

Trends in the Evolution of Baikal Amphipods and Evolutionary Parallels with some Marine Malacostracan Faunas

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I. SUMMARY

The taxonomically rich amphipod fauna of Lake Baikal (at present 257 described species and 74 subspecies) shows great ecological diversity and a variety of evolutionary directions. The main trends in the intralacustrine evolution of this group are: habitat partitioning by depth, substrate type or layer; trophic differentiation; differentiation by season of reproduction; transition to marsupial parasitism; the appearance of giant and dwarf forms; colonization of Baikal's gulfs; and geographical (allopatric) differentiation. Each of these ecological/evolutionary mechanisms operates at a different level in the taxonomic hierarchy. The prevalence of sympatric speciation in these amphipods is examined, and the occurrence of numerous cases of morphological convergence (parallelism) between Baikal and other, especially marine, amphipod faunas noted. Several examples of these parallelisms are given and are considered within the framework of nomogenetic evolution.

II. INTRODUCTION

The amphipods are among the most speciose groups within the macrofauna of Lake Baikal. To date, 257 species and 74 subspecies of amphipod have been described from this lake (Takhteev, 1997), only one of which is non-endemic or subendemic: the Palaearctic distributed *Gammarus lacustris* Sars, 1863, and this number constitutes almost 5% of the entire species diversity of the known freshwater amphipod fauna. Different groups within the amphipod fauna of Lake Baikal are at different evolutionary stages, some primitive, some advanced, and through studies of this fauna many evolutionary patterns can be identified.

However, until very recently, discussion of the mechanisms of speciation in Baikalian amphipods was conducted only in hypothetical terms, and while the diversity itself was enthusiastically catalogued by generations of taxonomists, the mechanisms whereby these forms arose remained poorly understood. This situation was due to two factors. First, evolutionary thought in Russia was long dominated by a dogmatic stereotype, namely, that speciation occurs only (or mainly) allopatrically. As a result, there was no tradition of diverse research on alternative speciation mechanisms. Secondly, modern approaches and technologies have been slow to become accepted and available to Russian biologists working in Baikal, and accordingly, very few karyological, genetic and molecular biological studies have been conducted on the amphipods of this lake (e.g. Salemaa and Kamaltynov, 1994; Mashiko *et al.*, 1997a, b; Ogarkov *et al.*, 1997). A non-speculative description of the mechanisms of speciation is impossible without such research.

Studies of the taxonomy of Baikal amphipods, their gross distribution patterns and ecological characteristics have been carried out since the 1940s (e.g. Bazikalova, 1945, 1948 a, b 1962, 1971, 1975; Bekman, 1959, 1983a, b, 1984, 1986; Mekhanikova and Takhteev, 1991; Tachteev, 1995; Tachteev, 1997; Takhteev and Mekhanikova, 1996; Weinberg and Kamaltynov, 1998a, b). For several species, biological parameters such as period of reproduction, growth rate, fertility, feeding, oxygen absorption ability, osmotic characteristics of the haemolymph, reaction to changes in hydrostatic pressure and thermopreferences have been investigated (Bazikalova, 1941, 1951, 1954; Bazikalova *et al.*, 1946a, b; Gavrilov, 1949; Bekman and Bazikalova, 1951; Bekman, 1962; Vilisova, 1962; Nikolayeva, 1964, 1967; Brauer *et al.*, 1980a, b; Rudstam *et al.*, 1992; Tachteev and Mekhanikova, 1993; Melnik *et al.*, 1993, 1995; Timofeev *et al.*, 1997; Zerbst-Boroffka *et al.*, 1998, 1999). Studies have also begun on the daily vertical migrations of various benthic species and the ecological role of these migrations (Bessolitsyna, 1999; Takhteev and Bessolitsyna, 1999). By identifying and defining trends in the intralacustrine evolution of this group of animals in Baikal, several striking parallels can be revealed between the development of Baikal's amphipod fauna and those of other water bodies, especially the sea.

One aspect that will be emphasized throughout this chapter is that the various evolutionary trends which are discussed below are often manifest at discrete levels within the taxonomic hierarchy: one trend may be expressed among species, another among genera, and yet another at the subspecies level. Similarly, the evolutionary trends seen among Baikal's amphipods have not proceeded uniformly: some pertain to a large set of species and genera, whereas others are observed in only a few taxa. However, it is also important to pay attention to the latter, as in other freshwater bodies these trends are sometimes much more evident. Some processes, for example the formation of a parasitic malacostracan fauna, are represented in Lake Baikal by earlier stages in comparison with the seas. Nonetheless, it is clear that in both cases this process has proceeded in a very similar direction.

