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The Cenozoic History of the Molluscan Faunas of the North Pacific Shelf

A.I. Kafanov

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The present work is the latest of a series of publications 134* [Kafanov, 1974 a-c, 1976, 1978, 1979 a-e, 1981; Kafanov and Popov, 1975; Skarlato and Kafanov, 1975, 1976] summarising the main ideas which have been advanced with respect to the evolution of the molluscan faunas that inhabited the shelves of the northern hemisphere during the Paleogene-Neogene epochs. Such a task presupposes consideration of a whole range of questions, among which an important place is occupied by an analysis of the paleogeographic situation during particular stages of geological history.

In a genetic approach to the study of the distributional features of a marine biota it is necessary to rely upon information concerning

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*The figures in the right-hand margin are page numbers of the original (Tr.).

(a) the shore line, the area and the bathymetric characteristics of the paleowater expanses; (b) the development of the climatic zonation, which determines the evolutionary dynamics of the latitudinal boundaries of geographic ranges of species and taxa higher than the rank of species; and (c) the distribution of the paleocurrents, since these introduce an interzonal element into the geographic range of the animals and plants and, to a considerable degree, influence the scale and directivity of prochoreses[1]. It is for this reason that the section dealing with the evolution of the Pacific Ocean molluscan faunas is preceded by a survey of contemporary ideas with respect to the paleogeography and paleoclimatology of the North Pacific. While the survey in no way claims to be complete, it may be found useful by biogeographers who, being faced with the diversity and frequently, 135 the contradictoriness of paleogeographic and geochronological interpretations, prefer for the most part to ignore the geological and paleontological literature.

In the stratal-time range adopted here the Quaternary includes the Apsheronian, the Calabrian and their analogues (lower boundary - about 1.8 million years [see: Troitskii, 1979]). The beginning of the Pliocene corresponds to the lower boundary of Gilbert's 5th

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[1] Following the example given by the Termiers [Termier and Termier, 1956], I make extensive use of the term "prochoresis" for designating migrations of organisms on the geological time scales.

paleomagnetic epoch and is drawn along the roof of the Pontian, the Messinian and their analogues (about 5.0 million years). The Miocene-Pliocene boundary has a similar character in the North Pacific also [Harper, 1978]. In the biostratigraphic plan the correlation scheme of the Paleogene-Neogene horizons of the North Pacific which was worked out by Gladenkov [1978] is taken as the datum.

Some of the paleogeographic features of the North Pacific in the Cenozoic

The most recent geological-geophysical, paleontological and biogeographic data lend support to the idea that the Pacific Ocean is of very great antiquity, dating, in the opinion of the vast majority of the investigators, to Pre-Cambrian time. However, even with respect to recent stages of geological history, its former shore line, area and bathymetric characteristics differed markedly from those of the present day.

Throughout the greater part of the Cenozoic, at the site of the Bering Strait and the present shelf of the Bering Sea there existed a single land mass (Beringia) which connected Eurasia with North America. The Bering land mass originated in the Late Cretaceous as a result of the Yanshan tectonic movements in Eastern Asia and the Laramic tectogenesis in the northwestern region of North America. It individuated the region represented by the Canadian Basin of the Arctic Ocean from the Pacific Thalassocraton.

There are no reliable data on the Paleogene inundation of the Bering-Chukotsk Platform. Mainly on the basis of an analysis of the continental flora and fauna, a pra-Bering Strait is believed to have existed in the Middle Eocene and at the end of the Early Oligocene [Hopkins, 1959; Hopkins et al., 1969; Flerov et al., 1974; Novodvorskaya and Yanovskaya, 1976]. Moreover, Paleogene links between the North Pacific and the Polar Basin have yet to be traced through finds of marine molluscs [Skarlato and Kafanov, 1976; Kafanov, 1979 c].

Right up to the end of the Middle Miocene a platform projection of the western part of Beringia extended as far as the Koryak Highlands, Eastern Kamchatka and the Komandorskie Islands, and it is probable that in the Early Oligocene it was directly connected with paleo-Kamchatka [The Geological Development..., 1968; Shantser, 1974; Vdovin, 1976]. The pre-Neogene unconformity and the stratigraphic discontinuities recorded in the region of the Komandorskie Islands and Obruchev's Uplift [Goryachev, 1965; Schooll et al., 1971, cited from: Shantser, 1974] attest to the existence there of a vast area (or areas) of land extending from the Maastrichtian to the Middle Eocene.

Throughout the whole of the Paleogene the contemporaneous water expanses consisting of the Sea of Okhotsk and the Sea of Japan were also the site of a vast area of land [The Geological Development..., 1968; Kulakov, 1972; Khudyakov, 1972; Aleksandrov, 1973; Rodnikov 136 and Rodnikova, 1974; Shantser, 1974; Sergeev, 1976]. There were some comparatively small sedimentation basins, connected with the open sea, in the regions of Sakhalin, eastern and western Kamchatka, Hokkaido and possibly the Kurile Islands (Late Eocene - Oligocene). Only in the Early-Middle Miocene did the basin occupied by the Sea of Japan begin to become silted up, while the Sea of Okhotsk platform, or at least its northwestern half, preserved a sub-aerial character until the Middle Pliocene (Okhotia). The final subsidence of the western part of Beringia occurred by the beginning of the Late Miocene.

Thus, in Paleogene time the North Pacific area was much smaller than it is today. This is completely in accord with a scheme [Flemming and Roberts, 1973] that makes provision for a causal link between epochs of tectonic-magmatic activity and global transgressive-regressive cycles. According to this scheme, throughout the Paleogene and the Neogene two global transgressive epochs were manifested. One of them corresponded to the Middle Eocene, the other, to the first half of the Middle Miocene - Late Miocene. In particular, the end of the Middle Miocene was marked by almost the largest transgression of all on the territory of the Japanese Islands. The vastness of it is corroborated by the close similarity which exists between the diatomaceous flora of Sakhalin, Kamchatka and North America, and also by a number of other paleogeographic discoveries [Tanner, 1968; Aleksandrov, 1973]. The epochs which were characterised by a fall in the eustatic level of the World's ocean, as registered by global equipotential surfaces, are correlated with the initial phases of the Danubian (25±2 million years), the Attican (9±3 million years) and the Caucasian (1.6±0.4 million years) epochs of tectonic-magmatic activity in the Cenozoic [Khain, 1971]. In addition, the overall picture of the fluctuations in the level of the ocean was greatly complicated by transgressive-regressive phenomena that were regional in character.

It has been established that two or three Neogene transgressions occurred in the Province of Beringia. The earliest inundation of the province is associated with the Late Miocene [Davies, 1929, 1934; MacNeil, 1957, 1965; Durham and MacNeil, 1967; Hopkins, 1967, 1972; Cohen, 1968; Coan, 1969; Shantser, 1974; Nelson et al., 1974; Biske and Baranova, 1976; Vdovin, 1976]. There is reliable information about the presence on the shelf of the Bering Sea, of shallow marine deposits dating from the Late Miocene to the Early Pleistocene [Hopkins et al., 1969]. Biske and Baranova [1976] consider that the origin of the Bering Strait was associated with regional tectonic movements that were activated during the Late Oligocene - Neogene period with the migration of geosynclinal zones in the direction of the Pacific Ocean. A Late Miocene transgression, mostly synchronous with the Pontian, occurred between 10 million and 5 million years ago; the Pliocene Beringian Transgression began about 3.5 million and ended about 2.5-2.1 million years ago.

The Late Miocene transgression that occurred in the province of Beringia does not yet have a definitive name, which has been the cause of notorious frustrations. Accordingly, I suggested that it be called the "Nuvok Transgression" (Report presented at the 14th Pacific Ocean Scientific Congress, Khabarovsk, 1979). This nomenclature corresponds to a similarly named formation located in the north of Alaska near Camden Bay and includes one of the oldest (from the Middle or Late Miocene to the Pleocene) marine Neogene deposits on the arctic littoral of North America.

The development of climatic provincialism and the character of the paleocurrents

The Cenozoic trend of paleotemperatures. Extending from the Late Cretaceous (Campanian-Maastrichtian) climatic pessimum right up to the end of the Paleocene, a climatic warming is known to have occurred in the northern hemisphere. After the Paleocene-Early Eocene climatic optimum the temperatures gradually declined. In the Pliocene this process led to the development of extensive continental glaciation over wide expanses of Eurasia and North America. The overall character of this trend [Keith and Weber, 1964; Bogdanov et al., 1978; Monin and Shishkov, 1979; Schnitker, 1980], interrupted by comparatively brief periods of warming and cooling, is confirmed by a large body of paleoclimatic data, collected by very different techniques of investigation[2]. The climatic changes that took place in the northern

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[2] It is considered probable that an association existed between episodes of tectonic activation and the transgressive-regressive and climatic cycles [Akhmet'ev, 1976; Krasilov, 1977 a].

part of the Pacific Ocean were similarly characterised.

Throughout the whole of the Cenozoic there was a permanent southerly migration of the northern tropic (the Tropic of Cancer) [Weber, 1964; Smith et al., 1973] (fig. 1). In the North Atlantic, however, and also on the Asiatic and American coasts of the North Pacific, the rate of this migration was evidently not the same (fig. 2,a)[3].

Beginning with the Late Cretaceous [Krasilov, 1976, 1977 a,b; Fot'yanova, 1977] and continuing until now, a difference is apparent in the trend of the isotherms along the Asiatic and American coasts of the North Pacific. This is confirmed by the position of the Tropic of Cancer during the Late Cretaceous - Paleogene (fig. 1,2,a). The Paleogene flora of Alaska were displaced northwards by approximately 10° in comparison with flora of the same type in Eastern Asia [Krasilov, 1976]. In the Paleocene they were characterised by the presence of palms and many kinds of subtropical plants [Wolfe, 1972].

Prior to the beginning of the Middle Miocene the climatic cooling was apparently more pronounced in the northeastern part of the Pacific Ocean, but during the remaining part of the Miocene and in the Pliocene, the opposite process was manifested. Northwards of

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[3] Fig. 2,a has been produced on the basis of fig. 1 and illustrates the relative rate of migration of the Tropic of Cancer on the meridians of Alexandria in Egypt (about 30° east long.), Awaji Island in the Inland Sea of Japan (about 135° east long.) and the region between Santa Maria and Santa Barbara in California (about 120° west long.).

the Tropic of Cancer this general picture was somewhat disrupted on account of the fact that a large part of the Asiatic coast of the North Pacific was constantly subject to the influence of the Siberian anticyclone, which became more intense during continental periods (that is, when the Beringian land mass existed). Therefore, during the Cenozoic the Beringian Province of North America at all times enjoyed a relatively warmer and more humid climate that did the Beringian Province of northeastern Asia [Buks, 1976]. Throughout almost the whole of the Cenozoic the North Atlantic was evidently warmer than the North Pacific. It is probable that, beginning with the Late Miocene (fig. 2,a), the very abrupt increase in the rate of migration of the Tropic in the North Atlantic dictated the development in the Pleistocene of the extensive continental glaciation of the northwestern part of Eurasia, Greenland and North America.

