COMPETITION AND ITS BEARING ON THE FRESH-WATER FAUNAS

BY

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The main dominant and competitive groups of fresh-water animals are: Ostariophysi among fishes, crabs among decapoda, Parabathynellidae among Syncarida, Unionacea (except Hyriidae) among mussels, Diaptomidae among Calanoid Copepoda and Streptocephalidae among Anostraca. South-East and East Asia were the main centers of evolution for these groups; North America was a secondary center for crayfishes and mussels, South America a second center for Ostariophysi. Archaic groups, eliminated by competitive ones, survive mainly in southern continents, especially Africa for fishes, Australia for Invertebrates. Some archaic and non-competitive groups lived once also in northern continents, while others seem to have dispersed through direct contact between southern continents.

In analysing the zoogeography of fresh-water fishes and terrestrial vertebrates, Darlington [3] concluded that one main feature of their distribution pattern is the presence of a few dominant and competitive families or higher taxa, all or most of which center in the Tropics of the Old World, showing the tendency to spread over the whole Megagea (e. g. Eurasia, Africa and North America) and to eliminate progressively the older groups, which survive mainly in peripheral areas. He explains in the same manner [5] the distribution of some old groups of Invertebrates, occurring in Australia, New Zealand and the southern top of South America.

One can distinguish not only among fishes, but among several higher taxa of fresh-water Invertebrates, dominant and competitive groups on one hand, archaic and non-competitive on the other, and their distribution reflects the effects of competition and of partial elimination of the last-named by the first ones.

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Fresh-Waters Fishes. As generally accepted by Darlington and other students, the Ostariophysi (excluding the Gonorynchiformes, recently included by Rosen & Greenwood [15] as a distinct series, Anotophysi, within Ostariophysi) are the dominant and most competitive group of fresh-water fishes. Their distribution indicates two main centers of differentiation and radiation : South-East and East Asia for Cyprinoidei and a few families of Siluriformes, tropical South America for Characoidei and other Siluriformes. A few families (Anabantidae, Mastacembelidae a.o.), original from South-East Asia, accompanied the Cyprinoidei in their dispersal, while all other orders and families of primary fresh-water fishes proved less competitive than Ostariophysi and were "vanquished" by them. The most important among the "vanquished" groups are the Osteoglossomorpha, which were once the dominant group and had a world-wide range ; the Jurassic East-Asian and Siberian *Lycoptera* belonged to them [6]. At present the Osteoglossomorpha are richely represented only in Africa, but a few survive also in South America, South Asia, Australia, even in North America. Among the other non-competitive fresh-water fishes are : the Percopsiformes, Amiidae and Lepisosteidae in North America (formerly also in Europe), four African families and the Holarctic Esociformes and Percidae.

One general conclusion of this distribution pattern is that primitive non-Ostariophysi were almost completely eliminated in the two dispersal-centers of Ostariophysi, and survived mainly in Africa, then in North America, a few also in Europe (Fig. 1).

Secondary fresh-water fishes are less competitive than primary ones, being abundant only in Central America, where primary fresh-water fishes are recent intruders [11] and in some special habitats, such as inland water bodies with special chemical features from arid areas and even great lakes (the African Cichlidae !).

Even less competitive are peripheral fishes, quite scarcely represented in continental areas, but abundant in islands where there are no, or only quite few primary, secondary and vicarious fresh water fishes (Madagascar, Lesser Sunda islands, New Zealand) as well as in parts of continents under very cold conditions, where the former primary fresh-water fauna was decimated (northern Siberia and Canada, probably cold South America too).

Higher Crustaceans. The only primary fresh-water Decapoda are the Crayfishes : Astacidae (Holarctic) and Parastacidae (southern continents, except Africa). Unlike primary fresh-water fishes, crayfishes proved less competitive than secondary fresh-water crabs (former Potamonidae ; according to the recent studies by Bott [1] [2] a.o. several families, each of them having distinct marine ancestors) and peripheral fresh-water prawns. The Parastacidae were totally eliminated from Africa (where they probably lived once) and tropical South America. Because of the competition of crabs, the Astacidae were not able to colonize tropical Asia (or were eliminated here, if once present). Among the Astacidae, the primitive subfamilies, Cambaroidinae and Astacinae have a disjunct range (North East Asia, Europe, western North America), having been eliminated in eastern Nort
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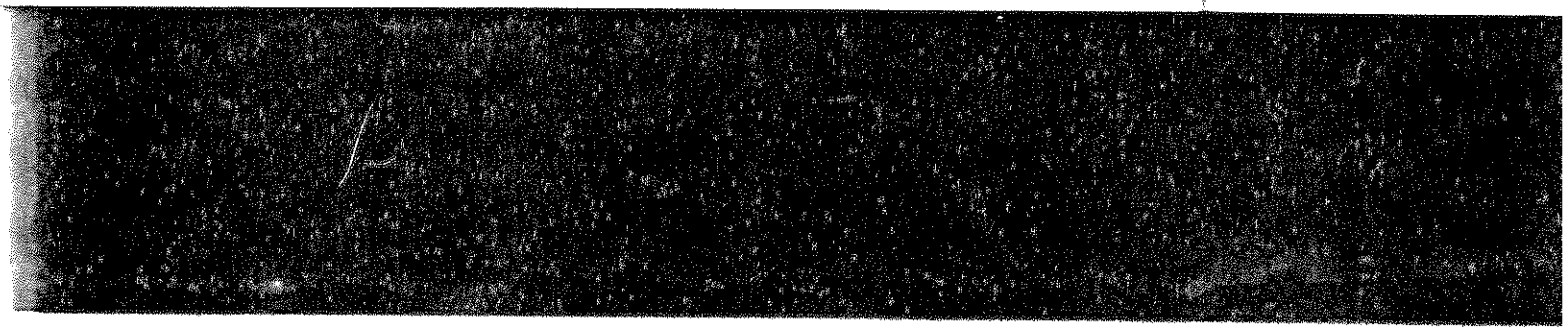

