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The ecological principle of evolutionary reconstruction as illustrated by marine animals

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Abstract

Analysis of the evolution, distribution and ecology of marine prosobranchs of the genera *Neptunea* and *Littorina* and amphipods of the genera *Anisogammarus* and *Gammarus* demonstrates the possibilities of ecological and palaeoecological methods in composing evolutionary reconstructions. A comparative study of historical climate changes and of palaeogeography in areas inhabited by certain taxonomic groups, coupled with information on the distribution and ecology of species belonging to these groups, allows us to determine the time and locality of the origin of diverse biogeographical groups of species and to trace the routes of their further distribution, even in those organisms which have no fossil remains. Species dwelling under conditions which correspond historically to the most ancient climate of their dwelling area prove to be more primitive than species dwelling under newly-formed climatic conditions. For instance, subtropical species of the genera under consideration, in the North-western parts of the Pacific and Atlantic Oceans, have proved to be more ancient and primitive than species inhabiting the upper boreal Pacific and Atlantic waters and the Arctic Ocean. Therefore, the palaeoecological analysis of the historical development of faunas from different regions of the globe, combined with the application of the morphological principle, can significantly contribute to a more detailed and precise understanding of the processes and trends of evolution which compose the phylogenetic schemes of the taxonomic groups under discussion.

Introduction

In order to understand the faunal and floral formations in different regions of the globe, the reconstruction of evolutionary schemes reflecting both the phylogenetic relations among organisms and the time and locality of the origin of diverse taxonomic categories is essential.

However, the majority of scientists assessing phylogenetic reconstructions — especially in regard to groups of organisms without fossils — make use of the morphological method only; this enables species to be categorized according to their degree of structural resemblance and the progressiveness of some of their peculiarities, but it produces no clues as to time and place of the origin of the species.

Although in no way depreciating the above-mentioned morphological principle for studying evolution and phylogeny of organisms, we consider it highly desirable to apply, in addition, ecological and palaeoecological information. The data available at present are based on the comparison of the distribution and ecology of modern species with fossil remains of similar taxonomic categories and the general characteristics of deposits of corresponding geological periods of the past. They provide, with a reasonable degree of certainty, a picture of climatic changes of the globe during the known geological epochs (Krishtophovich, 1932; Berg, 1947; Bruks, 1952; Ruchin, 1955; Schwarzbach, 1955; Gekker, 1957; Markov, 1960; Sinitzin, 1965, 1966; etc.). Palaeogeographical information from corresponding regions is essential in order to appreciate the patterns and rules governing the distribution of organisms in the said regions.

Sometimes it is possible to reconstruct the palaeogeographical picture of the past by analysis of the geographical distribution of modern species. The application of the biogeographical principle of the geological history of the Quaternary period (Lindberg, 1955, 1965) may be cited as an example of coordinated analysis of biogeographical and palaeogeographical data.

Material and method

The application of the palaeoecological method is based on the closest dependence of development of modern flora and fauna upon the history of climatic changes in various parts of the globe. The said dependence is determined by a decisive influence of physico-chemical factors upon the process of speciation and the subsequent distribution of the species.

Therefore, by comparing ecological data (especially on thermopathy) and data on the distribution of modern species with information concerning the history of climatic changes and palaeogeography in the dwelling regions of the species considered, we can evaluate the ecological situation and, hence, the locality and time of origin of those species, and we can trace the probable ranges of their distributions in the past and the trends of their evolution.

It seems obvious that species dwelling under the historically most ancient climatic conditions must be more primitive within their genus, and retain plesiomorphous (terminology of Hennig, 1950) peculiarities, while species whose distribution is based on newly-formed climatic conditions are phylogenetically younger, and exhibit apomorphous peculiarities. This assumption is confirmed by comparative-morphological and palaeontological data, and may be considered in the analysis of taxonomic categories of a higher rank.

Particularly striking and convincing evidence, which illustrates the application of the ecological principle, is received when the history of climatic changes in cold and temperate zones of the Northern hemisphere during the Tertiary and Quaternary periods is compared with the evolution of species dwelling in the same zones.

Geological and palaeoecological data provide evidence of a constant climatic cooling in the Northern Hemisphere, which has occurred over a relatively brief period of geological time.

The origin, formation and development of the fauna and flora, specific for temperate and cold climatic conditions, occurred under the impact of the said cooling, which was intermitted by short pulsations of temporary warming in several zones.

Simultaneously, the fauna of temperate latitudes may have been fundamentally formed during the course of the Tertiary period under the conditions of the gradual establishment of a temperate climate, while the fauna of the Arctic area, dwelling under lower temperature conditions, and even at temperatures below zero, may have developed in the Quarternary period at the time of glaciation in high latitudes of the Northern Hemisphere.