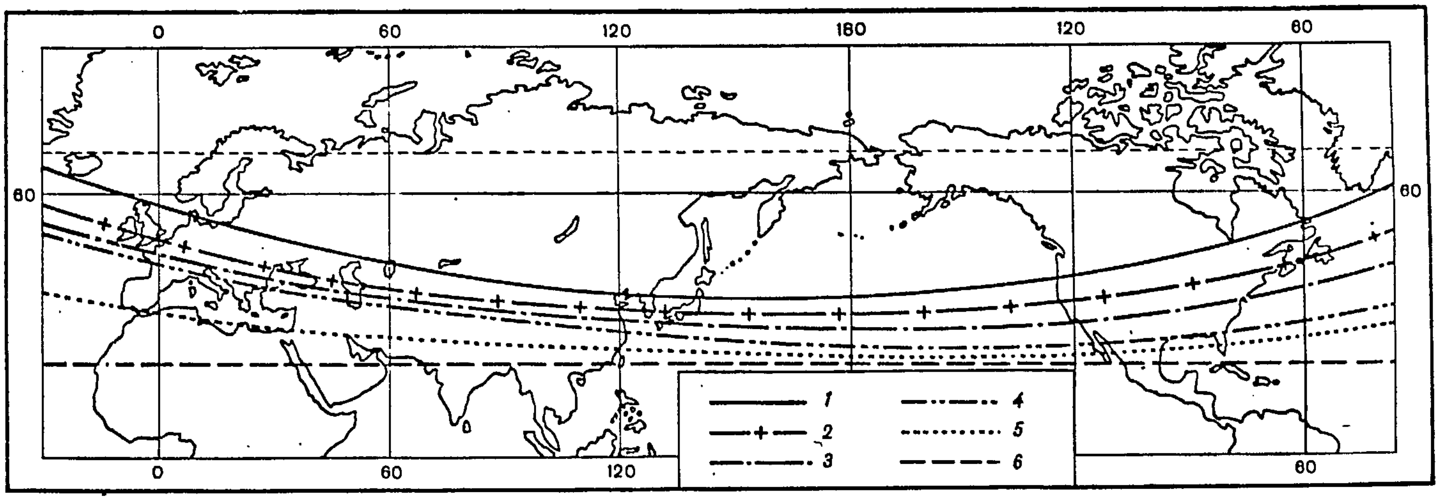

Fig. 1. Change in the position of the Tropic of Cancer during the Cenozoic [after Sinytsin, 1967, 1972, 1976].

1. Late Cretaceous; 2. Eocene; 3. second half of Oligocene;
4. Miocene; 5. first half of Pliocene; 6. present position.

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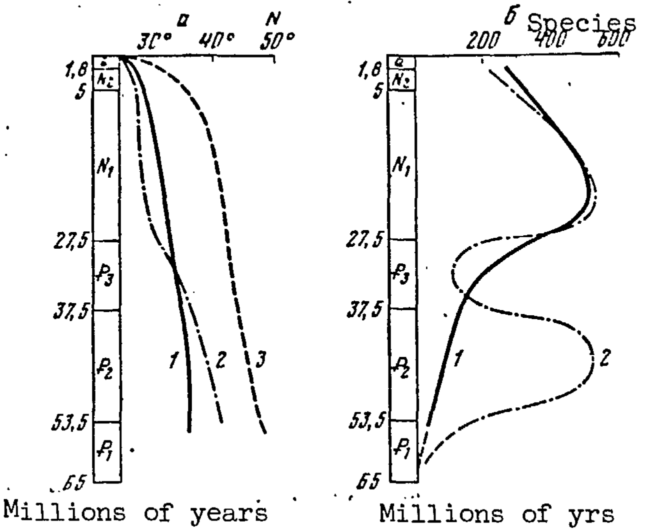

Fig. 2,a— Latitudinal rate of migration of the Tropic of Cancer during the Cenozoic.

1. at longitude 135°E (Japan); 2. at longitude 120°W (California), 3. at longitude 30°E (Egypt).

b - change in the number of species of bivalve molluscs in (1) Japan and (2) California during the Cenozoic [after: Keen and Benson, 1944; Hatai and Nisiyama, 1952, and "The Zoological Record" for subsequent years].

The Paleogene. "Prior to the Oligocene the climates of the Earth were comparatively equable with respect to the thermal regime: the temperature differences between the low and high latitudes were minor. The thermal zonation was indistinct and consisted of two zones: a 140 tropical and a boreal. The latter is a distinctive, now unknown, type of modified tropical climate, which, in contrast to the contemporaneous subtropical climate, was not subject to the systematic influence of temperate and arctic climates, as these did not as yet exist"

[Sinitsyn, 1972, p. 19]. From the end of the Eocene (Kizi Stage) to the end of the Oligocene (Blakeley Stage) the February mean water surface temperatures at the site now occupied by Los Angeles fell by no more than 2° [Durham, 1954], while the Tropic of Cancer continued to embrace the territory of southern Japan even in the second half of the Oligocene (fig. 1).

According to results of isotopic-oxygen determinations in planktonic and benthonic Foraminifera taken from core samples obtained during deep-water drilling operations, throughout the Paleocene the surface water temperatures in the equatorial part of the Pacific Ocean ranged from 22° (beginning of the Paleocene, about 65 million years ago) to 25° (second half of the Paleocene, 60-53.5 million years ago), and the temperatures near the bottom were 12-13° [Douglas and Savin, 1971]. Somewhat lower estimates of the paleotemperatures of the surface water during the Paleocene were obtained for the northern subtropical and subantarctic regions of the Pacific Ocean: by A.P. Lisitsyn at the latitude of southern Kyushu (32°N), 19-22° [Monin and Shishkov, 1979]; by Shackleton and Kennett [1975] off the southern shores of New Zealand, 18-20°.

In the Eocene, in the regions corresponding to what are now northern Japan and Sakhalin, a subtropical[4] or subtropical-temperate-

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[4] In using this term I am following the example of the vast majority of the authors, even though the conditionality of its use with respect to Paleogene climates is obvious [see Sinitsyn, 1972]. For Paleogene "boreal" and "subtropical" climates, use of the term "paratropical" [Wolfe, 1972] is preferable.

warm climate prevailed. According to Borsuk [1967], the northern boundary of the subtropical paleofloristic province lay somewhat to the south of 40°N. latitude (northern Honshu). Krasilov, however [1977b], takes the Eocene flora of the Aleksandrovsk region on northern Sakhalin (about 50°N. latitutde) to be the northern outpost of subtropical forests containing Dryophyllum and Cinnamomum. The Eocene Bibai flora on Hokkaido is considered to be one of the most thermophyllic floras of the southern half of the Far East and displays a transitional warm-temperate, subtropical, forested character with an important role played by palms and a small number of Arcto-Tertiary components. In its composition and biological type the flora of the Avgustovka River on Sakhalin (lower part of the Lower Due suite) closely resembles the Ube flora of southwestern Japan and the Raichikha flora of the Zeya-Bureya Basin [Flerov et al., 1974]. The climatic indices show that it corresponds to the Eocene climatic optimum and approximates to the floras of the present subtropical zone [Fedotov, 1977, 1979]. The freshwater molluscs of the Lower Due coaliferous suite on Sakhalin lived under climatic conditions 141 analogous to the present climate of southern China and the Indochinese Peninsula [Flerov et al., 1974].

From the marine molluscs in the Eocene of the southern part of the northwestern Pacific, two faunistic provinces are distinguished: a tropical, which embraced Taiwan and southwestern Japan, and a subtropical, which occupied northeastern Japan, Sakhalin, the Southern

Kurile Islands and possibly the southwestern extremity of Beringia [Oyama et al., 1960; Mizuno, 1962, 1964a; Takai et al., 1963; The Geological Development.., 1968; Zhidkova et al., 1974; Noda, 1975]. On Sakhalin, based on the composition of the molluscan fauna a comparatively warm marine basin containing a large number of subtropical species is recorded [Krishtofovich, 1964; Zhidkova et al., 1974]. The diverse character of the thermophyllic forms (Venericardia, Pitaria, Crassosirea, Brachidontes, Psephaea and others) affords evidence that the annual water temperature of the Sakhalin basins of the Krasnopolevian period may have reached 19° [Margulis and Savitskii, 1974].

Situated northwards of Sakhalin was a forested region containing a mixture of broad-leaved temperate, temperate-thermophyllic and evergreen trees. A modified subtropical climate in the Eocene is noted up to and including northeastern Kamchatka, Penzhino Bay [Flerov et al., 1974] and the Komandorskie Islands [Chelebaeva et al., 1974]. Pronina [1969] attaches great emphasis to the very warm water composition of the Eocene fauna of eastern Kamchatka, where Eocypraea, Cymatium, Conus, Miltha, Plicatula and fairly large numbers of corals have been recorded. Also indicative of this is the discovery of a palm on Kamchatka at latitutde 65°N. Further south, palms were a normal constituent of the flora [Fot'yanova, 1977]. Within Beringia, under modified subtropical climatic conditions there flourished thermophyllic broad-leaved and ancient coniferous trees containing a large proportion of evergreens. It was only the northern margins and the region of the present shelf of the Chukchee Sea that were characterised by a temperate-warm climate [Biske and Baranova, 1976].

An Eocene climatic optimum has also been established for the Pacific coast of North America [Wolfe, 1966, 1968, 1972; Wolfe and Hopkins, 1967; Axelrod and Bailey, 1969]. It has been suggested [Akhmetev, 1976] that it was global in character. It is more probable, however, that its distinctiveness was confined to the temperate and circumpolar latitudes. In particular, on the curve of the Cenozoic paleotemperatures of the upper layer of water in the western part of the Pacific, a curve which was plotted by Lisitsyn from the results of a layer-by-layer analysis of the oxygen isotopes in two columns of rocks obtained from deep-water drilling during the sixth voyage of the "Glomar Challenger", the gradual drop in the temperature, observed since the end of the Paleocene, corresponds to almost the entire Eocene [Monin and Shishkov, 1979]. This is especially interesting inasmuch as the portion of the paleotemperature 142
curve which corresponds to the Eocene was obtained on the basis of an analysis of a column of rocks obtained at latitude 19°N, while the portion of the curve corresponding to the Paleocene is based on analysis of a column obtained much further to the north, at latitude 32°.

The first Cenozoic phase of North Pacific climatic cooling began in the second half of the Eocene. It culminated in a temperature minimum which was most pronounced in the middle of the Oligocene (about 30 million years ago).

According to the results of oxygen isotopic determinations in the equatorial region of the Pacific Ocean the surface water temperatures decreased from 25° in the middle of the Middle Eocene (49 million to 45 million years ago) to 23° at the beginning of the Late Eocene (about 43 million years ago), to 18° at the Eocene-Oligocene boundary (about 37.5 million years ago), and to 17° in the middle of the Oligocene (32 million to 30 million years ago). The temperatures near the bottom were respectively 11-12°, 9°, 7° and 5° [Douglas and Savin, 1971]. For the equatorial part of the eastern Pacific, Emiliani [1961] obtained higher estimates of oxygen-isotope based paleotemperatures near the bottom: 10.4° in the middle of the Oligocene (30 million to 35 million years ago).

According to Lisitsyn [Monin and Shishkov, 1979], the Cenozoic paleotemperatures of the surface layer of water in the western part of the Pacific (about 19° N. latitude) were characterised by values of 17° for the Middle Eocene (about 45 million years ago), 15° for the late Eocene (about 40 million years ago) and 14° for the first half of the Oligocene (about 35 million years ago). In the South Pacific the surface water temperatures ranged from 18-20° in the Early Eocene to 7° in the Early Oligocene [Shackleton and Kennett, 1975]. The glaciation of Antarctica probably began at the end of the Oligocene [Kennett, 1977].

The identicality of the trends that led to changes in the climate in the northern and southern regions of the Pacific Ocean is indicative of the global character of the Paleocene-Early Eocene temperature maximum and the Middle Oligocene temperature minimum. Moreover, it is highly probable that both the maximum and the minimum were most pronounced only in the temperate and circumpolar latitudes.

It should be noted that the dating, character, and scale of the first Cenozoic climatic minimum are treated in the literature very ambiguously. On the one hand, this is a consequence of the differing notions that were held with respect to the ages of the geological formations in question. Thus, for the northwestern states of the U.S.A., a Late Oligocene warming of the climate has been established [Wolfe and Hopkins, 1966]. Fot'yanova [1977] ascribes to the same period the very pronounced cooling that occurred in the second half of the Paleogene, while Krasilov and Alekseenko write about a possible Oligocene climatic optimum in the southern Primor'ye region. Furthermore, Krasilov [1977], in discussing a possible link between cycles of tectonic activity and climatic cycles, apparently ascribes a global character to this optimum. Akhmetov [1976] considers that a Late Oligocene Aquitanian climatic minimum was clearly manifested 143 in regions forming part of a system of Cenozoic geosynclinal provinces, including the North Pacific. Meanwhile, according to the scheme of correlations of stratigraphic units of the Mediterranean Sea (Tethys and Paratethys), which was adopted at the Sixth Congress on Mediterranean Neogene Stratigraphy (Bratislava, 1975), the Aquitanian Stage belongs to the Lower Miocene. On the other hand, the ambiguity which is evident with respect to the datings and scale of the Late Paleogene climatic pessimum could be a consequence of a simplified approach [see Kafanov, 1979d] being taken to the evaluation of particular paleoclimatic indicators.