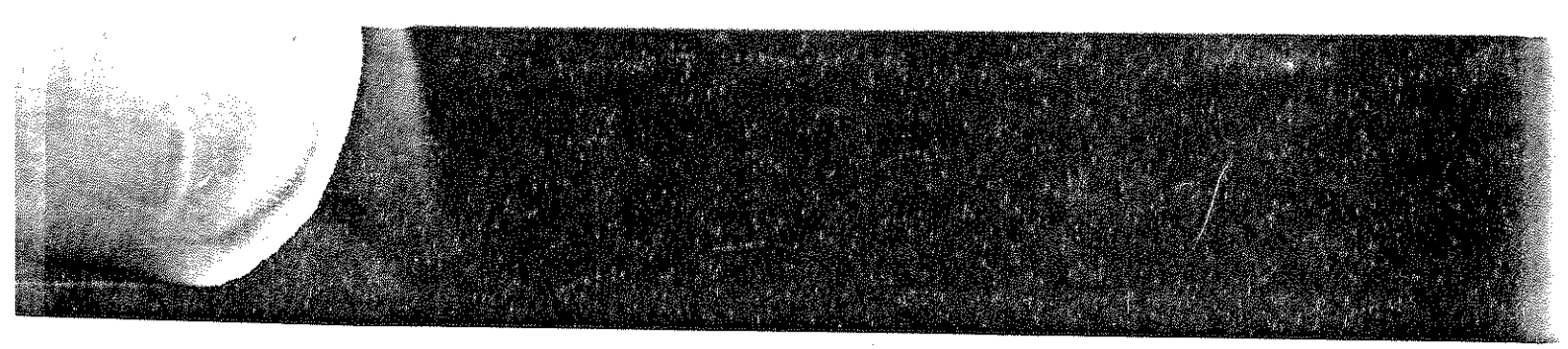

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The distribution pattern of fresh-water Isopoda and Amphipoda doesn't reveal the effects of competition between families or genera. Both groups live mainly in temperate and even cold areas; their absence or scarcity in tropical areas may be due to the competition by prawns.

One peculiar group of fresh water Isopoda, the Phreatoicoidea lives in Australia, New Zealand, India and the southern top of Africa. This distribution too seems to reflect elimination, at least from tropical Africa. Like Parastacidae, the Phreatoicoidea occur in northern Australia, where the competition by modern groups is much feebler than in other tropical areas.

The effects of competition are very evident in the distribution of the mainly hypogeous Syncarida [12], [13]. The most primitive order, Anaspidacea, is exclusively Australian, the second, Stygocaridacea, lives in southern South America and in New Zealand, while within the last order, Bathynellacea, the family Bathynellidae has a disjunct, bipolar range, occurring in the temperate zone of both hemispheres; it has been eliminated in the tropical zone by the more competitive Parabathynellidae [12].

Entomostraca. The effect of competition is evident also in the geographical distribution of the two exclusively fresh-water families of Calanoid Copepoda: Boeckellidae and Diaptomidae. The first family ranges in Australia (without reaching its northern corner), in New Zealand and southern South America and adjacent sub-antarctic islands; one species is isolated in Mongolia. The Diaptomidae are more differenciated in East and South-East Asia; they occur throughout Megagea and in tropical and warm-temperate South America; two species (none of them endemic) reach northern Australia. Some genera are Holarctic, but only one of them, *Arctodiaptomus* has a wider range in America, reaching its warm-temperate parts; the other Holarctic genera are mainly Palaearctic, a few of their cold-adapted species living also in Alaska and northern Canada.

It is quite reasonable to conclude that Boeckelidae had once a much wider range, being eliminated later by the Diaptomidae from the whole Megagea and from tropical South America; the single Mongolian species is a relict in a part of the former range (Fig. 3).

Among the Anostraca, one family, Streptocephalidae, seems to be in an expansive stage, radiating from tropical Africa. The range of Branchinectidae (Holarctis and cold-temperate South America) may suggest a former wide range and subsequent elimination from the tropics; yet this cold-adapted family could also have reached temperate South America by slow dispersal along the Andean high plateaux.

Fresh-water Mussels. The main distribution pattern of fresh-water mussels is the occurrence of Unionacea (except Hyriidae) in the Megagea, with maximum of differenciation in East- and South-East Asia (not in India !) on one hand, in North America on the other, the occurrence of Hyriidae, a family of Unionacea, in South America, Australia (with New

Guinea) and New Zealand and of Mutelacea in South America, Africa and India. The Megageic Unionacea are evidently a competitive group. There is no evidence of a former occurrence of Mutelacea outside their present recent; yet one can assume that Unionacea entered relatively recently in India and Africa and already began to eliminate the Mutelidae from these countries. The South American Hyriidae are apparently offshoots of North American immigrants which arrived here at the end of Cretaceous-beginning of Palaeocene [14]; the genera to which they belong became extinct from North America, where they may have been eliminated by more modern Unionacea (Fig. 4).