A review of the system of gastropods of the genus *Neptunea* Bolten (Golikov, 1963, 1964) and amphipods of the genera *Gammarus* s.l. (sea- and brackish-water species) and *Anisogammarus* Derzhavin (Tzvetkova, 1969; and in press)[1], has been completed by the present authors. A thorough analysis of the morphology, ecology and distribution of the species composing these genera, which inhabit mainly the boreal and Arctic seas, enables the comparison of the application of morphological and palaeontological principles on the one hand and the application of ecological and palaeoecological principles on the other hand, with a view to revising the conception of the evolutionary development of both of these genera.

Neptunea species are particularly abundant in the fossil deposits of the Tertiary and Quarternary periods; this affords an opportunity of testing the correctness of the application of the palaeoecological method both by comparative-morphological and by palaeontological evidence.

In the analysis of the evolution of species belonging to the genera *Gammarus* and *Anisogammarus*, because of paucity of fossil remains, the comparative-morphological principle of comparing plesiomorphous and apomorphous peculiarities of different species has been chiefly used as control. Additional criteria for assessing time and locality of the origin of a species and of the corresponding climate were provided by minimal intraspecific variability, corresponding to the ecological environment of the origin and primary adaptation (Golikov, 1963).

In *Neptunea* species, we considered the development of the axial sculpture; it depends upon temporary decreases in growth rate during periods of increased environmental variability. The axial sculpture of species inhabiting comparatively warm waters and that of intraspecific forms is weakly developed, while that of cold-water species (with contracted spawning period) is highly developed.

While establishing phyletic correlations between species, we made considerable use of morphological peculiarities of the various species, with due consideration to the fact that the morphological principle, coupled with the ecological principle, enables the construction of the most correct temporal and spatial evolutionary schemes.

Results

The climate of the area of present temperate and cold latitudes of the Northern Hemisphere in the early Paleogene period was relatively stable — similar to that of the modern subtropics.

Apparently, under the impact of the first stages of climatic cooling in the late Eocene, the genera *Neptunea* and *Anisogammarus* evolved in comparatively cool subtropic waters from ancestral forms in the area of present Northern Japan. The genus *Gammarus* evolved in the basin of the Atlantic Ocean — the Tethys Sea. Evidence of this process is provided (1) by the distribution of modern, most primitive species, which are similar to the initial forms; these live under conditions similar to their ancestors. (2) The discovery of the first fossil residues of the genus *Neptunea* in the Upper Eocene and the Oligocene deposits of the Japan Islands *(N. altispirata, N. sitakaraensis)*, and of the genus *Gammarus* in the lower Oligocene deposits of the Paris basin *(G. alsaticus)*.

The hypothesis that the locality and time of origin of the genus *Anisogammarus* resembles those of *Neptunea* is supported by comparative-morphological and palaeoecological analyses of the former's evolution and distribution, which have been influenced by similarly changing conditions and which proceeded in a way similar to those of the *Neptunea*.

The relatively constant temperature conditions which prevailed in the Northern part of the Pacific and Atlantic Oceans during the Paleogene period, must have allowed the primitive species of the genera under

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[1] The genus *Anisogammarus* consists of 3 subgenera: *A. (Anisogammarus)* Derzhavin, *A. (Eogammarus)* Birstein, and *A. (Spinulogammarus)* Tzvetkova, subgenus nov.; the latter includes 7 species with spines both on the urosome and the metasome: *A. jesoensis*, *A. spasskii*, *A. ochotensis*, *A. oregonensis*, *A. subcarinatus*, *A. atchensis* and, probably, *A. annandalei*; the type-species of the subgenus is *Gammarus ochotensis* Brandt, 1851.

study to disperse widely towards the North. At the same time, or at the very beginning of the Neogene period, species of the said genera, dwelling in relatively warm waters, may have penetrated to the Pacific *(Neptunea* and *Anisogammarus)* and Atlantic *(Gammarus)* coasts of North America.

The probability of interchange of faunistic elements which dwelt on the coasts of Japan with those of the Pacific Ocean on the coasts of North America in the Paleogene and early Neogene periods, is affirmed by many authors (Smith, 1904, 1919; Grant and Gale, 1931; Kristophovitch, 1932; etc.).