This chapter utilizes information from literary sources and original data to present, for the first time, a descriptive synthesis of the basic trends of the intralacustrine evolution of the amphipods of Lake Baikal. Much of this information is dispersed among (sometimes obscure) publications in Russian, and is here gathered together and presented in English for the first time. First, several examples of evolutionary trends displayed by Baikal amphipods are presented, with emphasis on the, in many respects, parallel character of development of this fauna and amphipod faunas of the seas. Then, the evolutionary trends seen among the amphipods of Lake Baikal are interpreted within a nomogenetical evolutionary framework. It is hoped that this chapter will draw the attention of biologists to the unsolved problems and the rich potential of studies on the amphipod crustaceans of Lake Baikal.

III. BASIC TENDENCIES IN THE EVOLUTION OF BAIKALIAN AMPHIPODS

A. Bathymetric Segregation

The great depth of the lake, which is oxygenated throughout, offers many opportunities for bathymetric segregation, and this is shown by several polytypic and oligotypic genera of Baikal amphipods, e.g. the polytypic genus *Poekilogammarus* (Tachteew, 1995) and the genera *Acanthogammarus*, *Echiuopus*, *Eulimnogammarus* (*sensu* Bazikalova, 1945) and *Odontogammarus*, and also to a lesser degree in other genera. However, it is appropriate to mention here that the number of abyssal forms, those occurring at depths greater than 500 m, is insignificant. Although Bekman (1984) listed 18 such forms, ongoing research has reduced this list; with few exceptions Bekman's data included only species occurring rarely, and even those described from single occurrences, i.e. species whose true depth range is unknown. While the abyssal zone (> 500 m depth) might not be as well populated as previously believed, the shallower waters, especially those of the littoral and sublittoral

zones, harbour an amphipod fauna which is abundant and taxonomically diverse.

Most species and subspecies of amphipod can be placed in one of three groups: (i) littoral (coastal, strongly stenobenthic, inhabiting only the first few metres of depth); (ii) sublittoral (found in the tens of metres of depth, and which do not occur in shallow waters or extreme depths; and (iii) those taxa that are eurybenthic and inhabit a wide range of depths, often hundreds of metres, but may sometimes be encountered even in the sublittoral zone.

Although quantitative ecological studies are few, several examples of bathymetric segregation, where different species inhabit different depth ranges, have been documented. The depth ranges of these species often overlap, but usually one species, or subset of a species, prevails at shallower depths and a different species, or subset thereof, prevails at greater depths. For example, two species of the genus *Garjajewia*, *G. cabanisii* (Dybowsky, 1874) and *G. sarsi* Sowinky, 1915 (Figure 1), co-occur over a significant range of depths, but the relative abundance of each varies with depth (Tachteev and Mekhanikova, 1996).

The disparity seen between the amphipod faunas of the littoral and abyssal zones is largely due to such depth partitioning. How this is achieved is

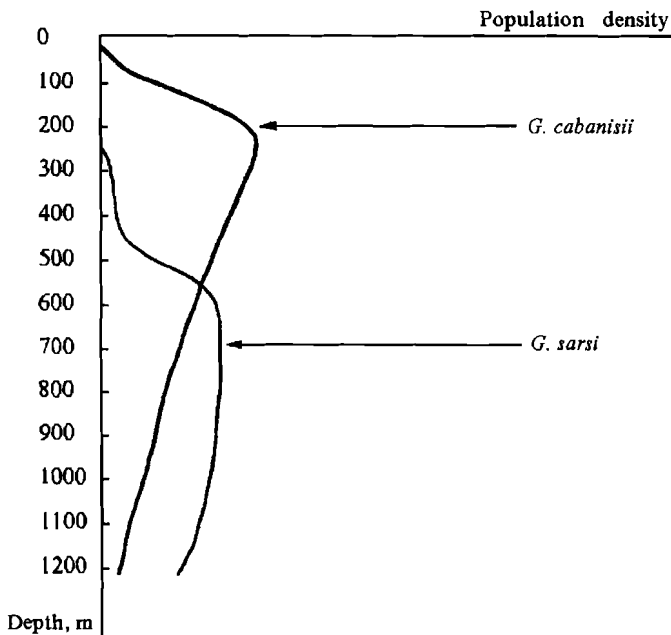


Fig. 1. Bathymetric partitioning shown by two allied species, *Garjajewia cabanisii* and *G. sarsi*.