The distribution pattern of fresh-water Prosobranchiates does not indicate clear effects of interfamiliar competition.

Plecoptera. Like other aquatic insects (and also like fresh-water mites), the stony flies have terrestrial origin and the adults have the possibility to cross water-sheds; I consider them therefore less significant for fresh-water zoogeography than primary aquatic animals. Their general geographical distribution was presented by Illies in several papers [7—9]. The most primitive families have an "amphinotic" range, occurring in Australia, New Zealand and cold South America, while the modern families are Megageic, with maximum of differenciation in East- and South-East Asia and to a less degree in North America; quite few stony-flies live in Africa. Illies explained this distribution accepting a Gondwanian origin, respectively a Trans-Antarctic dispersal of the primitive families. But this distribution reflects also the effects of competition: in South America the primitive families were eliminated from the tropics by the modern families (or these ones prevented the northwards dispersal of the former), while the absence of modern families in Australia allowed the survival of the primitive ones.

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Darlington [3], [4] concluded that all or most of the dominant families within the five classes of continental Vertebrates dispersed from "the Old World tropics". The distribution pattern of the few fresh-water groups discussed above proves that not all the Old World tropical zone was the dispersal center of the competitive groups, but only South East Asia (including partially also warm-temperate East Asia but excluding India). This is quite evident in the case of Cyprinoidei (which reached Africa only during the Pliocene), of Unionacea, of Diaptomidae and of modern Plecoptera; the only dominant group which apparently dispersed from Africa was the Anostracan family Streptocephalidae, while the dispersal center of secondary fresh-water crabs and prawns seems to have been the whole tropical zone, the Old and the New World families of fresh-water crabs having evolved independently from distinct marine ancestors [1], [2] and the same is true for prawns.

Far from having been a dispersal center for dominant fresh-water groups, Africa was colonized rather recently by these groups (e.g. Cyprinoidei and Unionacea) and has retained many archaic groups, especially among fishes (in no other continent do the Osteoglossomorpha and other archaic groups survive in such a great number as in Africa); also the Mutellacea live in Africa and in its southern top a few Phreatoicoidea; only the Parastacidae became extinct.

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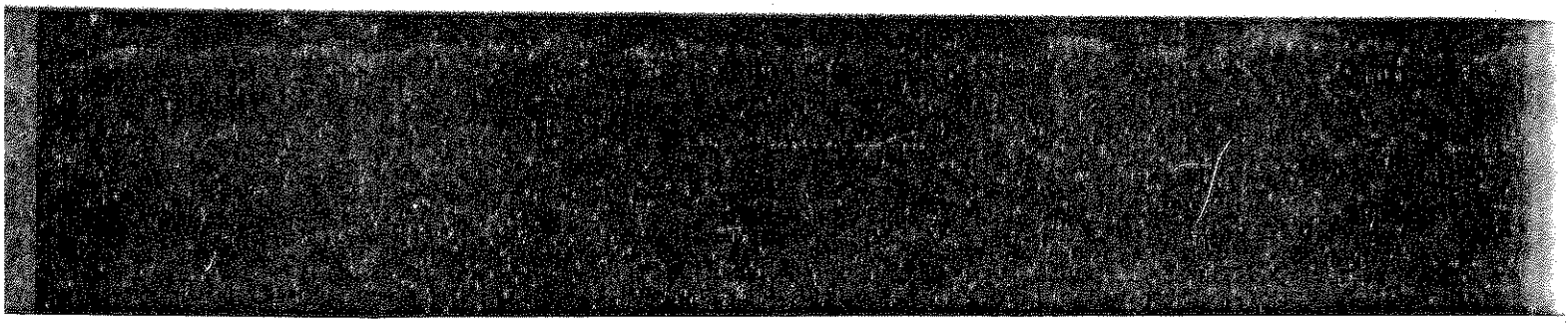

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The dominant groups which evolved in and radiated from South-East Asia dispersed over the whole Megagea, a few ones (e.g. the Diaptomid Copepoda) over most of the World, including northern Australia. For some dominant groups of fresh-water Invertebrates of probable South-East-or East-Asian origin, temperate eastern North America represents a center of secondary evolution and radiation: e.g. for Unionacea and for Cambarine crayfishes.

The Ostariophysi, which are the dominant group of fresh-water fishes, had a second center of radiation, quite independent from the South Asian: tropical South America (for Characoidei and 13 families of Siluriformes). But while the Cyprinoidei dipersed from South-East Asia throughout the whole Megagea (except Madagascar), the Characoidei reached only Africa and Central America. Already the wider range reached by the fish taxa original from South East Asia suggests that these are more successful than those of South American origin. This is confirmed by the fact that in Africa the Characoidei remained less speciose than the Cyprinoidei, in spite of their much older age. A quite different situation occurred in Central America, which was colonized rather recently by primary fresh-water fishes, both from South and from North America [11]; there are, in Central America, only 3 fish species of North American origin, as against 101 of South American descent [10]. The South American fish fauna proved, in Central America, to be much more competitive than the North American, which is a branch of the Megageic fauna, having thus a remote South Asian origin. This may be explained by the geographical position of Central America which lies very close to the radiation center of the South American fish fauna and quite far from South Asia. The North American fish fauna is only a pale reflexion of the very competitive South Asian one; although dominated by Ostariophysi (Cyprinoidei and Ictaluridae) of remote Asian origin, North America is, after Africa, the continent which retained the greater number of archaic fish families (Hyodontidae, Percopsiformes, Amiidae, Lepisosteidae). The aquatic Invertebrates of Central America have, on the contrary, North American affinities: all genera of fresh-water mussels, the crayfishes, apparently also all or most snails. This is a consequence of the above mentioned fact that North America is a center of secondary radiation for crayfishes and fresh-water mussels, but not for fresh-water fishes. The fresh-water crabs of Central America belong to two families occurring also in South America, one of which, Trichodactyllidae, seems to be of Central American origin and to have colonized South America later on [2], like Poeciliidae and perhaps other secondary fresh-water fishes.