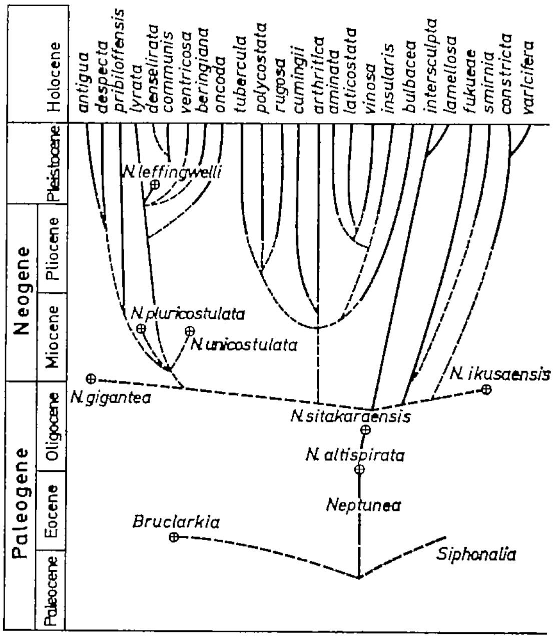

Fig. 1. Evolution of species of the genus *Neptunea* Bolten. ⊕ fossil species; - - - - - phyletic relations between species; ——— duration of existence of species

The first modern species evolved in subtropical waters in the early Miocene; at present they dwell under analogous conditions *[Neptunea intersculpta, N. fukueae, Anisogammarus (Eogammarus) turgimanus, A. (Spinulogammarus) annandalei, Gammarus (Pephredo?) locusta]*. These species are closely related to the fossil ancestral forms of the corresponding genera, and may have evolved directly from them (Figs. 1, 2, and 3).

The Pacific species originated in waters washing the Miocene coastline in the region of the present Northern Japanese Islands (Fig. 4). The discovery of the first fossils of *Neptunea intersculpta* in this region — as well as the palaeoecological climate in this area during the early Miocene, which corresponds to the present climatic conditions with minimum intraspecific variability of species which are subtropical by origin — provides evidence for the validity of this hypothesis.

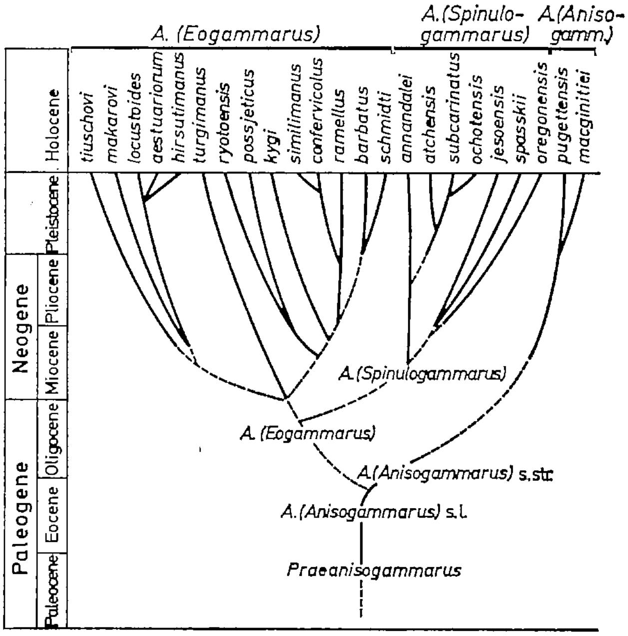

Fig. 2. Evolution of species of the genus *Anisogammarus* Derzhavin. Symbols as in legend to Fig. 1

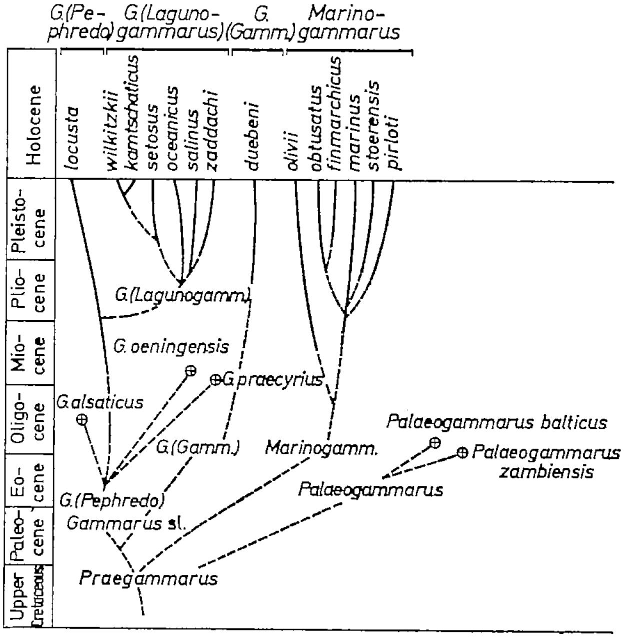

Fig. 3. Evolution of species of the genus *Gammarus* Fabricius s.l. Symbols as in legend to Fig. 1

The Lusitanian-Mediterranean species *Gammarus (Pephredo?) locusta* may have originated in the remnants of the Tethys Sea. Approximately at the same time, and under similar conditions, the most primitive representatives of the genus *Marinogammarus*, at present inhabiting the Northern Atlantic Ocean *(M. marinus, M. olivii)*, may have evolved.