The differences between the marine molluscan faunas of southwestern Japan and northeastern Japan and Sakhalin in the Oligocene persist for the most part. However, whereas in the Early Oligocene the boundary between the tropical-subtropical and the subtropical-temperate-warm water faunas traversed northern Honshu, by the end of the Oligocene this province corresponded to the boundary between the subtropical-temperate-warm water- and temperate-warm water faunas [Takai et al., 1963; Mizuno, 1964a; The Geological Development..., 1968].

The genesis of the North Pacific Current. On the Pacific coast of North America the cooling was more drastic than it was on the Asiatic coast (fig. 2,a). In California the rate of migration of the Tropic of Cancer was maximal in the Oligocene. Analysis of the marine molluscan faunas affords evidence in this connection of a pronounced cooling that occurred at the Eocene-Oligocene boundary and in the Early Oligocene [Addicott, 1970; Tipton et al., 1974]. Probably, the formation of a steep thermal gradient between the Californian waters and the waters washing the eastern seaboard of the

Japanese islands aided in the genesis of the North Pacific Current during the Oligocene. Attesting to this, in particular, are a number of findings.

The composition and diversity of the Paleogene molluscan faunas affords clear evidence of the existence of sharp paleogeographic disparities between northern and northeastern Honshu, on the one hand, and western Honshu, on the other [Mizuno, 1962, 1964b]. Here, the molluscan faunas of northern and northeastern Honshu more closely resemble the molluscan faunas of Sakhalin and Kamchatka, whereas the molluscan faunas of western Honshu are characterised by a much greater abundance of species and closely resemble the molluscan faunas of southern Japan and Taiwan. A distinctive feature of the Paleogene-Neogene faunas of the northern part of Kanto province (the Pacific coast of Honshu northwards of Cape Inubo as far as the town of Iwaki) is the transitional character between the faunas of western, central and northern Japan. These differences are discovered when analysing assemblages of molluscan faunas consisting of various taxa and also separate genera or higher ranking taxa. For example, the Oligocene finds of Cardiidae of the subfamily Clinocardiinae within the Japanese Islands are limited almost exclusively to the regions of northern and northeastern Honshu [Mizuno, 1964b; our data].

The analogous positioning of the biogeographic provinces along 144
the Sea of Japan and the Pacific coasts of Honshu has persisted to

this day. It is mainly determined by the system of currents washing the Japanese islands. The powerful, warm Tsushima Current extends along the entire west coast of Japan. The Kuroshio washes southeastern Japan, swinging eastwards approximately in the vicinity of Cape Inubo, and the northeastern coast of Honshu is under the influence of the cold Kurile Current (the Oyashio) (fig. 3,a).

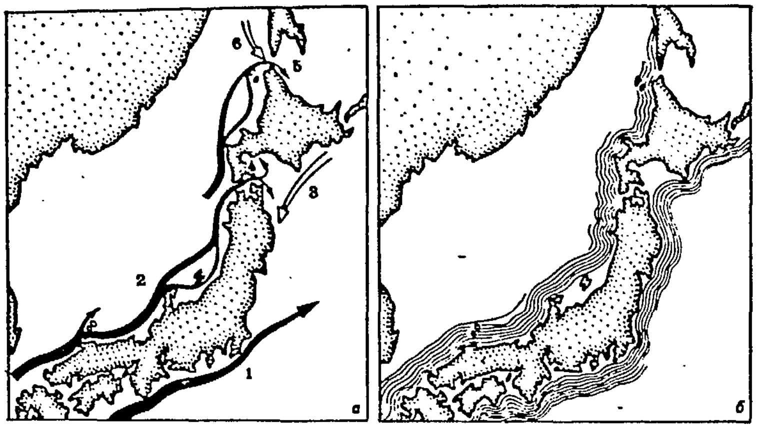

Fig. 3,a. - position of the warm (dark arrows) and cold (light arrows) currents off the coasts of Japan [after Khidaka, 1974].

1. The Kuroshio; 2. The Tsushima; 3. The Oyashio (Kurile Current),
4. The Sangarian; 5. The La Pérouse (Soya); 6. The Liman Current.

b - decrease in the number of bivalve molluscan species off the coasts of Japan from south to north [after Kuroda and Habe, 1952, and the "Zoological Record" for subsequent years]. Each isoline corresponds to approximately 15 species.

Possibly serving as a fairly reliable indicator of the distribution of the currents off the Pacific and Sea of Japan coasts of Honshu is the change in the number of species of bivalve molluscs (see fig. 3 a and b).

The forking of the main branch of the Tsushima Current in the vicinity of Noto Hanto Peninsula and Sado Shima Island is accompanied by a reduction there in the diversity of the molluscan species. The substantial decrease in the number of them in the vicinity of Boso Island reflects the sharp swing to seaward of the main branch of the Kuroshio Current and coincides with the southern boundary of the Pacific boreal region adopted by Skarlato [1974]. Near northeastern Honshu (northwards of Iwaki) the diversity of species increases somewhat on account of the southward penetration with the waters of the Kurile Current of relatively cold water-broadly boreal and boreal-arctic species. Between these regions, off the northern coast of Kanto Province between approximately Cape Inubosaki and Iwaki, the total number of species declines owing to the decrease in the relative share of both the subtropical-low boreal and the broadly 145
boreal and boreal-arctic components.

Thus, the differences between the Paleogene molluscan faunas of northeastern, northwestern and southern Honshu are most probably associated with the distributional pattern of the currents during the particular geological period. Since the Kuroshio forms part of the main system comprising the general circulation of the Pacific Ocean, it can be assumed that, overall, the principal characteristics of the hydrodynamic regime in the southern part of the northwestern Pacific and North Pacific had already begun to be manifested in the Oligocene.

The Neogene. The second Cenozoic warming in the North Pacific occurred at the end of the Early- and the beginning of the Middle Miocene. It was not as pronounced as the Paleocene-Early Eocene warming but was distinctly manifested over all of northeastern Asia [Ikebe and Chiji, 1969; Shmidt and Sinel'nikova, 1971; Gladenkov, 1972 and 1978; Kartashova, 1974; Biske and Baranova, 1976; Petrov, 1976; Fradkina, 1976; Krasilov et al., 1977; Fot'yanova, 1977; Chinzei, 1978; Itoigawa, 1978; Masuda, 1978] and also in northwestern America [Dorf, 1955, 1970; Wolfe and Barghoorn, 1960; Wolfe and Hopkins, 1967; Addicott, 1969, 1974, 1976; Additcott et al., 1978]. An Early-Middle Miocene warming is also established for the temperate and high latitudes of the southern hemisphere [Devereux, 1967; Margolis and Kennett, 1970]. It was probably global in character [Russell, 1968; Douglas and Savin, 1971; Monin and Shishkov, 1979].

The Miocene temperature maximum was ascertained by analysing the distribution of the marine molluscs, echinoderms, plankton and various representatives of the terrestrial fauna and flora, and also from oxygen isotopic determinations. In particular, the generic composition of the marine molluscan fauna of the Pestsov suite on Chukotka, which is the most warm water-inhabiting of the Neogene marine fauna of the northeasternmost part of the USSR, is typical today of basins situated 20°-25° further south, off the northern coasts of Japan and California (Crassatella, Taras, Turritella and Voluta, numerous

Arcidae, Ostreidae, Glycymeridae and others), while in the Middle Miocene deposits of western Kamchatka the remains of subtropical Echinoidea have been discovered. In Japan, typically warm water-inhabiting families of bivalve and gastropod molluscs, benthos-inhabiting and planktonic Foraminifera, and also reef-building corals became widely distributed during this period (15.5 to 16 million years ago) [Itoigawa, 1978]. According to paleofloristic data, a noticeable warming occurred in the Early and Middle Miocene even on the arctic littoral of Asia and in the lower reaches of the rivers Yana and Omoloi [Kartashova, 1976].

The main portion of the Miocene optimum corresponds to the period of accumulation of the deposits constituting the Il'inskoe suite on western Kamchatka, the Sertunai horizon of Sakhalin, the Nisikurosawa Stage of Northern Japan and the Burdigalian Stage of the Mediterranean Sea. In the North Pacific it corresponds to the beginning of a major trangression both in Japan and the Sakhalin- 146 Kamchatka region[5] and is characterised by a far northward penetration of typically warm water, benthic faunas [Tai and Serova, 1977].

According to potassium-argon datings, the period in which the Miocene climatic optimum occurred was between 18 and 15 million years ago [Addicott, 1969, 1970, 1976]. In Japan this period was of very brief duration, lasting from one to two million years, with the transition from warm water to relatively cold water conditions occur-

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[5] The Miocene Transgression was probably global in character [Tanner, 1968].

ring about 14 million years ago [Chindzei, 1978]. The latter writer [1978] does not rule out the possibility that this process was regional and was associated with the closing of the Korea Strait. At the same time, the data of Douglas and Savin [1971] with respect to the equatorial Pacific also attest to the extreme brevity of the Early-Middle Miocene temperature maximum. These data yield the following estimates of the paleotemperatures of the surface waters: 18° for the beginning of the Miocene (about 27.5 million years ago), 22° for the Early-Middle Miocene (16-15 million years ago) and $18\text{-}19^\circ$ for the Late Miocene (10.5-5 million years ago). For the waters near the bottom they are respectively 5°, 7° and $3\text{-}4^\circ$. Emiliani [1961] gives an estimate of 7° for the temperature near the bottom in the Lower and Middle Miocene.

In the Early-Middle Miocene (Il'inskaya suite) the mean annual temperatures off western Kamchatka at a depth of 0-30 m were 13.5°. At depths of 30-100 m the perennial mean temperatures in August-September were 4.5° in the Early-Middle Miocene (Il'inskaya suite of western Kamchatka)[6], 8.5 to 10° in the Middle Miocene (Kurasi and Okbykai suites of southeastern Sakhalin) and 7 to 9.5° in the Early-Late Miocene (lower subsuite of the Maruyama suite of southeastern Sakhalin); at depths of 0-30 m in the Early-Late Miocene (lower subsuite of the Maruyama suite of southeastern Sakhalin) they reached 16° [Kafanov, 1981]. The mean temperatures resulting in accretion of Ciliatocardium ciliatum shells as determined by oxygen isotopic

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[6] These values most probably pertain to the more bathypelagic facies.

analysis, proved to be 9.4±0.5° in lower Maruyama specimens [Kafanov, 1979e].

In the tropical latitudes the Miocene temperature maximum was evidently much less pronounced than in the temperate and circumpolar latitudes. Major disparities in the rate of migration of the Tropic of Cancer off the Asiatic and American littorals of the North Pacific (fig. 2a) were reflected in the paleoclimatic history of the Early and Middle Miocene in the more northerly regions of northern Kamchatka and the northern part of the Gulf of Alaska.

In the Gulf of Alaska near Yakataga (about 143° west long.), traces of local coastal and valley glaciation (the Yakataga 147 glaciation) are already manifest at the end of the Early Miocene. The thickness of the deposits making up the Yakataga Formation is as great as 5,000 m, and the Yakataga glaciation is the most protracted (end of the Early Miocene - Holocene) and probably, the earliest coastal marine glaciation to have originated in the Cenozoic history of the northern hemisphere. Judging from the distribution of the moraines in the Yakataga Formation it is assumed that, in the Early Miocene, large icebergs broke away from the mountain glaciers descending into the Gulf of Alaska [Derkson, 1976] and that, in the northeastern part of the Bering Sea, ice floes were abundant. The foot of the glacial marine deposits in the Yakataga Formation is estimated to date from the end of the Early Miocene or, at the latest, the first half of the Middle Miocene - about 20 million years ago [Huene and

Kulm, 1973; Plafker and Addicott, 1976]. It is true that Armentrout et al., [1978] draw the lower boundary of the glacial marine diamictites level with 12 million years ago and, on the basis of potassium-argon datings, they consider the glaciation to be at least 5.1-6.8 million years old.