Most dominant and competitive groups of fresh-water animals have thus a Megageic or Holarctic distribution, with maximum of differentiation in South-East or East Asia. The non-competitive, "vanquished" groups range on the contrary mainly in southern continents; the present range of many of them is "Gondwanian" or "Notogeic" (= Transantarctic). The greatest number of archaic fresh-water fish families live (or survive) in Africa, only two of them in Australia, one also in tropical South America, none in Madagascar, New Zealand or cold South America (except eventually the Percichthyidae, if recognized as distinct family and not included within the marine Serranidae). The archaic groups of fresh-water

Invertebrates survive mainly in Australia (even in its tropical corner), New Zealand and cold South America, with maximum of differenciation in Australia (Phreatoicoidea, Parastacidae), quite few of them in Africa and India (Mutelacea, Phreatoicoidea).

In debating the conditions which favour the evolution of dominant animal groups, Darlington [3], [4] concluded that both tropical climate and large areas were favorable to this evolution. A combination of both conditions is present (and was present in Tertiary times) in the Old World tropics. Yet, as shown above, the evolution center for dominant fresh-water groups was only South East Asia (excluding even India) which is not exceedingly large but had (contrary to Africa) favorable tropical climate since the Mesozoic. Also tropical South America (the second evolution center for Ostariophysi) is rather large and had constantly a favorable climate, while eastern North America is the largest warm-temperate area on the northern hemisphere.

Many dominant groups of fresh-water animals actually need warm or at least temperate climate: for ex. Ostariophysi, fresh-water mussels, crayfishes became extinct or diminished under cold climate in areas in which they were once richly represented, such as Siberia, northern Canada, etc; fresh-water crabs became extinct even in Central Europe. Also Parabathynellidae are confined to the tropical and warm-temperate zone, while Streptocephalidae are mainly tropical and their representants in the temperate zone develop, unlike most other Anostraca, during the hot months. The Diaptomidae seem to be the only dominant group of fresh-water animals living in arctic conditions, but its adaptation to these conditions develops quite slowly: Palaearctic species able to live in cold climate colonized North America, their offspring adapted to temperate, then to tropical climate, reaching tropical and partially temperate South America, but has not yet re-adapted to the cold climate of southern South America.

Many archaic, "vanquished" groups survive in temperate or cold conditions: lampreys, Boeckelidae, Parastacidae (partially!), archaic Plecoptera, even Esociformes and Percidae (both groups lived in Europe and North America also under tropical or subtropical conditions, but most of the recent species are cold-adapted).

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The role of competition in the genesis of recent faunas was emphasized by the supporters of the permanence of continents, who believe that all animal groups at present confined to the southern land masses were once distributed also on the northern continents, where they were later eliminated (Dahl's "Verdrängungtheorie"). This view was adopted in recent years mainly by Darlington [3] [4], even when accepting continental drift for a remote period [5]. He thinks that the present range of these taxa does not reflect Mesozoic Palaeogeography, showing that some groups now confined to southern, mainly cold areas, have fossil representatives in northern continents (*Nothofagus*) and he believes the same is true for groups without fossil record.

At least one group of fresh-water animals whose distribution is mainly "Transantarctic" has left a relict colony in North East Asia: the

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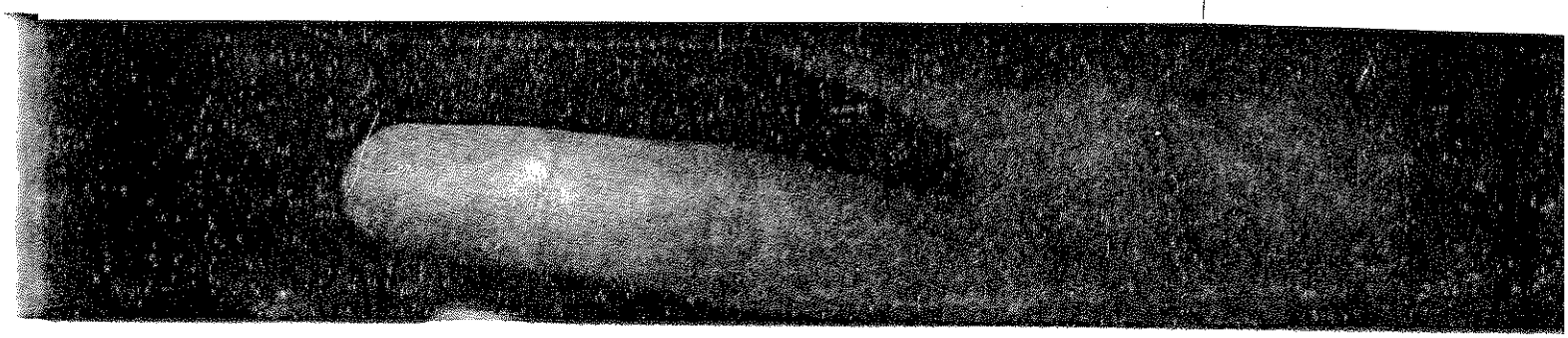