A typical example of the application of the ecological principle in evolutionary reconstruction is the palaeoecological analysis of origin and distribution of widely spread boreal Pacific species. These species may have evolved in the middle Miocene in the somewhat cool waters of the coasts of Beringia, from ancestral forms which had widely spread. The borders between climatic zones were only slight at that period; this fact made it possible for the species which originated in that area *[Neptunea lyrata, Anisogammarus (Anisogammarus) pugettensis, A. (Eogammarus) locustoides, A. (Eogammarus) makarovi]* to spread far to the South along the coasts of the Asian and American continents.

The increased cooling which ensued, and the establishment of sharp border-lines between the temperature regime of the high-boreal and the low-boreal Pacific waters, forced these species in the southern part of the area to migrate to greater water depths *(Neptunea lyrata)* or to shift their breeding period to a cooler time of year. Such space-time relationships of widely spread boreal Pacific species is based on the analysis of palaeoecological data, and confirmed (1) by the discovery of the first fossil residues of *N. lyrata* in the middle Miocene deposits of Kamchatka, Southern Alaska and Oregon, and (2) by the remarkably primitive structure of modern boreal species dwelling both along the Asian and American coasts studied by the present authors.

If we assume that these species have been formed in the southern part of that area, in waters with sufficiently high summer temperature, the possibility of their spreading into the Bering Sea becomes highly improbable as, in this region, even the summer temperatures do not rise over 6° to 8 °C; such temperature conditions must have prevented the breeding of organisms of subtropical and low boreal origin, as their breeding temperature is firmly fixed (Orton, 1920; Runnström, 1927, 1929; Hutchins, 1947; Kinne, 1963, 1970; and others); their breeding temperatures were probably fixed during the process of species formation. It seems rather unreasonable to assume that the widely-distributed boreal species of the Pacific Ocean may have evolved in a more recent geological period, as even in the late Miocene there existed already firmly fixed faunistic provinces, resulting from the establishment of sharp border-lines between climatic zones, which would have prevented further distribution of the species which evolved under the given hydrological conditions of a certain province or climatic zone. Later, widely boreal species of the Asian coasts *[Anisogammarus (Eogammarus) tiushovi, A. (Eogammarus) kygi, A. (Spinulogammarus) spasskii]* evolved directly from species widely distributed on the coasts of both continents, or from allied ancestral forms on the coasts of Kamchatka. The fact that these coastal species do not

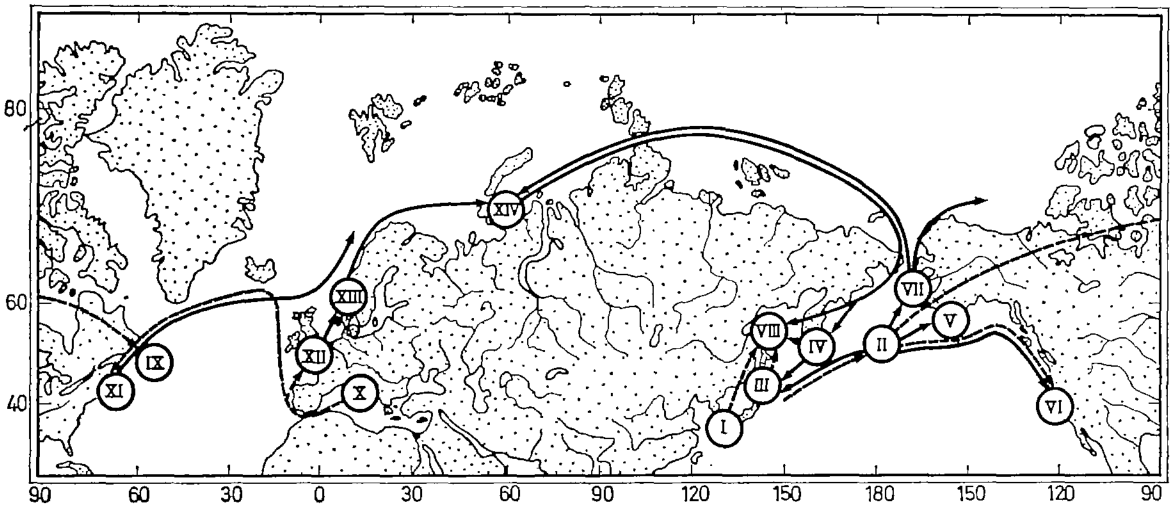

Fig. 4. Centres of origin (circles) and distributional paths (arrows) of different biogeographical groups. Species of genera *Neptunea, Anisogammarus, Gammarus* and *Littorina*. *I:* Pacific Asiatic subtropical; *II:* Pacific widely distributed boreal; *III:* Pacific Asiatic low boreal; *IV:* Pacific Asiatic widely distributed and high boreal; *V:* Pacific American widely boreal; *VI:* Pacific American low boreal; *VII:* boreo-arctic; *VIII:* Okhotsk high boreal; *IX:* Atlantic high boreal; *X:* Mediterranean-Lusitanic subtropical; *XI:* Atlantic American low boreal; *XII:* Celtic low boreal; *XIII:* European widely boreal; *XIV:* Arctic. ———: contemporary paths; — — —: ancient paths

dwell off the American coast may be a result of the distribution barrier constituted by the great depths which had already been formed by this time in the southern part of the Bering Sea.