Evidence that substantial cooling occurred during the period when the deposits making up the Yakataga Formation were beginning to form is afforded by a number of lithological characters, and also by the sharp dissimilarities which were manifested between the paleofaunistic assemblages of this formation and the deposits of the Poul Creek Formation underlying it [Clark, 1932; Miller at al., 1959; Addicott, 1969; Bandy et al., 1969; Denton and Armstrong, 1969; Lagoe, 1978]. The cause of the unusually early beginning of the Yakataga glaciation, in addition to the greatly enhanced development of climatic provincialism in the northeastern Pacific region, the latter a consequence of the intensive southward migration of the Tropic of Cancer (fig. 2,a), was the specific regimen of the increased humidity of the coastal regions, as well as the substantial amplitude of uplift of the mountain ranges [Biske and Baranova, 1976; Plafker and Addicott, 1976]. Moreover, the powerful transgression in the Middle Miocene led to an increase in the areal extent of the sea basins. In the process, warm ocean currents reached the subpolar latitudes, leading to heavy snowfalls.

It should be noted that the Yakataga glaciation was distinctly local in character. This is apparent when comparing the Middle Miocene molluscan faunas of the Gulf of Alaska region, which apparently inhabited cold waters, and coeval molluscan faunas of western Washington, where representatives of many subtropical genera are present [Plafker and Addicott, 1976; Ariey, 1978]. Thus, the fauna of the Clallam Formation (end of the Early Miocene) in northwestern Washington was a northern outpost of a temperate-warm water faunistic province embracing the coast of Oregon and a large portion of Washington [Addicott, 1976].

The climatic cooling continued from the Late Miocene to the Pleistocene inclusively. In the course of the Late Miocene Nuvok Transgression the northern part of the Pacific Ocean was linked with the Polar Basin. This led to an influx of cold waters into the North Pacific, strengthened the role of the currents in the processes 148
of heat transfer, and increased the scale of the Yakataga glaciation. It was probably also at this time that the parasubarctic circulation evolved in the northern half of the Bering Sea.

Against the background of the general climatic cooling that followed the Early-Middle Miocene temperature optimum, yet another optimum is noted to have occurred at the end of the first and the beginning of the second half of the Pliocene, albeit on a much smaller scale. A moderate increase in the temperature of the surface waters at this time is clearly apparent in the scheme proposed by Douglas and Savin [1971]. An Early-Middle Pliocene temperature optimum is found to have occurred in the Central [Burkle et al., 1978] and North

Pacific [Durham, 1950; Keller, 1978], Japan [Chinzei, 1966], Sakhalin and Kamchatka [Krishtofovich and Il'ina, 1960; Menner, 1962; Gladenkov, 1972, 1978; Zhidkova et al., 1974], on the northern shores of the Gulf of Alaska [Armentrout et al., 1978] and in California [Kammer, 1979].

Attesting to this is the low boreal habit of the molluscan assemblage in the Enemten suite on Kamchatka [Gladenkov, 1978; Sinel'nikova et al., 1979] and the presence of many low boreal and low boreal-subtropical constituents (Glycymeridae, massive Anadarinae and others) in the second half of the 4th packet of the Maruyama suite on southern Sakhalin. Of course, in this connection it is necessary to take into consideration that in recent years there has been an intensive reevaluation of the age of the Neogene formations in the region. Even data from as recently as ten years ago are proving to be highly unreliable. Additional arguments in favour of the existence of an Early-Middle Pliocene climatic optimum are provided by an analysis of the Neogene prochoreses of the North Pacific molluscan faunas (see below).

Having regard to the dextral and sinistral shapes of the Foraminifera, the advent of relatively thermophyllic species and the results of oxygen isotopic determinations, the Pliocene optimum is dated to the period extending between 4.2-4.3 and 3.2-3.4 million years ago [Armentrout et al., 1978; Burckle et al., 1978; Keller, 1978]. In the Late Pliocene the temperatures gradually declined, reaching values typical of the present day.

The Principal Stages in the Cenozoic History of Shelf-Inhabiting Molluscan Faunas

Paleocurrents and the directional orientation of the prochoreses. The ideas which are usually advanced with respect to the directional orientation, scales and intensity of prochoreses of marine organisms inhabiting the benthos are limited to establishing the almost total dependence of the migrations on physical geographic factors. The latter are identified as the presence or absence of continental or marine biogeographic barriers (land bridges, bathypelagic troughs etc.), the development of a climatic zonation that has determined the evolutionary dynamics of the latitudinal boundaries of the geographic ranges, and in particular, the direction and magnitude of the paleocurrents. Paleontologists and specialists in the field of historical biogeography accept as *à priori* a practically instantaneous (on geological time scales) dispersion of organisms by means of the currents, 149
which is one of the central dogmas of classical biostratigraphy.

It will be shown below that one of the most typical features in the evolution of the Paleogene-Neogene molluscan faunas of the North Pacific was the mainly unilateral orientation of the prochoreses from the Asiatic towards the American coast throughout a large portion of the Cenozoic and from the North Pacific towards the Polar Basin at the time of the Late Miocene Nuvok Transgression and the Pliocene Beringian Transgression. Assuming that a North Pacific Current had already become established in the Oligocene (see above), the unilateral orientation of the Paleogene-Neogene prochoreses is at first sight very easy to explain. At the same time the orientation and scales of the prochoreses are by no means always directly linked with the direction and magnitude of the paleocurrents [Kafanov, 1979b,c]. I shall cite several facts in support of this thesis.

In the Cretaceous and the first half of the Paleogene there existed a circumglobal equatorial current, which crossed the Pacific, the Tethys and the Caribbean Basin from east to west before returning again to the Pacific [Gordon, 1973]. At that time the extensive trans-Tethys prochoreses were by no means unilateral (from the southeast Asian region to the Mediterranean Sea) but rather bilateral in character. By far the largest part of the eastern Tethys elements has been preserved in the recent and Neogene molluscan faunas of Japan and the Indo-Malayan Archipelago. Mizuno [1964a], based on an analysis of more than 200 species of Paleogene-Early Neogene molluscs of western Japan, has confirmed the conclusion reached by Davies [1934], which was that the Paleogene molluscan fauna of Japan, notwithstanding the progressing trend towards the evolution of endemic forms, contains a definite proportion of Mediterranean relics. Kilmer [1978] showed that 42% of the 126 genera and subgenera of Gastropoda and Pelecypoda known to be present in the Pliocene deposits of Hokkaido and northern Honshu have a North Pacific origin, 40% originated in the Tethys, and 1% (Mercenaria) in the Atlantic, while 17% are accounted for by North Pacific Mesocenozoic autochthones. Moreover, among the genera in Japan which are known to date from the Eocene and the Oligocene, the Mediterranean predominate over those of North Pacific origin. If it is thought that the dispersion of these forms was assisted by a circumglobal current, it would be necessary to assume that they had travelled almost right the way round the world: from the region of the Mediterranean Sea to Japan by way of the Atlantic, Central America, and the Pacific. This assumption is not borne out by existing paleontological materials.

In principle, the peculiarities of the North Pacific circulation, the main features of which had begun to be manifested by the end of the Paleogene, ought to have promoted an intensive transfer of 150 planktonic larvae of molluscs of Asian origin in the direction of the American coast and thereby smoothed away the faunistic differences between the two regions. However, at least from the Late Miocene the evolution of the molluscan faunas of the northwestern and northeastern Pacific has proceeded along largely independent paths. Also referred to the Late Miocene is the individuation of the independent Oregon faunistic subprovince [Watkins, 1974].

Throughout the Paleogene and the Neogene the inflow of Pacific waters into the Polar Basin by way of the Bering Strait was at all times much less than the inflow of Atlantic waters. At the same time, in the composition of the contemporaneous fauna in the Arctic proper, bivalve molluscan genera of North Atlantic origin account for about 17.5% and genera of North Pacific origin, about 70%. Genera of uncertain origin account for 12.5% of the total, and in these it is impossible to infer a clear predominance of forms of North Pacific origin [Kafanov, 1974c, 1979c; Skarlato and Kafanov, 1975, 1976].

It is usually considered that sea currents play a decisive role in the distribution of molluscs with a planktonic larva. However, the Cenozoic prochoreses of Neptunea [Golikov, 1963; Strauch, 1972; Nelson, 1978], possessing bottom-dwelling egg capsules and developing directly, are in principle no different from those of Mya [MacNeil, 1965; Strauch, 1972], the Clinocardiinae [Kafanov, 1974b] and Serripes, possessing a pelagic stage in ontogenesis. In the Plio-pleistocene sections of England and Iceland, these four groups all appear at practically the same time [Gladenkov, 1978]. Finally, a principally unilateral orientation of the trans-Bering migrations from Asia to America has been established for a whole series of representatives of the continental fauna [Flerov et al., 1974] and flora [Yurtsev, 1974], the distribution of which bears no relation to sea currents.

Thus, drawing solely upon physical geographic factors in order to explain the peculiarities of prochoreses is proving to be manifestly inadequate. Biotic factors were just as important, and possibly even decisive, to the resettlement of bottom-dwelling fauna. The possibility of new water areas becoming populated was controlled by competitive pressure on the part of the aboriginal population, with the result that migrations were more easily accomplished in a direction in which the species diversity was less and the ecological niches were not as fully occupied [Briggs, 1974a,b; Kafanov, 1978, 1979b,d].

Furthermore, the potentialities for achieving migrations materialised to varying degrees in the progressive, conservative, and relict elements of the communities [Kafanov, 1974a, 1978, 1979d].

The principally unilateral direction of the prochoreses of the North Pacific molluscan faunas throughout a large part of the Cenozoic was evidently the result of two further factors. Due to the cyclonic direction of the currents in the North Pacific dating from the second half of the Oligocene, in the western part of the North Pacific circulation the development of climatic provincialism surpassed in scale and outstripped in time the similar climatic changes on the Pacific littoral of North America. The Pole had shifted from the present position. At that time, Japan was situated 151 in higher latitudes than California (fig. 2a). The process which resulted in a transformation of the Northern Japan - Sakhalin Paleogene molluscan fauna and the acquisition by it of a relative "predilection for cold" began earlier than was the case with the molluscan faunas of the American coast. It is for this reason that the invasion of the higher latitudes, and in particular, the cooled waters of the Northeastern Pacific, by the Asian forms surpassed in scale and outstripped in time the prochoreses of the American forms in the northwestern Pacific.

The second factor influencing the principally unilateral orientation of the prochoreses throughout a large part of the Cenozoic was as follows. The Northern Japan-Sakhalin Paleogene centre of formation of the relatively cold water molluscan faunas had a decisive influence on the evolution of the vast majority of the Neogene and recent molluscan faunas in the northern hemisphere. This stemmed from the historical continuity of the peculiarities of the exceptionally rich and highly endemic fauna of the Indo-West Pacific region [Kafanov, 1978]. The Central American tropical molluscan fauna and the Northwestern American (Washington-Oregon) Paleogene centre of formation of the molluscan faunas with which it is genetically linked were characterised by a lower rank and degree of endemism, just as they are today. The potentialities for diverging, increasing the diversity of the species and expanding into new regions were therefore greater in the Northern Japan-Sakhalin Paleogene molluscan fauna than in the Northwestern American fauna.

A discussion of the principal stages in the Cenozoic history of the North Pacific shelf-inhabiting molluscan faunas is best begun by analysing the dispersion characteristics of several prolific groups that are well represented in the fossil record. In this respect the best studied of all are Mya, Neptunea, and the sub-family Clinocardiinae. Representatives of these three groups are widely disseminated in the Cenozoic marine deposits of the North Pacific and the European Subarctic. In many stratigraphic units they are zonal forms or are indicated as the most typical species. They are also important when determining the boundary of the Paleogene and Neogene in the northwestern part of the Pacific mobile belt, while in the North Atlantic they serve as the most striking witnesses of Neogene trans-Arctic prochoreses of North Pacific invertebrates.