Boeckellidae. Osteoglossomorpha too have a few recent and fossil representatives on the northern hemisphere, in spite of their predominant Gondwanian range. The distribution of both groups can thus be explained by dispersal through the North. But Parastacidae, Mutelacea, the snail family Ampullaridae (South America, Africa, South Asia, with fossil record only within the present range) indicate rather a Gondwanian, or at least an Africano-Brasilian dispersal route. For Phreatoicoidea and for the Amphipod family Hyalellidae (Australia, New Zealand, South America, with infiltrations in North America) one can assume independent colonization from the sea. Transantarctic dispersal can be assumed for archaic Plecoptera, for Stygocaridacea and eventually for Hyriidae. The last named family may have reached South America from the North, as accepted by Parodiz [11], but in Australia it probably arrived from South America, by an Antarctic route (a dispersal from Asia is quite improbable, because of the absence of fresh-water mussels in the Lesser Sunda islands). Myers [11] demonstrated that Characidae are recent intruders in Central America and their occurrence in South America and Africa cannot be explained by an independent colonization from the North : being a competitive group, they could not have become extinct in Central America, if once present there. I have an objection in this problem. The sister-group of Characoidei are the Cyprinoidei, whose dispersal-center was not India, but South East and even East Asia, e.g. areas which originally belonged to the northern land-mass, not to Gondwana. The common ancestors of Characoidei and Cyprinoidei must once have lived also in the northern continents, dispersed over most of the world (except Australia), became extinct on most of range, except South America (or Africa) and South East Asia, where they evolved in Characoidei and Cyprinoidei, getting in the same time the characters which made them competitive. Remote, non competitive ancestors of Characoidei may once have lived also in Central America. But the recent Characoidei from South America and from Africa are too closely related for accepting an independent origin from some remote, not competitive northern ancestors and a direct dispersal, by contact between both continents, is quite probable.

Among the animal groups with mainly or exclusively "Gondwanian" range, some probably dispersed by direct continental contact (e.g. continental drift), others may have been eliminated in the north by more competitive groups. Both cathegories are archaic, noncompetitive groups : it is natural that Mesozoic groups (the only which could use continental drift) cannot compete with modern groups which evolved during Tertiary times in South East Asia. I think the indisputable fact that the modern groups, with South-East or East-Asian origin have the tendency to colonize the whole world, eliminating the older groups, is not incompatible with a Gondwanian, respectively an Africano-Brezilian or Notogeic origin and dispersal of some (not all !) archaic groups. It is even possible that in Mesozoic times Gondwana was the main center of differentiation and dispersal for dominant animal groups.