Under the influence of subsequent, long-term, thermal pulsations in the late Miocene, which resulted in the formation of fixed borders between climatic zones in the waters washing the Asian continent in the region of Kamchatka and Northern Sakhalin, the most erythermal high boreal species *[Neptunea pribiloffensis, Anisogammarus (Eogammarus) tiushovi, A. (Eogammarus) kygi]* evolved from widely distributed boreal forms or from common ancestors. This hypothesis is supported by the conformity of the palaeoecological conditions in the late Miocene in this region, with the breeding temperature and the conditions of minimum variability of the species concerned reflecting the conditions of their primary adaptation; additional evidence in favour of this hypothesis is provided by the fact that fossil residues of *N. pribiloffensis* have been found in the upper Miocene deposits of Northern Sakhalin and Kamchatka. The morphological analysis of the phyletic correlations of these species leads to the same conclusions.

It is highly probable that, in the late Miocene, a brief lowering of the Bering platform may have occurred, which offered the first opportunity for the sublittoral species *Neptunea lyrata* and *N. pribiloffensis* to penetrate into the Northern Atlantic Ocean. An analysis of the history of the formation of the genera of the bivalve molluscs *Mya, Macoma* and some other organisms, leads us to assume that the Bering Strait was formed during the late Miocene period, and that the most eurybiont elements of the boreal Pacific fauna may have migrated to the Northern Atlantic Ocean during the same period (MacNeil, 1965; Coan, 1969; and others). However, migration of boreal Pacific species in the late Miocene to the coasts of Central Europe and their giving rise to boreal Atlantic species seems highly improbable, as subtropical climatic conditions predominated, to judge from the Lusitanian-Mediterranean characteristics of the fossil fauna of these regions. Apparently, the process of speciation and the spreading of boreal species in the Atlantic Ocean must have occurred later or in the second part of the Pliocene period, but the genetic material for the formation of these species may have been supplied by populations of later Miocene emigrants from the Pacific Ocean, which spent the warm period in higher latitudes. The genus *Anisogammarus* may not have migrated to the North Atlantic Ocean; these forms are fully adapted to the littoral zone.

The first lower-boreal species *[Neptunea arthritica, N. bulbacea, Anisogammarus (Spinulogammarus) jesoensis* and *A. (Eogammarus) possjeticus]* formed in the late Miocene or at the very beginning of the Pliocene, during the next pulsation of climatic warming in the area of present Northern Japan; at this time, sharply defined borders already existed between the low-boreal and high-boreal waters. These shallow-water species, dwelling in well-warmed sea areas, prefer temperature conditions which correspond approximately to those existing in the whole aquatoria of the lower-boreal waters at that period.

Somewhat later, *Neptunea cumingii*, subtropical in origin, may have evolved in more southern areas; it has spread exclusively throughout geologically younger Northern Chinese seas and in the Japanese Sea. In the middle of the Pliocene, approximately in the area of present Sakhalin (judging by palaeoecological information and the thermopathy of modern species), another group of the low-boreal species, distributed in the cooler waters, may have evolved: *Neptunea constricta, N. polycostata, N. tuberculata.* Approximately at the same time, species of high-boreal origin *[Anisogammarus (Spinulogammarus) spasskii, A. (Eogammarus) barbatus]*, dwelling in comparatively warm waters, formed on the coasts of Kamchatka. They spread southwards along the Asian coast up to the Southern Kuril Islands and Southern Sakhalin; on the coasts of America, the Oregon species *Anisogammarus (Eogammarus) ramellus, A. (Eogammarus) confervicolus* and *A. (Spinulogammarus) oregonensis* evolved.

Both the first and the second group of species must have originated from widely distributed Pacific species or from descendant forms inhabiting the greater part of the present temperate Pacific waters up to the middle Miocene period; they evolved after sharp borders became established between climate zones and faunistic provinces.

Later, but apparently before the period when permanent connections between the Pacific Ocean and the Polar Basin were established (but directly after a marked cooling had occurred), the high-boreal species *(Neptunea vinosa, N. laticostata, N. insularis, N. oncoda, Anisogammarus (Eogammarus) schmidti* and *A. (Spinulogammarus) subcarinatus* on the coasts of Kamchatka, and *Neptunea aminata, N. smirnia, Anisogammarus (Anisogammarus) macginitiei* and *A. (Spinulogammarus) atchensis* on the coasts of the Aleutian Islands and of Alaska) may have evolved, judging by their present-day distribution.

