D), elongation of pereonite 4 (E). A: Holidoteinae; B: Pseudidotheinae; C: Arcturinae *(Pleuroprion)*; D: Arcturinae *(Antarcturus)*; E: Arcturinae *(Arcturella)*.

A)

B)

Fig. 5A: Palaeogeography during Upper Cretaceous (90–80 my) with the presumed distribution of sero-lids (from Wägele, in press).B: A, B, C: radiation centers of serolids; R: Gondwana – relict region, distri-bution of Plakarthriidae and Bathynataliidae. Open arrows: presumed distribution – routes of deep-sea genera. Black arrows do not indicate a path but the enigmatic disjunct distribution of *Heteroserolis* (from Wägele, in press).

idae) contain only few species with a relict distribution in the south of South America, Africa, and in the Australian region. Within the Serolidae 4 monophyla can be discerned, which radiated mainly in South America, Australia, or in Antarctica (Fig. 5B), while shelf species are absent in South Africa (Fig. 3B, 5B). It seems that crown group Serolidae evolved *after* the separation of Africa (90 m. y. b. p., see Fig. 5A). Vicariance by continental drift and local dispersal seems to be the best explanation for present-day biogeography of serolids. The phylogenetic analysis shows that part of the deep-sea serolids are not derived from Antarctic ancestors, but belong to a South American monophylum (Wägele in press). The monophyly of the group with predominantly Antarctic species indicates that special adaptations are required to successfully inhabit the polar environment.

The historical development of the Arcturidae is basicly similar to that of the Serolidae: the less derived, phylogenetic older taxa (Holidoteinae, Xenarcturinae, Pseudidotheinae; Fig. 4) occur in the south of Africa, South America, New Zealand, and in the Subantarctic region (Fig. 4). The phylogeny of the Arcturinae is still unknown in detail. Most species of the northern hemisphere are more specialized than the Antarctic ones: their pereonite 4 is usually elongated and the filter-basket is shortened (Wägele 1989, see Fig. 4E). These data suggest that suspension-feeding of arcturids evolved in the Southern Ocean (Wägele 1989).

Conditions that favour speciation in the South Polar Ocean can be studied in the case of *Ceratoserolis trilobitoides*, an eurybathic serolid with circumpolar distribution. Local populations from different localities vary in morphology and colouration (Wägele 1986). Specimens of *neighbouring* populations can be discerned by their morphology, while the variability *within* a population is small. As already mentioned populations also differ in egg numbers and size (southern populations having larger eggs). Despite oceanic currents and the relative uniformity of water temperature, populations are obviously isolated from each other, gene exchange is reduced. Low reproductive rates, the absence of pelagic dispersal stages, low mobility of adults favour this isolation. Bottom morphology and currents can function as barriers, as in the Filchner depression.

Acknowledgements

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