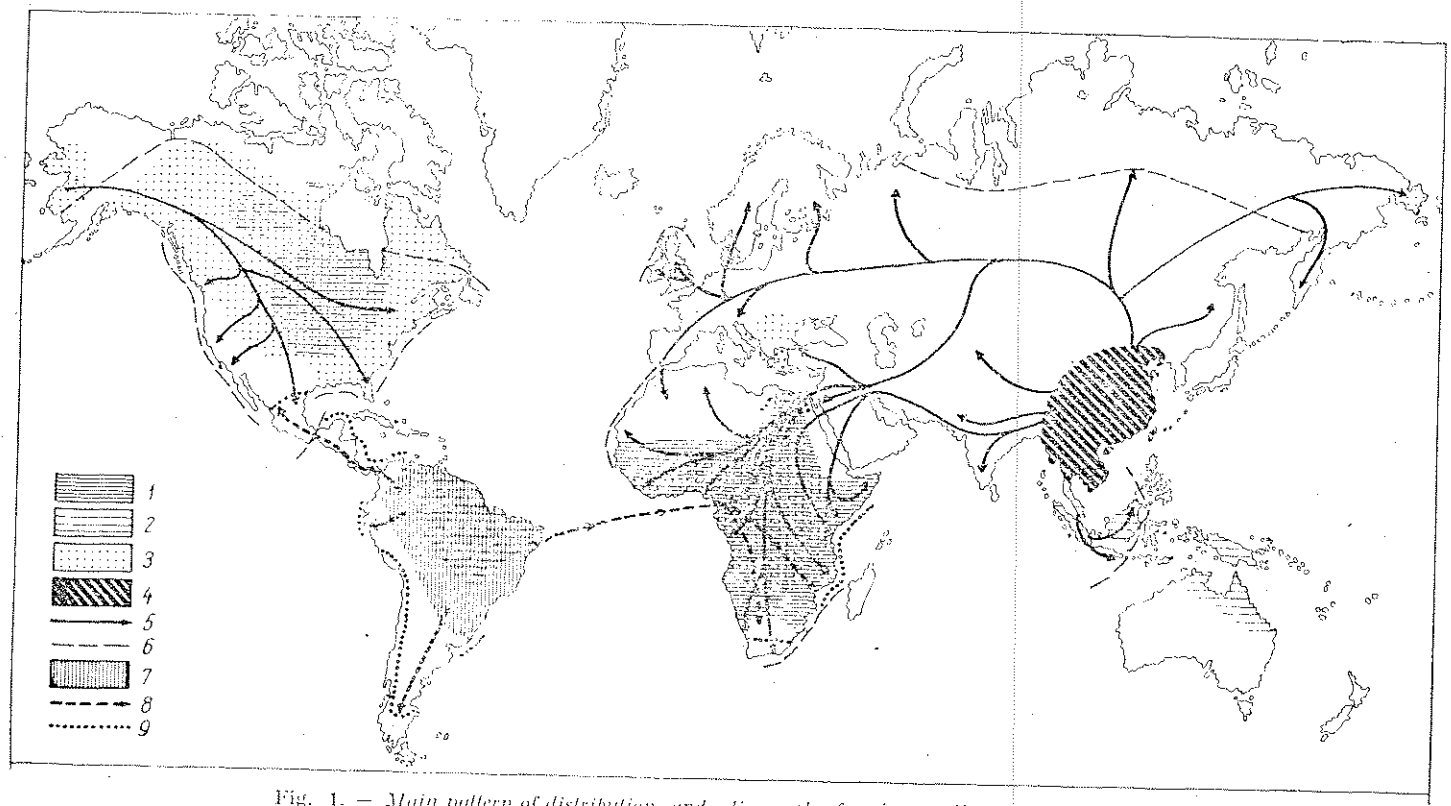

Fig. 1. — *Main pattern of distribution and dispersal of primary Fresh-water Teleosts.* *1*, Osteoglossomorpha, numerous; *2*, Osteoglossomorpha, rare; *3*, Other archaic Teleosts (Denticipitidae, Kneriidae, Phractolaemidae, Umbridæ, Percopsiformes); *4*, Dispersal center of Cyprinoidei; *5*, Dispersal routes of Cyprinoidei; *6*, Limit of Cyprinoidei; *7*, Dispersal center of Characoidei; *8*, Dispersal routes of Characoidei; *9*, Limits of Characoidei.

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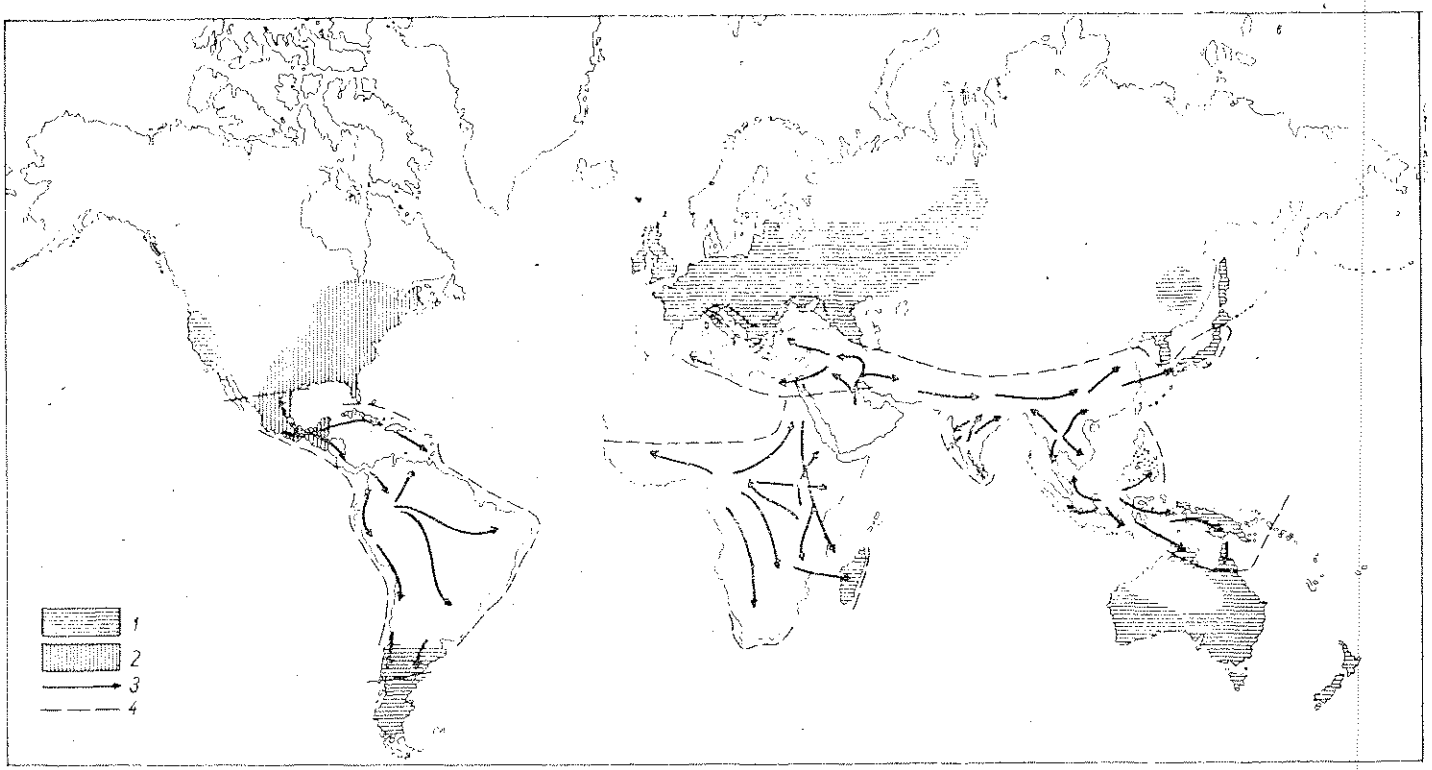


Fig. 2. — *Distribution and dispersal of Crayfishes and of Fresh-water Crabs.*
1, Non competitive Crayfishes (Astacinae, Cambaroidinae, Parastacidae); *2*, Competitive Crayfishes (Cambarinae); *3*, Dispersal routes of the different families of Freshwater Crabs; *4*, Limits of Freshwater Crabs.