The phyletic relationships of these species are revealed in their evolution. They have been evaluated by means of palaeoecological analysis of the succession of origin and distribution and on the basis of comparative-morphological information. For instance, *Neptunea smirnia* may have evolved from its morphologial relative *N. fukueae*, which migrated with the waters of the Kjuro-Shive to the coasts of America in the first part of the Miocene. The cooling in the northern part of the Pacific Ocean, which occurred in the late Miocene and the Pliocene, resulted in the formation of *N. smirnia*, and in the extinction of descendant forms of *N. fukueae* in the intervening areas.

The submergence of the Bering-Chukotsk platform joined together with water masses of the Pacific Ocean and the Polar Basin. Further cooling of the northern part of the Bering Sea facilitated the formation of the boreal-arctic species *Neptunea beringiana*, *N. ventricosa* and *N. communis*. These species evolved from *Neptunea lyrata* or from related, now-extinct forms. On the basis of thermopathy and the present-day distribution of *N. beringiana* (North-west to the Island of Bennet, North-east to the Island of Victoria), this species must have evolved in the region of Western Alaska and the Pribiloff Islands; in these regions, fossil residues of *N. beringiana* have been found in Pliocene deposits. *Neptunea ventricosa* and *N. communis*, which are widely distributed in the Arctic and high boreal Pacific waters, evolved one after the other (at first *N. ventricosa*) in the northeastern area of the Bering Sea, or in the southern part of the Chukotsky Sea. Species of the genus *Anisogammarus* (apparently because of their genotypical adaptation to the littoral zone) may not have given rise to any boreal-arctic forms.

The cooling of the North Atlantic Ocean, which began in the middle Pliocene period and gradually increased, resulted in the formation of boreal water-masses, and formed a corresponding fauna in this ocean. Apparently, parallel to the formation of the upper boreal water masses off the coasts of America, *Neptunea despecta* — morphologically related to *N. pribiloffensis* — may have evolved from descendants of the latter, who had penetrated into the Atlantic coastal waters in the late Miocene (or, less probably, in the second part of the Pliocene, after the secondary migration of this species into the Atlantic Ocean).

The variability, ecology and present-day distribution of *Neptunea despecta* provides evidence of the area and time of its origin. The migration of *N. despecta* to the coasts of Europe during the period of pronounced climatic changes, which occurred along the coasts of this continent in the late Pliocene, resulted in the formation of *N. antiqua* from this species. Judging by the ecological peculiarities and the time and place of the discovery of the first fossil residues of this species, *N. antiqua* must have originated in the aquatorium of present-day Southern England.

Ecological information and the distribution of modern species of the genus *Gammarus* s.l., supported by comparative-morphological analysis of the phyletic correlations between evolutionary advanced and primitive species, show a definite similarity between the locality and period of the formation of boreal species of this genus and those of Atlantic species of the genus *Neptunea*. However, boreal conditions in the Northern Atlantic Ocean resulted in the formation of an independent sub-genus, *Lagunogammarus* Sket (partim) (Sket, 1971), during the evolution of the genus *Gammarus*. The first representatives of this sub-genus evolved during the second part of the Pliocene, from the most ancient of the present-living species of *Gammarus*, i.e., the Lusitanian-Mediterranean *Gammarus (Pephredo?) locusta*.

The brackish-water living, comparatively thermophile, species *Gammarus (Lagunogammarus) salinus* may have originated first. The brackish-water species *G. (Lagunogammarus) zaddachi*, which has spread somewhat wider than the former species, but is less thermophilic, presumably evolved later from this species or from common ancestors.

In the late Pliocene, under sharply changing hydrological conditions, the eurybiont species *Gammarus (Lagunogammarus) oceanicus* may have evolved; this species has now spread far to the North. Approximately at the same time, or somewhat earlier, the eurybiont brackish-water boreal species of another very ancient, chiefly fresh-water living subgenus, *Gammarus (Gammarus) duebeni* may have evolved.

The evolution of the genus *Marinogammarus*, influenced by a similarly changing environment, is analogous to that of the genus *Gammarus*. The Celtic species *M. pirloti* and *M. stoerensis* were presumably the first to evolve within this genus from the Lusitanian-Mediterranean *Marinogammarus marinus*, while in the late Pliocene period, in cooler waters, the lower boreal *M. obtusatus* originated, followed by the less eurybiontic high-boreal *M. finmarchicus*.