The history of Mya. According to Fujie [1962], MacNeil [1965], Strauch [1972] and Bernard [1979], the history of Mya is as follows. The oldest representative of the genus - M. ezoensis Nagao et Inoue - was discovered in Upper Eocene deposits of the Wakkanabe Formation of the Ishikari group on Hokkaido. In the Early-Middle Oligocene the 152 geographic range of the genus increased markedly in a northward direction and the first Mya appeared in the Gulf of Alaska region. This is shown by an analysis of the geophysical and geochronological range of M. kusiroensis Nagao et Inoue. This species is reported from the Sitikara Formation of the Urokhoro group on Hokkaido, and also from the upper part of the Acila shumardi zone on Popov Island (Alaska Peninsula) and the lower and middle portions of the Poul Creek Formation in the Yakataga District (Southern Alaska). Until the Late Miocene the southern limit of Mya resettlement along the American littoral of the North Pacific was confined for the most part to the boundaries of the Gulf of Alaska. Recorded as having been there at that time are M. salmonensis Clark (Poul Creek Formation; in the Northwest Pacific - the Lower Oligocene Poronai Stage in southern Sakhalin and Hokkaido), M. cuneiformis (Böhm) (lower part of the Yakataga Formation and the Middle Miocene beds containing Mytilus middendorffi on Kodiak Island; in the Northwest Pacific - the Middle Miocene deposits of Sakhalin and the following Miocene formations: Tikubetsu, Kawabata, Numanuti, Kokodzura, Togesita, Nakayama, Wakkanai, as well as the Honbetsu and Takihawa Pliocene formations of Hokkaido and Northern Honshu), and perhaps also M. grewingki

Makiyama (Poul Creek Formation?; in the Northwest Pacific - the Oligocene-Early Miocene deposits of Sakhalin, Hokkaido and Northern Honshu). In California, all of the known *Mya* - *M. truncata* L., *M. dickersoni* Clark, *M. arrosis* MacNeil and *M. fujiei* MacNeil - are recorded in almost every instance as not predating the Late Miocene. Very occasional finds of the latter species have been reported for Middle Miocene deposits [Adegoke, 1967a]. At the time of the Nuvok Transgression, at least one of the true *Mya* - *M. arenaria* L. - penetrated into the North Atlantic, which is documented by fossil remains of it in the deposits of the Late Miocene Yorktown Formation in Virginia. Strauch [1972] considers that *M. arenaria* may have penetrated into the North Atlantic from the North Pacific by way of the Panamanian Isthmus region. This hypothesis, as Bernard remarks with full justification [1979], is in no way proven paleontologically.

On the whole, this pattern of resettlement by *Mya* within the North Pacific is corroborated by an analysis of the geochronological distribution of species extending from the Miocene to the present time. Thus, *M. truncata* originated off the Japanese islands in the Miocene, but it was only in the Pliocene that it appeared off California. *M. arenaria* is noted to have been present in Japan from the Middle Miocene and, in spreading, reached California in the Late Miocene. The problem becomes more complex when interpreting finds of "*M.*" *producta* Conrad in the Middle Miocene Choptank and Kirkwood formations in Maryland and New Jersey respectively. MacNeil [1965] emphasised that this species stands apart from the other known representatives of the genus, and Strauch [1972] instituted for it a monotypical subgenus Atlantomya. Mya (Atlantomya) producta is an independent line of evolution of Mya. Inasmuch as there are no data on Early and Middle Miocene submergences of the Bering-Chukotsk Platform, Early and Middle Miocene prochoreses of forms that had a North Pacific origin into the North Atlantic by way of the Panamanian Isthmus region must be acknowledged as probable. In that event, of course, the extreme rarity of Mya finds in the Middle Miocene deposits of the southern part of the Pacific littoral of North America becomes difficult to explain.

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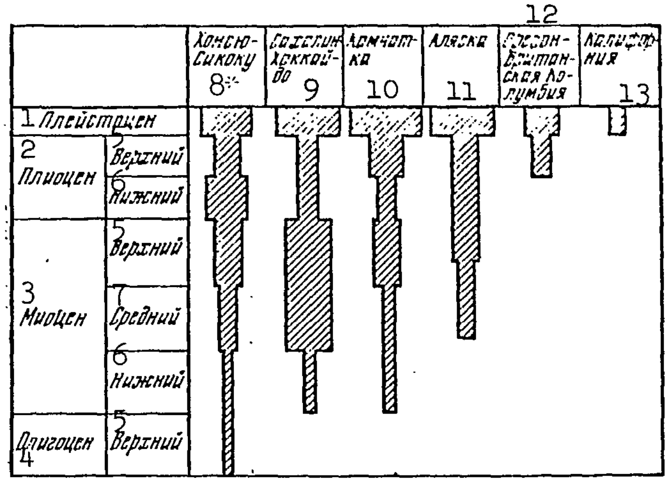

Fig. 4. Chronostratigraphic range of Neptunea s. str. in the Cenozoic of the North Pacific [after Nelson, 1978 with amendments]

Key:
1 - Pleistocene
2 - Pliocene
3 - Miocene
4 - Oligocene
5 - Upper
6 - Lower
7 - Middle
8 - Honshu-Shikoku
9 - Sakhalin-Hokkaido
10 - Kamchatka
11 - Alaska
12 - Oregon-British Columbia
13 - California

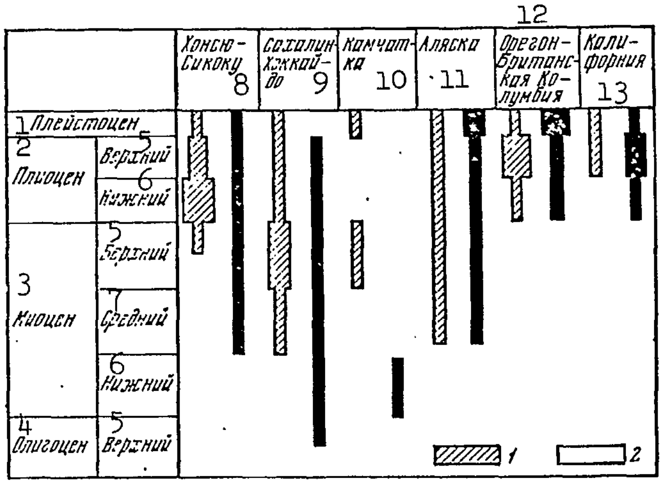

Fig. 5. Chronostratigraphic range of (1) *Neptunea* (*Sulcosipho*) and (2) *Neptunea* (*Golikovia*) in the Cenozoic of the North Pacific [after Nelson, 1978 with amendments].

Key:

1 - Pleistocene
2 - Pliocene
3 - Miocene
4 - Oligocene
5 - Upper
6 - Lower
7 - Middle
8 - Honshu-Shikoku
9 - Sakhalin-Hokkaido
10 - Kamchatka
11 - Alaska
12 - Oregon-British Columbia
13 - California

The history of Neptunea. Another group of molluscs, the initial stages of whose formation are associated with the Paleogene Northern Japan-Sakhalin Province, is the genus *Neptunea* [Hopkins, 1959; Golikov, 1963; Strauch, 1972; Nelson, 1973, 1977, 1978]. Confined to this region are the most ancient fossil finds of representatives of all three *Neptunae* subgenera: *Neptunea* s. str., *Sulcosipho* and *Golikovia* (figs. 4,5)[7]. As early as the Early Oligocene, the first species of

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[7] The data depicted in fig. 4 do not contradict this conclusion, as the Oligocene finds of *Neptunea* in the "Honshu-Shikoku" region originate precisely from the northern part of Honshu which is included within the Northern Japan-Sakhalin Paleogene Province.

N. (N.) pribiloffensis (Dall) group are singled out. Until the end of the Oligocene the geographic range of the genus was limited to the Shikoku, Honshu, Hokkaido and Sakhalin regions. In the Early Miocene it expanded as far as Kamchatka. Off southern Alaska the first N. (Neptunea), N. (Sulcosipho) and N. (Golikovia) are seen in the Middle Miocene (Yakataga and Topsy Formations). The two latter subgenera are reported in British Columbia, Washington and Oregon, dating from the Lower Pleistocene deposits, and the nominative subgenus from the Upper Pliocene deposits. Off California, N. (Golikovia) are reported as dating from the Early Pliocene, N. (Sulcosipho) - from the Late Pliocene, and N. (Neptunea) - from the Pleistocene. As will be seen, the history of Neptunea in the North Pacific very closely resembles that of Mya.

The history of the Clinocardiinae. Data published by the author [Kafanov, 1974b,c, 1976; Kafanov, 1979] show that the history of this group of molluscs is as follows.

The oldest representatives of the sub-family are assigned to the genus Ciliatocardium (fig. 6). At the present time, the immediate ancestors of this genus have not been ascertained and the initial stages in the phylogenesis of the group are almost wholly problematic. Most probably, Ciliatocardium owes its origin to certain Early Paleogene Trachycardiinae. Pointing to this, in particular, are the structural peculiarities of the costae of the first fossil representatives of the genus and the rudiments of acicular or spiny costal ornamentation (a typical character of the Trachycardiinae), observed in juvenile individuals and from time to time, in adult Ciliatocardium specimens - the contemporaneous C. ciliatum (Fabricius).

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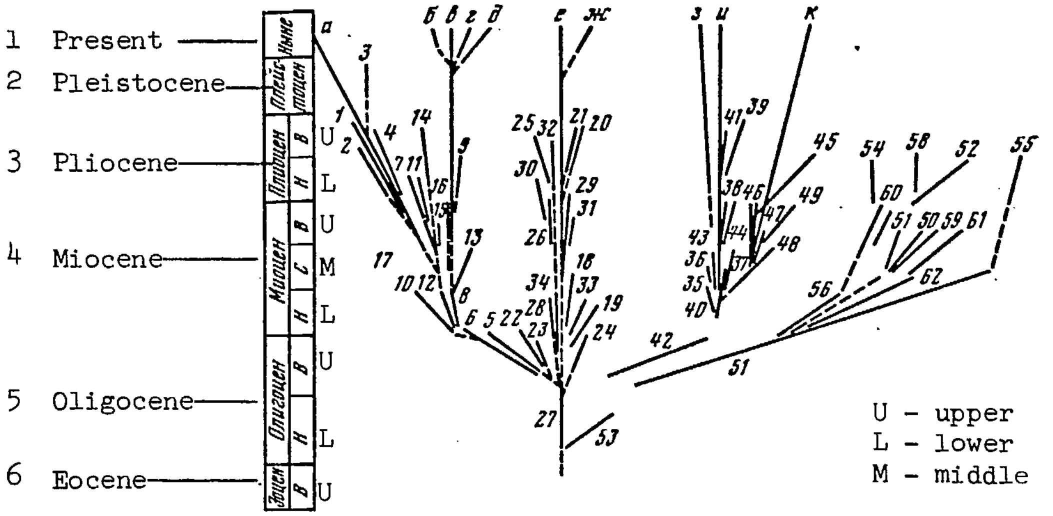

Fig. 6. Schematic representation of the phylogeny of the Clinocardiinae.
The numerals denote the fossil representatives of the sub-family (check list not given), the letters - the present representatives:
а — *Clinocardium nuttallii* (Conrad); б — *Keenocardium blandum* (Gould); в — *K. californiense* (Deshayes); г — *K. buelowi* (Rolle); д — *K. fucanum* (Dall); е — *Ciliatocardium ciliatum* (Fabricius); ж — *C. likharevi* Kafanov; з — *Serripes laperousii* (Deshayes); и — *S. groenlandicus* (Bruguiere); к — *Yagudinella notabilis* (Sowerby)

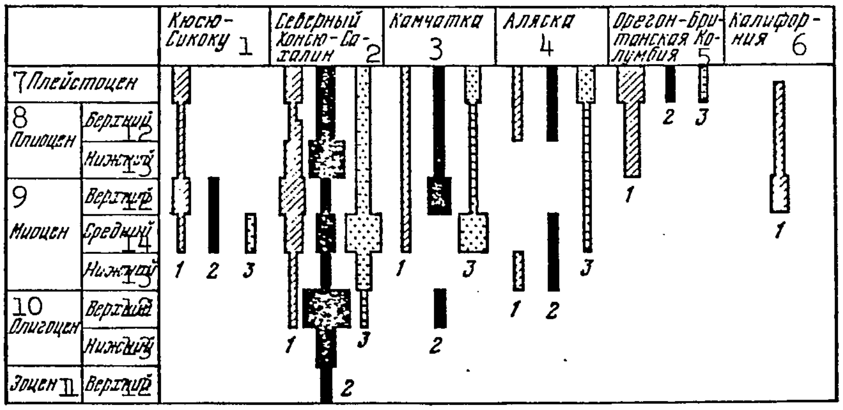

Fig. 7. Chronostratigraphic distribution of the genera (1) Keenocardium, (2) Ciliatocardium and (3) Serripes in the Cenozoic of the North Pacific.
Key: 1. Kyushu Shikoku, 2. Northern Honshu-Sakhalin, 3. Kamchatka,
4. Alaska, 5. Oregon-British Columbia, 6. California,
7. Pleistocene, 8. Pliocene, 9. Miocene, 10. Oligocene,
11. Eocene, 12. Upper, 13. Lower, 14. Middle.