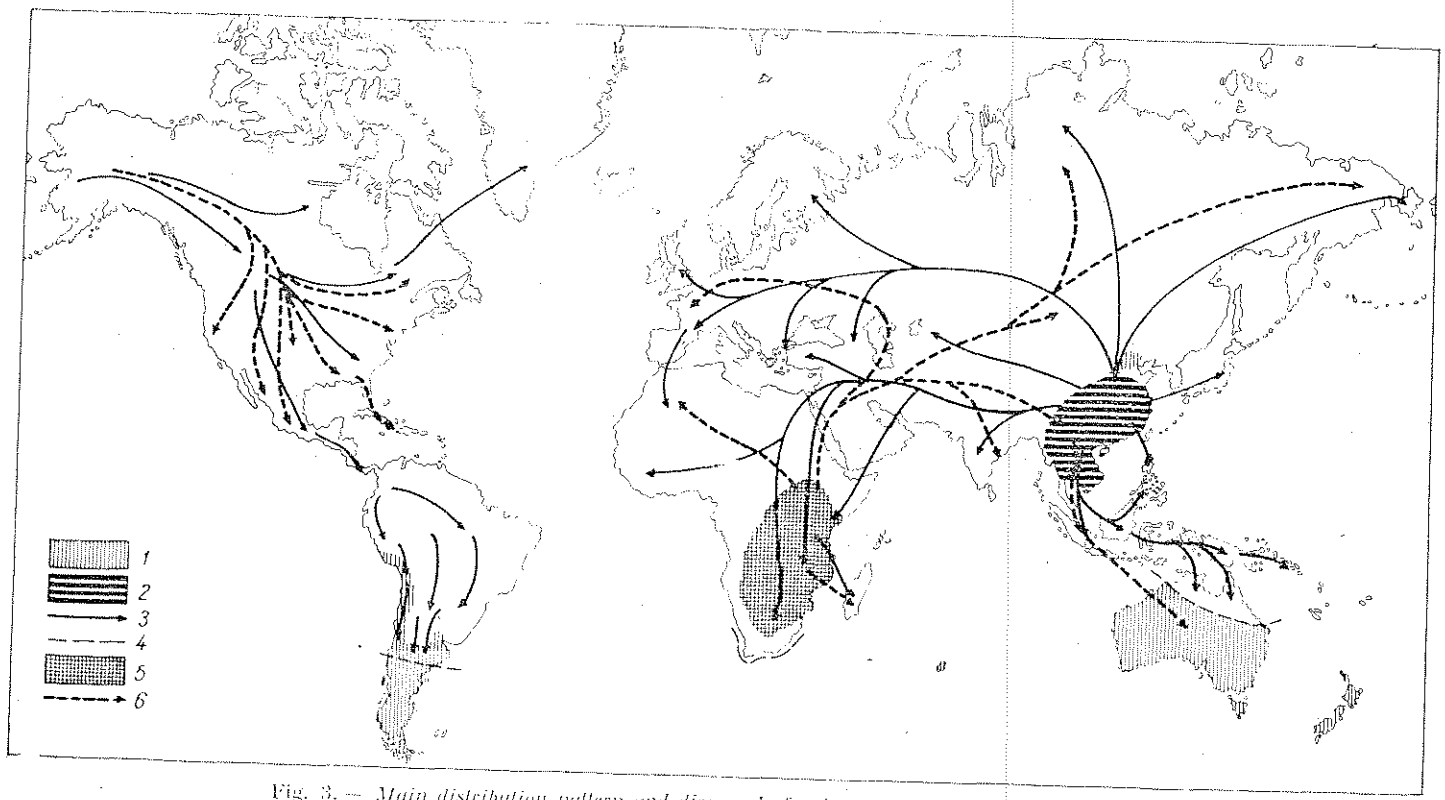
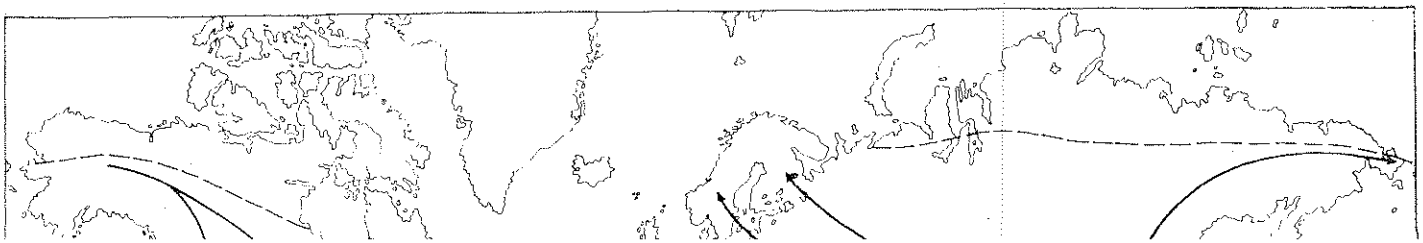


Fig. 3. — *Main distribution pattern and dispersal of primary Fresh-water Calanoida and of Streptocephalidae.*