The arctic species obviously formed in Arctic waters masses, which were formed by Pleistocene glaciation in the higher latitudes of the Northern Hemisphere. *Gammarus (Lagunogammarus) setosus*, distributed throughout a vast arctic-boreal area, and continuously adapted to the littoral zone, may have been the first species to originate from *G. (Laguno gammarus) oceanicus* or from related ancestors. Later, apparently at the height of glaciation, *G. (Lagunogammarus) wilkitzkii* must have evolved; this species had begun to dwell under the lower surface of the drifting ice cover and had inhabited the central parts of the Polar Basin, and might have penetrated to the high boreal waters of the Pacific Ocean during the period of intraglacial sea transgression. The arctic *Neptunea denselirata*, known in its fossil form from the glacial deposits of Western and North-western Norway and, on the basis of ecological and morphological evidence, one of the recently formed species of the genus *Neptunea*, presumably originated from *N. communis* in the Pleistocene period, during the period of increasing glaciation.

Great and vigorous geological events in the western part of the Okhotsk Sea, and the establishment of glacial conditions there in the second part of the Pleistocene resulted in a powerful outbreak of speciation in this part of the Pacific aquatorium. Some of the glacial Okhotsk Sea species evolved at that time from the genetic stock of relatively ancient, lower boreal and subtropical species *(Neptunea varicifera, N. lamellosa)*, while others derived from widely distributed boreal and upper-boreal Pacific species *[Anisogammarus (Eogammarus) aestuariorum* sp. nov., *A. (Eogammarus) hirsutimanus, A. (Spinulogammarus) ochotensis]*. The single exclusively pacific, glacial-Okhotsk Sea species of the genus *Gammarus, G. (Lagunogammarus) kamtschaticus*, derived from *G. (Lagunogammarus) wilkitzkii*, which penetrated to the Okhotsk Sea from the Arctic during the late Pleistocene.

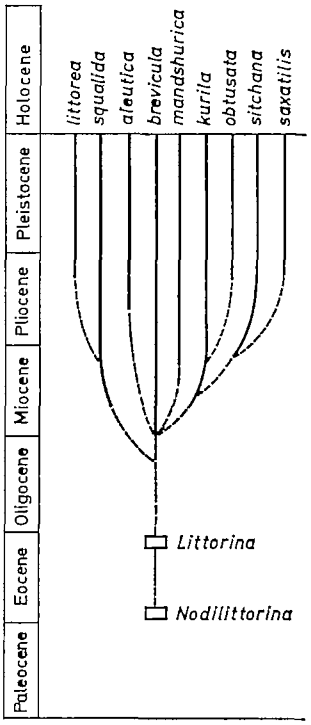

Fig. 5. Hypothetical scheme of evolution of the genus *Littorina* Ferussac. Symbols as in legend to Fig. 1

We offer a conjectural scheme of the evolution of the genus *Littorina* as an additional illustration of the use of ecological and palaeoecological information for the reconstruction of temporal-spatial evolutionary schemes, based on a detailed analysis of comparative-morphological and palaeontological data. The majority of species of this genus (Fig. 5) dwell in the littoral zone, and their origin and development can serve as a good illustration of convergency in the direction of evolution and distribution, together with those of the littoral genera *Anisogammarus* and *Gammarus*.

The genus *Littorina* seems likely to have originated in the somewhat cooled subtropical waters between the Eocene and the Oligocene off the Asian coasts, were Japan is presently situated. The most ancient of modern species of this genus, *Littorina brevicula*, which is, by reason of its thermopathy, subtropical and, therefore, subtropical in origin, may have originated in the early Miocene in comparatively cooled subtropic coastal Asian waters. This species has the greatest affinity (within the genus) to representatives of the more ancient genera of the family, inhabiting subtropical and tropical waters. *L. brevicula*'s ancestors, and probably *L. brevicula* itself, have spread widely throughout the northern part of the Pacific Ocean. After the separation of the low-boreal water mass off the coasts of Asia in the second part of the Miocene, *Littorina mandshurica* may have derived from these forms; the ecologic peculiarities of *L. mandshurica* correspond to the conditions established at that time in the lower-boreal biogeographical province. Somewhat earlier, the temperate eurythermal species *L. kurila*, off the coasts of Beringia, was derived from ancestors common to *L. brevicula* and probably common to *L. mandshurica;* the genotypical peculiarities and primary adaptation conditions afforded this species an opportunity to spread throughout boreal Pacific waters.

Simultaneously, and in the same area as *Littorina kurila*, another widely distributed Pacific boreal species, *L. (Algaroda) squalida*, may — as a result of increased cooling in the northern part of the Pacific Ocean — have originated from other, apparently more ancient forms, which gave rise to the sub-genus *Algaroda*, and sufficiently spread until the middle Miocene.

The late Miocene cooling may have caused the formation off the coasts of Alaska of the species *Littorina sitchana* (probably directly from *L. kurila*), which has mainly spread throughout American coastal waters.