The author linked the initial stages in the emergence of *Ciliatocardium* with the Paleogene basins of northern Japan and Sakhalin [Kafanov, 1974b]. Taking the opposite position to this, Savitskii [1978] maintained that *Ciliatocardium* is the youngest group of molluscs and that its emergence in the Northern Japan-Sakhalin Province dates only from the Early Miocene. Recent data on the geological history of the genus make it possible to fill in the details of the overall picture of its evolution (figs. 7,8).

The greatest diversity of Paleogene *Ciliatocardium* spp. is confined to Sakhalin. Even in the upper half of the Krasnopolevian suite in the central part of the western Sakhalin sedimentation basin (Middle?-Late Eocene) there are numerous minute *C. asagaiense* (Makiyama), which are widely disseminated in the deposits of the
Shebuna and Lesogorsk stratigraphic horizons of southern Sakhalin 157
(Late Eocene-Oligocene). The upper boundary of the stratigraphic range of the species on Sakhalin is the roof of the Srednearakai sub-suite (Oligocene).

C. asagaiense, described from the Asagaya Formation and widely developed in Oligocene deposits of the Pacific coast of the northern half of central Honshu, brings together the Paleogene *Ciliatocardium* faunas of Sakhalin and northern Japan. Moreover, in the upper half of the Gastellovskaya suite on Sakhalin, fossil remains of *C.* cfr. *makiyamae* (Kamada) are found, the type locality of which is also placed within the Asagaya Formation. Outside of Sakhalin and northern Japan, Paleogene remains of *Ciliatocardium* spp. have been authentically found only in the upper part of the Tigil' series in western Kamchatka - *C. snatolense* (Krishtofovich).

Thus, the waters which covered the present territories of Sakhalin and northern Japan in Paleogene time must be presumed to have been the centre of origin and dispersion of the genus. At the same time, some differences are to be seen in the composition of the *Ciliatocardium* fauna in these regions. An endemic *C. mutuense* (Nomura et Hatai) is present in the Oligocene Isomatsu Formation on northern Honshu and, in the northern part of Sakhalin (the Shmidt Peninsula), the deposits of the Machigarskaya suite contain a unique assemblage of the species, including *C. matchgarense* (Makiyama), *C. schmidti* (Khramova) and *C. yamasakii* (Makiyama). Consequently, whereas the initial appearance of the *Ciliatocardium* spp. is confined to the second half of the Eocene, the evolution and flourishing of the genus fall within the Oligocene. It was precisely at this time that, concurrent with a substantial widening of the geographic range, it attained its maximum species diversity.

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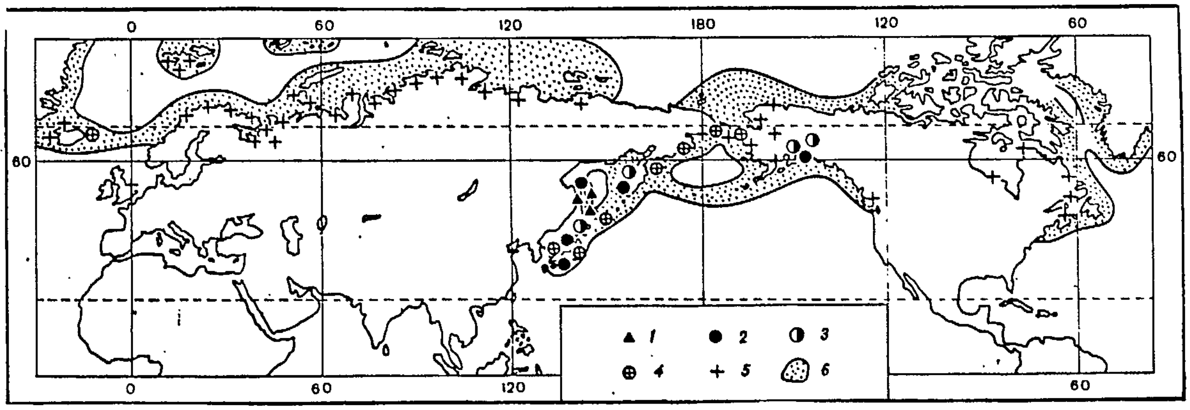

Fig. 8. Geochronological and geographic range of *Ciliatocardium*.

1 - Eocene; 2 - Oligocene; 3 - Miocene; 4 - Pliocene;
5 - Plio-Pleistocene and Pleistocene; 6 - present range.

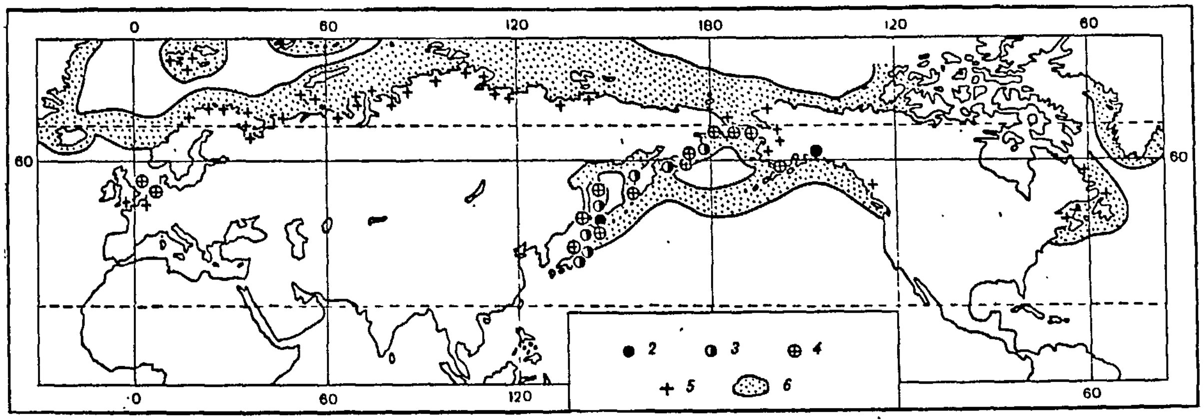

Fig. 9. Geochronological and geographic range of Serripes.

1 - Eocene; 2 - Oligocene; 3 - Miocene; 4 - Pliocene; 5 - Plio-Pleistocene and Pleistocene; 6 - present range.

The Miocene stage of evolution of Ciliatocardium is fixed quite clearly in the geological record . On Sakhalin, C. shinjiense (Yokoyama) is found in the Bora suite and the second half of the Dagi suite, while a massive representative of the genus, which has not been described but is 3 to 4 times larger than the Oligocene spp., occurs in the upper regions of the Arakai suite and the lower subsuite of the Bora suite; on Hokkaido, C. ainuanum (Yokoyama) is found in the Haboro Formation.

In the Late Miocene (lower part of the Maruyama suite), finds of the Neogene subspecies C. ciliatum - now a widely disseminated boreal-arctic species - were recorded for the first time. Together with C. shinjiense it brings together the Miocene Ciliatocardium fauna of Sakhalin and Japan. On Kamchatka, representatives of the genus are rare and often problematic.

At the beginning of the Miocene the first prochoreses of 158
Ciliatocardium spp. towards the North Pacific coast of America were accomplished, as evidenced by finds of *C. yakatagense* (Clark) in the upper(?) part of Poul Creek Formation in Southern Alaska. However, in the northeastern part of the Pacific *Ciliatocardium* did not become widely distributed. There, the southern limit of the geographic range of the genus did not and does not currently extend beyond the coasts of British Columbia (Vancouver Island). Except for *C. yakatagense*, all the positive finds in the Neogene are limited to the presence of *C. ciliatum* in the Beringian beds of the Pribiloff Islands.

The Pliocene history of the genus is also of great interest. In the Early Pliocene on Sakhalin - beds containing *Fortipecten takahashii* Yokoyama - *C. uyemurai* (Kanehara) is fairly widespread. This species is distributed everywhere in the Pliocene deposits of southern and central Sakhalin (on the east and west coasts). Its dimensions make it one of the largest representatives of the genus. It is characterised by clearly defined diagnostic features and can serve as a zonal species of the Pomyrskaya stratigraphic horizon. In northern and northeastern Honshu there were the endemic form *C. hataii* (Hasayaka) - the Ishiguma Formation, and *C. iwatense* (Chinzei) - the Kubo Formation. At the time of either the Late Miocene Nuvok Transgression or the Pliocene Beringian Transgression, *C. ciliatum* gained access to the Polar Basin by way of the Bering Strait region, after occupying vast expanses of the North Atlantic Shelf and the shelves of the epicontinental seas of the Arctic Ocean.

Thus, it can be argued that *Ciliatocardium* had its beginnings in the Northern Japan-Sakhalin Paleoprovince in the Eocene - Oligocene and became widely distributed in the Neogene. Throughout the entire geological history of the genus, new species that had a relatively narrow stratigraphic range (Division-Subdivision) were continually forming.

In the Late Oligocene three other genera of the sub-family *Clinocardiinae* are seen to stand apart from the genus *Ciliatocardium*: *Keenocardium*, *Serripes* and *Profulvia* (figs. 9-11). The main characteristics of their evolution in the Paleogene-Neogene basins of the North Pacific are similar to those of *Ciliatocardium*.

The species *K. hopkinsi* (Kanno) and *P. hamiltonense* (Clark), reported from the Late Oligocene-Early Miocene Poul Creek Formation in Southern Alaska, and also *C. yakatagense*, are substantially different from the Asiatic representatives of the respective genera. This affords a basis for assuming that at the end of the Paleogene and the beginning of the Neogene there existed off Southern Alaska a special faunistic centre, in which the Northern Japan-Sakhalin Paleogene molluscan fauna became transformed. Serving as one of the grounds for this assumption is the fact that all the American Neogene *Keenocardium* spp. bear a resemblance to *K. hopkinsi*, while differing essentially from the Asiatic species of the genus.

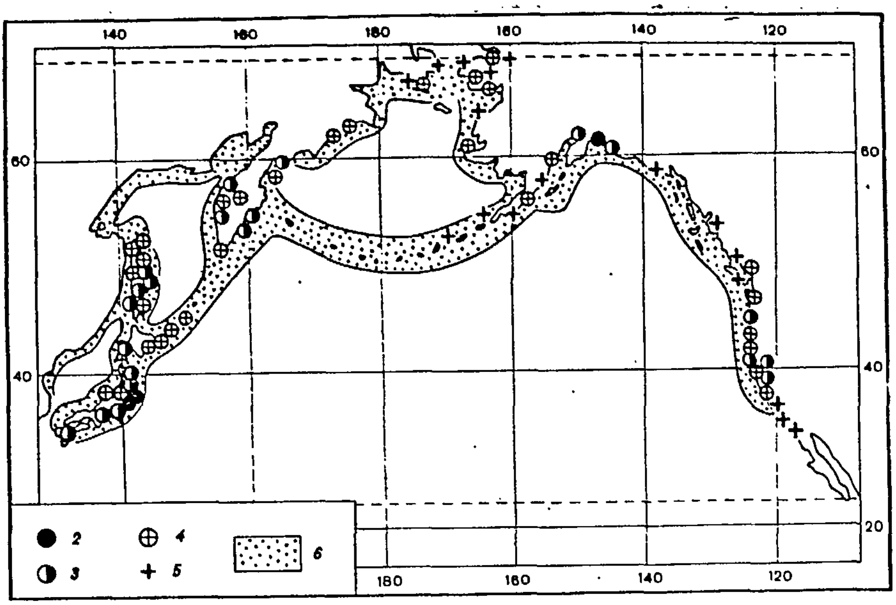

Fig. 10. Geochronological and geographic distribution of Keenocardium. The symbols are the same as in fig. 8.