1, Boeckellidae (non-constitive); *2*, Dispersal center of Diaptomidae; *3*, Dispersal routes of Diaptomidae; *4*, Limits of Diaptominae; *5*, Dispersal center of Streptocephalidae (constitive Anostraca); *6*, Dispersal routes of Streptocephalidae



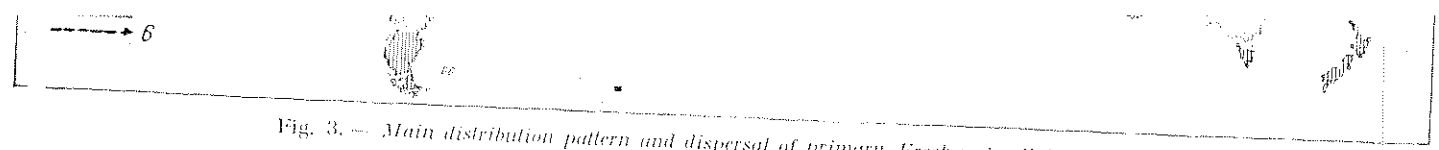


Fig. 3. — *Main distribution pattern and dispersal of primary Fresh-water Calanoida and of Streptocephalidae.*

1, Boeckellidae (non-competitive); *2*, Dispersal center of Diaptomidae; *3*, Dispersal routes of Diaptomidae; *4*, Limits of Diaptomidae; *5*, Dispersal center of Streptocephalidae (competitive Anostraca); *6*, Dispersal routes of Streptocephalidae

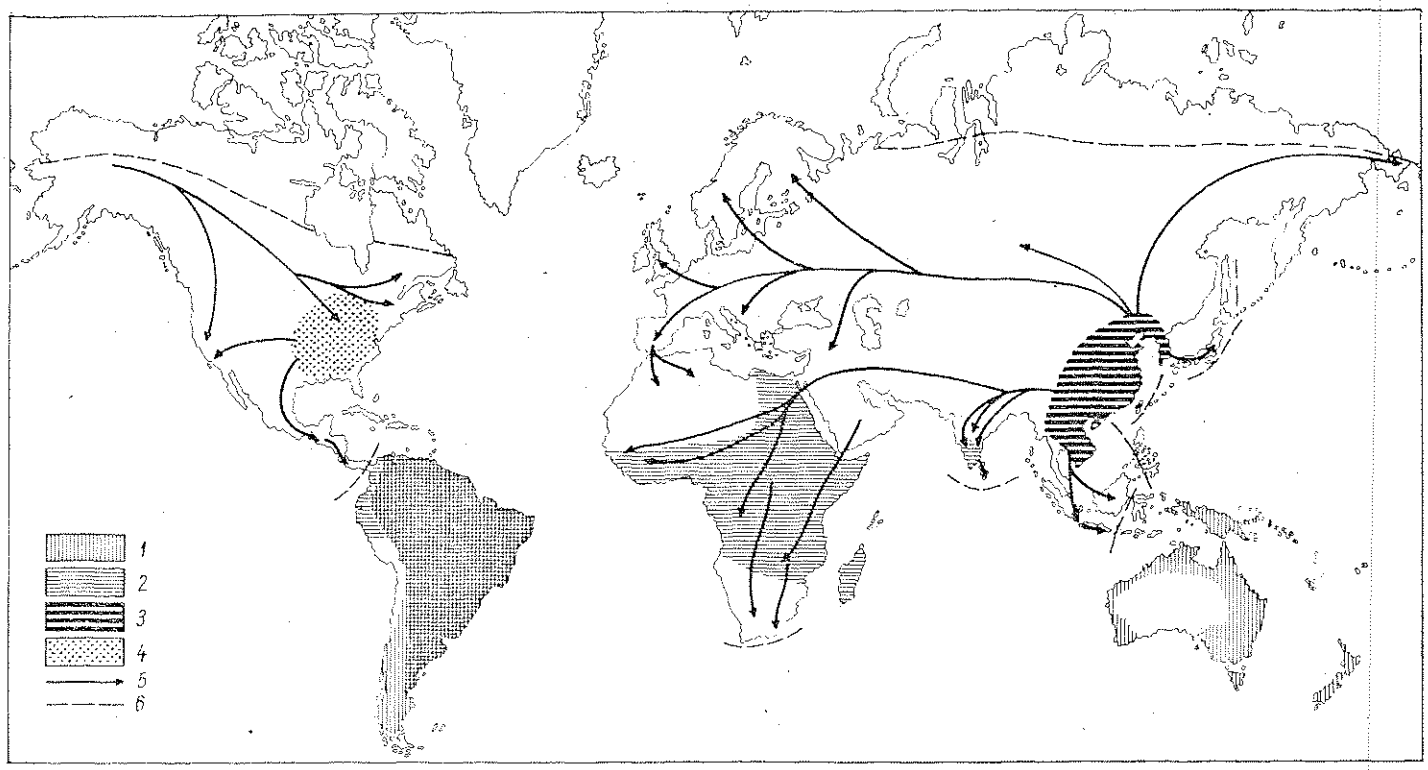


Fig. 4. — *Distribution and dispersal of Fresh-water Mussels*

1, Hyriidae (non-competitive); *2*, Mutelacea (Mutelidae and Aetheriidae, non competitive); *3*, Main dispersal center of competitive Unionacea; *4*, Secondary dispersal center of competitive Unionacea; *5*, Dispersal routes of Unionacea; *6*, Limits of competitive Unionacea.