Probably at the same time, *Littorina kurila, L. sitchana* and *L. squalida* penetrated along the northern coasts of America to the Northern Atlantic Ocean.

Already in the Pliocene period in the region of the Aleutian Islands, the high-boreal species of *Littorina aleutica*, morphologically allied with *L. brevicula*, may have derived from *L. brevicula* or from common ancestors.

In the second part of the Pliocene period, the establishment of boreal climatic conditions in the Northern Atlantic Ocean and the migration of the descendants of species which had already penetrated to the coasts of Europe from the Pacific Ocean, may have resulted in the formation of boreal Atlantic species — *Littorina obtusata* from the descendants of *L. kurila, L. saxatilis* from the descendants of *L. sitchana* and *L. littorea* from the descendants of *L. squalida*, respectively.

Discussion

A distinct convergency in the evolution of the genera under consideration can be seen — the biogeographical groups of species were formed at similar localities and at the same periods. The formation and distribution of the genera *Gammarus* and *Anisogammarus* illustrate parallel evolutionary development with homological lines (Vavilov, 1922; Tzvetkova, 1969) and with similar ecological niches occupied by bionomically analogous species.

The boreal waters of the Northern Atlantic Ocean are inhabited by a fauna which is less abundant than that of the boreal waters of the northern part of the Pacific Ocean; this can be easily accounted for, since boreal conditions were established first in the latter aquatorium and then in the former — consequently, the fauna within the former aquatorium developed during a shorter period of time. Moreover, the shorter meridional extent of an aquatorium with boreal conditions such as the Atlantic Ocean, as compared to the Pacific Ocean, may have had some influence.

The study of the process of formation of the genera under investigation provides evidence of the fact that virtually all modern species of these genera originated from the former geological epochs at the time of vigorous geological shocks and sharp hydrological condition changes in the greater part of the aquatorium in which the species under consideration dwell.

The process of species formation was followed by a pronounced increase in variability of the paternal species, by greatly increased selection, which influenced the production of formative processes of a series of species at the time of environmental pulsation (the species are partly preserved in fossil remains), and by an increase in intraspecific variability of ancestral forms.

A wide intraspecific variability at the edges of these areas can be observed even among modern species (Golikov, 1960, 1968), but the comparative stability of climatic conditions of the Holocene hinders the formation of new species due to specific homeostatic reactions and genotypical conditioning in regard to the faunal distribution ranges.

Similarity of time and place of formation and of time course of distribution of different animal groups, conditioned by similarly changing environmental factors, adds much to, and proves the correctness of, the evolutionary reconstructions presented. This is true for each of the genera under consideration. It justifies the construction of time-space schemes, also for groups of organisms without fossil remains.

Common climatic histories in the dwelling regions of highly dissimilar groups of organisms, which in coinciding areas required similar environmental conditions and which have developed under the influence of the same environmental factors, leads to the hypothesis that the evolutionary scheme of the genera analysed represents part of a more general process in the formation and development of the whole fauna of the areas of cold and temperate waters of the Northern Hemisphere considered.

Summary

1. We suggest the application of an ecological method of constructing time-space schemes of evolutionary trends. This method is based on the principle of close dependence of the distributional range and the dwelling conditions of modern species upon (1) climate (environment) effective during their formation; (2) primary adaptation; (3) subsequent distribution as influenced by historical changes of the climate in the dwelling region.

2. Application of the ecological method is illustrated by the analysis of the evolutionary development of gastropods of the genera *Neptunea* and *Littorina*, and amphipods of the genera *Anisogammarus* and *Gammarus*, distributed throughout the cold and temperate waters of the Northern Hemisphere.

3. The validity of the ecological principle of evolutionary reconstructions gains support from comparative-morphological and palaeontological information, and from the degree of intraspecific variability, which proves to be minimal under conditions approaching those existing at the time of the formation and primary adaptation of the species considered.

4. Species still dwelling under conditions corresponding to their most ancient climatic environment are more primitive than those inhabiting areas with, historically, more recently formed climatic conditions. In the northern parts of the Pacific and Atlantic Oceans and in the Polar Basin, species of the genera under study, subtropical by origin, prove to be more ancient and primitive than those inhabiting the high-boreal and Arctic waters.

5. Convergency and parallelism in the evolutionary development of diverse animal groups, which occur under similarly changing environmental conditions, and which manifest themselves in the similarity of time and place of the formation of analogous biogeographical groups of species, lead us to assume that the evolutionary trends of the genera analysed are a part of the formation and development of the fauna of cold and temperate waters of the whole Northern Hemisphere.

6. The ecological principle combined with palaeoecological data allows the reconstruction of time-space evolutionary schemes even for groups of organisms for which no fossil remains are available.

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