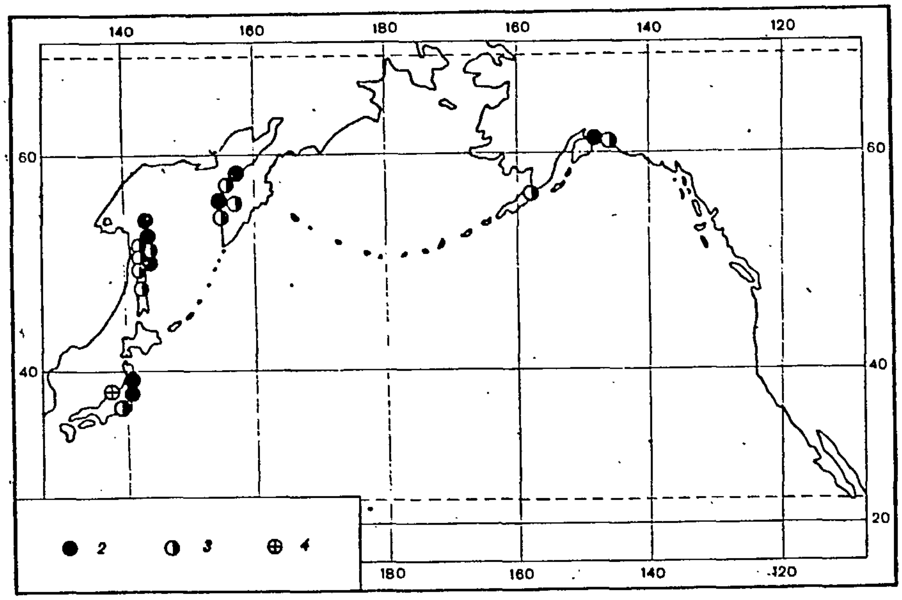

Fig. 11. Geochronological and geographic distribution of Profulvia. The symbols are the same as in fig. 8.

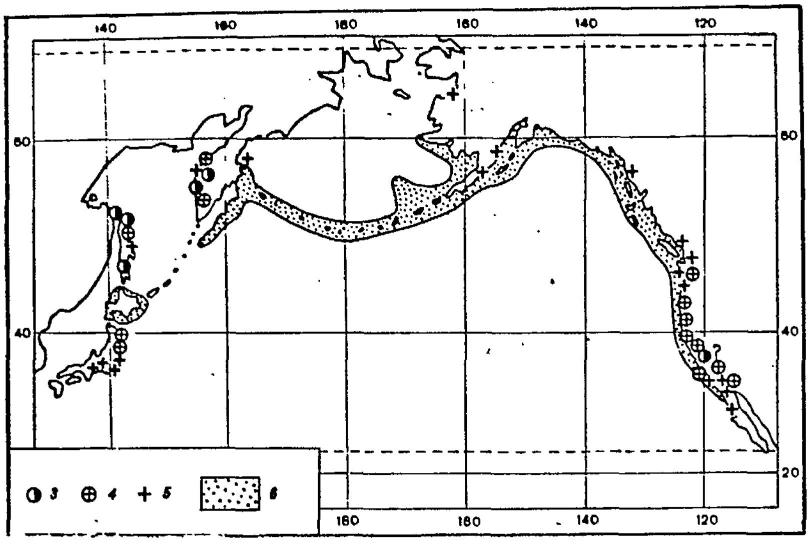

Fig. 12. Geochronological and geographic distribution of <u>Clinocardium</u>. The symbols are the same as in Fig. 8.

There are two opposite points of view with respect to the geological history of <u>Clinocardium</u>. Up to now, fossil finds of <u>Cl</u>. <u>nuttallii</u> and in general, of all the true <u>Clinocardium</u> spp., in the Far East have been authentically reported only from the Pleistocene deposits of Sakhalin and Kamchatka [Slodkevich, 1938]. Kilmer [1973], after making a special study of the problem of the geological and geographic distribution of <u>Cl</u>. <u>nuttallii</u>, reached the conclusion that all the indications of its presence in the Neogene deposits of the Far East were unsubstantiated. On the Pacific coast of North America the earliest finds of <u>Cl</u>. <u>nuttallii</u> were ascribed to the Upper Miocene San Pablo group - the "Margaritan Stage" of Addicott [1976] - in the San Francisco Bay region [Clark, 1915]. Nevertheless, Kilmer [personal communication] doubts the validity of identifiying these forms with <u>Cl</u>. <u>nuttallii</u> and ascribes the initial appearance of this species in the North American Neogene sections to the Pliocene Purisima and Etchegoin formations in California. Accordingly, the place of origin of the species is considered to be the North Pacific and the time of the transoceanic migrations, the Late Pliocene and the Pleistocene.

We discovered Cl. nuttallii in the deposits of the Il'inskaya and Enemten suites of the Tochilo geological section of Western Kamchatka, and in those of the Upper Due suite on Sakhalin. In view of Cl. (Fuscocardium) cfr. pseudofastosum (Nomura) also being 161 reported from the Il'inskaya suite and a new, as yet undescribed, species of Clinocardium s. str. being reported from the Lower Maruyama subsuite, the time of appearance of the genus must be considered to be the middle of the Miocene, and the origin of its trans-Pacific migrations is ascribed to the Late Miocene (fig. 12). Just such a pattern of migration by Clinocardium was suggested by myself in an earlier article [Kafanov, 1974b].

As will be seen, the three groups of molluscs discussed have a number of similar characteristics with respect to their geographic and geological distribution. An analysis of these characteristics will be furnished below.

The Paleogene prochoreses. In the Paleogene, mainly during the first half of it, there occurred extensive bilateral prochoreses of molluscan faunas between the Asiatic and American coasts of the northern part of the Pacific (fig. 13, a,b). This is indicated in a large number of paleontological and biogeographic studies [Chamberlin, Salisbury, 1914; Dall, 1921; Woodring, 1926; Tegland, 1933; Davies, 1934; Hatai, 1936, 1939; Durham, 1944; Krishtofovich, 1954, 1969; Uozumi, 1957; Durham, Sasa, 1961; Masuda, 1962; MacNeil, 1965, 1973; Shikama, 1967; Borzunova et al., 1969; Pronina, 1969; Kamada, 1973; Chelebaeva et al., 1974; Addicott, 1976; Kilmer, 1978; Nelson, 1978; and others]. The migration routes most probably extended along the southern margin of the Komandorskii-Aleutian island arc. Pronin [1973] considers that the pre-Neogene unconformity and the stratigraphic breaks at the Paleogene-Neogene boundary, which were recorded both in the vicinity of the Aleutians and the Komandorskie Islands, attest to the existence there of a vast area of land at the end of the Oligocene and the beginning of the Miocene.

It is thought that a continental regime also prevailed at that time within the Kurile-Kamchatka Chain [Sergeev, 1963; Goryachev, 1965]. If these findings are corroborated, then it will probably be necessary to conclude that the origination of the Paleogene-Neogene Asiatic-American prochoreses of molluscs and other groups of benthic animals may have been linked to a greater degree with northern Japan than with Sakhalin.

The diversity of the molluscan species in the southern part of the North Pacific (Japan and California) increased on account of the links that were preserved during the Paleogene with the faunas of the Tethys [Davies, 1934; Keen, 1950; Mizuno, 1964a; Hirayama, 1973] and the Atlantic [Schenck and Reinhart, 1938; Hertlein, 1941;

Durham, 1950; Durham and Allison, 1960; Woodring, 1966]. A part of the groups migrated from the Pacific coast of North America to Japan. Thus, the Cassididae in Japan (to latitude 44° N) date from the Early Miocene and are represented by eight species. Today, 19 Cassididae spp. are known to be present there but these do not extend northwards of southern Honshu (not beyond latitude 35° N). In California, Oregon, Washington and southeastern Alaska, this family is known to date from the Late Cretaceous-Early Eocene (more than 16 species), but contemporaneous forms are found only to the south of latitude 32° N [Kanno, 1973]. Judging from the fossil record [Schenck, 1936; Slodkevich, 1967], Acila (Truncacila) gained access to Kamchatka and Sakhalin in the Early Miocene, also from northwestern America.

Prior to the beginning of the Neogene, dissimilar tendencies were 162 manifested in the change in the diversity of the species constituting the molluscan faunas of Japan and California; these faunas are now situated at approximately the same latitude (fig. 2, b). In the Eocene the number of species off the Californian coast greatly exceeded the number off the coasts of Japan. The reasons for this have not yet been clarified. Kilmer [1978] also concludes that in the Eocene the number of genera and subgenera in Japan was less than the number in the Late Cretaceous and that subsequently it began to increase rapidly. In his opinion, Japan broke away from the Asian mainland in the Oligocene and began to move southeastwards, into a region washed by a warm paleo-Kuroshio Current. In the process, the archipelago sealed off the young Sea of Japan from the open ocean. If we accept the phenomenological "Wallace principle" (an increase in the diversity of the species with movement from the high latitudes towards the tropics), then the differences in the richness of the molluscan faunas of Japan and California can also be attributed to paleoclimatic causes. In the Eocene, California was situated in lower latitudes than were 163 the Japanese islands (cf. figs. 1, 2,a).

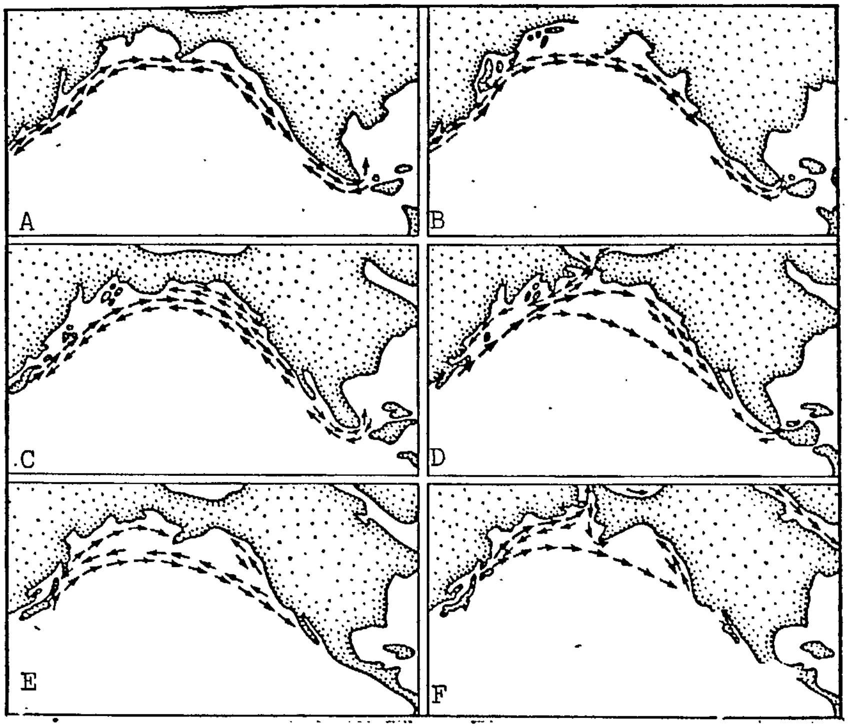

Fig. 13. Scheme of the Cenozoic prochoreses of the molluscan faunas inhabiting the North Pacific shelf regions.

A - Eocene;
B - Oligocene;
C - Early-Middle Miocene;
D - Late Miocene;
E - Early Pliocene;
F - Late Pliocene..

The thickness of the arrows denotes the relative intensity of the prochoreses.

There are important findings compelling one to assume that prochoreses are more easily accomplished in the direction of regions with a lower diversity of species and where the ecological niches are not as fully occupied [Briggs, 1974b; Kafanov, 1978, 1979a,b,d]. In the event that this is so it would be necessary to assume that, in the Eocene, the orientation of the prochoreses was principally unilateral: from the Pacific coast of North America towards Sakhalin and Japan. This is indicated, in particular, for several groups of molluscs, for example the Cassididae and *Acila* (*Truncacila*). Overall, however, the picture of the Eocene prochoreses indicates an intensive bilateral interchange of faunas between Asiatic and North American coasts. This was possibly linked with currents not yet established which constituted the North Pacific circulation in later stages of geological history.

As was indicated earlier, the Oligocene temperature minimum was more pronounced off the coast of California than off Japan. This led to a decrease in the diversity of the species making up the Californian molluscan fauna, which became relatively less rich than off the coasts of Japan. The appearance of the first elements originating from the Northern Japan-Sakhalin Paleogene centre of formation of molluscan faunas is recorded in the Gulf of Alaska region at the end of the Oligocene.

The Neogene prochoreses. At the end of the Paleogene and especially in the Early Miocene, unilateral prochoreses in the North Pacific from the Asiatic to the American coasts (fig. 13,b) are already in evidence. This is indicated in a number of groups of bivalve and gastropod molluscs [Grant and Gale, 1931; MacNeil, 1965; MacNeil et al., 1961], which include Acila (Lacia) [Slodkevich, 1967], Swiftopecten [Masuda, 1960, 1962, 1971, 1972, 1973; Kanno, 1971; Sinel'nikova, 1975], Ancillopsis (MacNeil, 1964), Turcicula (Noda, 1975) and Beringius (MacNeil, 1973). On the Pacific coast of North America the nautiloid genus Aturia is not found in deposits pre-dating Middle Miocene time [Schenck, 1931], but is noted in the Eocene of Japan [Yokoyama, 1911; Nagao, 1926]. Finally, the most striking examples are furnished by an analysis of the geochronological and geographic distribution of Mya, Neptunea and the Clinocardiinae (see above).

A similar picture emerges when we examine the Paleogene and Early Neogene Cardiidae of Japan, Sakhalin and the Pacific coast of North America [Kafanov and Popov, 1975]. In all of the groups whose distribution at that time was bounded by the northern part of the Pacific Ocean - the Clinocardiinae and Nemocardium (Keenaea), the earliest authentic fossil finds are confined to the Asiatic coast. The far eastern Laevicardium do not have analogues among the North American forms. Schedocardia, Vasticardium, Nemocardium s. str. and Nemocardium (Pratulum), found in the Paleogene-Neogene deposits of North America, are derivatives of the Mesozoic-Cenozoic fauna of the 164
Tethys. Plagiocardium, Vepricardium, Fragum, Ctenocardia (Afrocardium), Nemocardium (Frigidocardium) and Nemocardium (Trifaricardium) are Indo-West Pacific relicts of the Tethys (or recent derivatives of the latter)

and are not noted in North America. At the end of the Oligocene a very small number of representatives of the genus Profulvia (earlier - the "Papyridea") gained access to Alaska from the northwestern Pacific. Thus, analysis of the geographic and geochronological distribution of the Cardiidae confirms the principally unilateral character of the prochoreses in the Late Paleogene-Early Neogene of the North Pacific.

Beginning with the Early Miocene an approximate parity was established between the number of species of bivalve molluscs on the Asiatic and American coasts of the North Pacific (fig. 2,b). The temperature maximum of the first half of the Middle Miocene weakened the significance of the North Pacific circulation in the redistribution of heat, and this was accompanied by a revival of the bilateral migrations of the Asiatic and American components of the relatively thermophyllic fauna (fig. 13,c). Thus, the Middle Miocene faunistic assemblage of the Rakitinskaya suite in eastern Kamchatka is closely similar in generic composition and has both identical and similar species to those of the assemblages of the Middle Miocene Astoria Formation in Oregon and Washington and its equivalent Temblor Formation in California [Pronina, 1969]. The vast majority of the bivalve molluscs of the Middle Miocene Shumnovskaya suite of Paramushir Island are known to be present in the coeval deposits of Sakhalin, Kamchatka, Northern Japan and North America [Zhidkova et al., 1972]. Mytilus middendorffi, which is one of the index species of bivalve molluscs in the Middle Miocene deposits of the Pacific coast of North America

[Durham, 1953; MacNeil, 1973; Addicott, 1974], has been discovered in very large numbers at the base of the Goryachii Klyuchi suite* dating from the Middle Miocene in eastern Kamchatka [Krishtofovich, 1969]. The tropical-subtropical genus Liracassis was widely distributed at that time along both margins of the North Pacific [Kanno, 1973]. The penetration of the North American coasts by Nanaochlamys is possibly linked with the Middle Miocene [Sinel'nikova, 1975].

Paleographic changes occurred in the North Pacific in the second half of the Middle Miocene and the Late Miocene. The formation of the central part of the Aleutian Trench, which began approximately 10 million-14 million years ago [Ninkovich et al., 1969; Hays and Ninkovich, 1970], and was continued in the eastern half during the Pliocene [Huehne and Shor, 1969], the active growth of the island arcs and the submergence of the Bering-Chukotka Platform resulted in some redistribution of the sea currents and accentuated the climatic cooling that followed the Early-Middle Miocene temperature maximum. In the Southern Alaska region, the local coastal- and mountain valley Yakataga glaciation evolved. The "cold spot" in the northeastern part 165 of the Gulf of Alaska served as a barrier to the distribution of the relatively warm water elements and sharply weakened the faunistic links that had existed between the Asiatic and American coasts in the first half of the Middle Miocene (fig. 13,d).

It is to this period that Watkins [1974] dates the formation of the independent Oregon faunistic province or subregion, as it is called by Soviet investigators [Golikov and Kusakin, 1962; Kusakin,

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*The meaning of which is "hot springs" (Tr.).

1971; Vasilenko, 1974; Skarlato, 1974]. In particular, Skarlato [1974] considers one of the most striking characteristics of the contemporaneous Northern Japanese (Ainu) subregion to be the presence there of the endemic genus Crenomytilus. In the northeastern Pacific the earliest fossil finds of representatives of this genus are dated to the Oligocene (Kirker tuff, the upper part of the San-Emigdio Formation, and the San Juan Bautista Formation) and are confined to central and southern California. Moreover, the genus Crenomytilus is widely distributed in the Miocene of California and more or less common in the Pliocene deposits (Addicott, personal communication). In Japan it has been reported from the Oligocene [Nomura and Hatai, 1936], the Miocene [Yokoyama, 1925, a,b, 1926; Kuroda, 1931] and the Pliocene [Yokoyama, 1925,b] and, in contrast to the northeastern Pacific, it persisted there until now. It is probable that the trans-Pacific migrations by Crenomytilus underwent an abrupt weakening in the Late Miocene, since the Late Miocene and Pliocene American C. coalingensis, C. kewi and certain other species are differentiated from the Oligocene and Early Miocene species, both Japanese and North American.

These paleogeographic peculiarities of the end of the Middle and the whole of the Late Miocene were conducive to relatively cold water forms, such as Serripes groenlandicus [MacNeil, 1957] penetrating towards Southern Alaska. They contributed to the isolation of the American Neogene Keenocardium spp., and, analagously to the other groups of molluscs [Addicott, 1974], led to intensive southward migrations of the latter, even as far as southern California.

It is very important to note that the second half of the Middle Miocene and especially the Late Miocene was a period in which many groups of molluscs, including Mya, Neptunea and the Clinocardiinae (see above) gained access to the southern part of the northeastern Pacific. The direction and period of the Neogene prochoreses of Swiftopecten are reconstructed in like manner [Masuda, 1959, 1960, 1962, 1972, 1973; Kanno, 1971; Sinel'nikova, 1975]. Although this genus is younger (Early Miocene), the earliest fossil finds of the Californian species assigned to it are also dated to the Late Miocene [Adegoke, 1967b]. The same is indicated for Lyropecten and Patinopecten (Lituyapecten) [Addicott, 1974]. Addicott [1976] dates to the Early-Late Miocene the initial occurrence of Buccinum, Neptunea, Protothaca, Siliqua and certain other genera in the American geological sections, and Watkins [1974] dwells at length on the presence of molluscan assemblages of Japanese origin in the Upper Miocene deposits of California. Thus, on the basis of a number of characteristics, the 166 second half of the Middle Miocene and the Late Miocene must be considered to be the period in which the amphi-Pacific disjunctions began to form [Kafanov, 1974b]. Many Asiatic genera that originated later were unable to penetrate the northeastern Pacific any further than the southeastern part of the Gulf of Alaska. The protracted period of isolation (about 10 million years) of the Asiatic and American populations of Pacific species that had previously been widely distributed led to the origination of unique "pairs of species"

[Skarlato, 1955; Coan, 1969; Sirenka, 1973], although as regards the amphi-Pacific forms, an objective solution of the question "species or subspecies" is in the vast majority of cases almost impossible.

In the light of the foregoing discussion the views of Andriyashev [1939a,b, 1944], Skarlato [1955], D'yakonova [1955], Lindberg [1956, 1972] and Ushakov [Uschakov, 1971] with respect to the period in which the amphi-Pacific type of marine faunal distribution evolved, stand in need of some amendment. Aside from the repeated interchange of faunas that occurred between the northwestern and northeastern Pacific, the inhomogeneity which these authors noted with respect to the degree of difference between taxonomic categories in amphi-Pacific animals could also have been due to differences in the rate of morphological divergence of the various taxa and to the more ancient, principally Late Miocene, rather than Pleistocene, origin of the amphi-Pacific disjunctions. More recently, judging from the lists of bivalve molluscs [Keen, 1937; Skarlato, 1974, and also "The Zoological Record" for subsequent years], the high species-endemicity of the contemporaneous molluscan faunas of the Asiatic and American coasts of the North Pacific is being confirmed. The possibility that a part of the amphi-Pacific ranges is a consequence of the most recent anthropogenic introductions [Bonnot, 1935, et al.] should not be ruled out.

Currently, the predominant direction of the Pliocene prochoreses of the North Pacific molluscan faunas is not completely clear (fig. 13, e,f). Paleontological data, based principally on the Pectinidae, are disclosing not only Asiatic-North American [Grant and Gale, 1931; Masuda, 1959, 1971, 1972, 1973; MacNeil, 1967, 1973; Masuda and Addicott, 1970; Sinel'nikova, 1975] but also North American-Asiatic prochoreses [Masuda, 1962; MacNeil, 1967; Sinel'nikova, 1975]. It is highly probable that, as in the first half of the Middle Miocene, the latter were manifested to a greater degree at the time of the Pliocene climatic optimum. The beginning of this latter conforms approximately to the period when the deposits of the second half of the 4th packet of the Maruyama suite on Sakhalin accumulated.

The foregoing critical survey of the Cenozoic history of the molluscan faunas inhabiting the shelf regions of the North Pacific does not, of course, claim to be complete, and new paleontological data will perhaps modify our ideas concerning the time and direction 167 of prochoreses of certain groups of molluscs. Nevertheless, the main characteristics of the evolution of the Pacific molluscan faunas in the Cenozoic can already be considered to be more or less established. Included among these are the following.

Throughout the greater part of the Paleogene there was an extensive bilateral interchange of faunas between the Asiatic and American coasts of the North Pacific.

Since the end of the Paleogene and especially in the Early Miocene, principally unilateral prochoreses of molluscan faunas from the Asiatic to the American coast are observed. The revival of the opposite migrations occurred mainly at the time of the Miocene and Pliocene climatic optima.

The principally unilateral character of the Cenozoic prochoreses within the North Pacific was due to three main causes: (1) the character of the North Pacific circulation of waters, which had become established by the end of the Paleogene; (2) the success of the prochoreses accomplished in the direction of regions with a lower diversity of species and where the ecological niches were not as fully occupied; (3) the earlier process of transformation of the Paleogene Northern Japan-Sakhalin molluscan fauna and the acquisition by it of a relative "predilection for cold".

The evolution of the main part of the amphi-Pacific disjunctions is dated to the second half of the Middle and especially the Late Miocene.

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