unknown. Experimental studies have shown that in several littoral species of the genera *Pallasea* and *Eulimnogammarus*, the first changes in behaviour (increased locomotory activity) were evident only at pressures of 15 atmospheres or more, which corresponds to the pressure at depths in excess of 150 m (Brauer *et al.*, 1980b). As such, at the shallower depths inhabited by most amphipod species, differences in hydrostatic pressure play only a minor, if any, role in effecting isolation of species. Similarly, the increase of water depth during the formation of the Baikal basin seems not to have played a major role in the origin of the new forms of amphipods. In this context, it should be noted that Lake Baikal has become an ultra-deep-water lake (with depths more than 500 m) only since the Pleistocene (Popova *et al.*, 1989).

B. Differentiation by Season of Reproduction

This discussion is restricted to closely related forms, living at shallow depths, and which are characterized by temporal segregation of their periods of reproduction and brooding of eggs (Figure 2). For example, species such as *Gmelinoides fasciatus* (Stebbing, 1899), *Micruropus wohlii* (Dyb., 1874) and *Eulimnogammarus cyaneus* (Dyb., 1874) reproduce in the period from summer to autumn, whereas during the winter to spring period, other species, such as *Eulimnogammarus verrucosus* (Gerstfeldt, 1858), *E. viridis* (Dyb., 1874), *E. maackii* (Dyb., 1874), *E. marituji* (Bazikalova, 1945), *Pallasea cancellus* (Pallas,

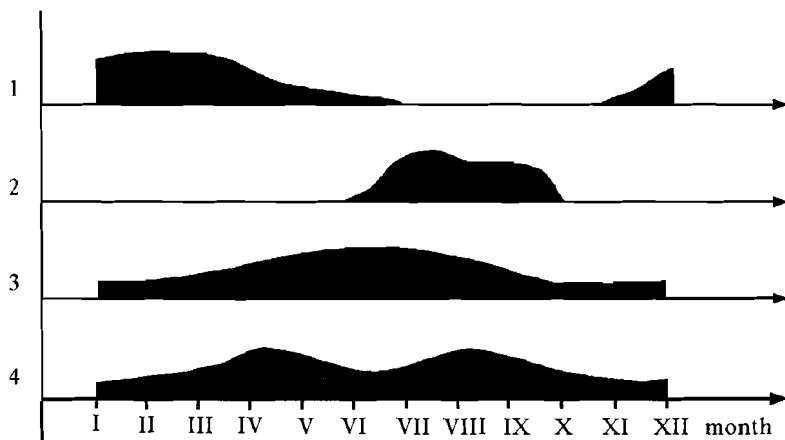


Fig. 2. Examples of differentiation by the season of reproduction. 1, *Eulimnogammarus viridis* (Dyb., 1874), a shallow-water inhabitant; 2, *E. cyaneus* (Dyb., 1874), a shallow-water inhabitant; 3, *Ommatogammarus albinus* (Dyb., 1874), a deep-water inhabitant; 4, *Macrohectopus branickii* (Dyb., 1874), a pelagic species. Based on data given in Bazikalova (1941) and Melnik *et al.* (1995).

1776) and *P. cancelloides* (Gerstf., 1858) (Bazikalova, 1941; Gavrilov, 1949), reproduce. In contrast to the shallow-water inhabitants, many deep-water, benthic amphipods, such as several species of *Garjajewia*, *Paragarjajewia*, *Ommatogammarus* and *Acanthogammarus*, and also the pelagic amphipod *Macrohectopus*, reproduce continuously during the year. However, even in these taxa one or two seasonal maxima in reproductive output are usually evident (Figure 2).

What cues determine the different seasonality of reproduction in these species, and what is the adaptive advantage of this behaviour? Bazikalova (1941) proposed that the temperature conditions of the reproductive period are encoded in the hereditary "memory" of a species. Bazikalova posited a relationship between a species' reproductive period and its phylogenetic history and, based on this, identified three discrete groups of amphipods: (i) species with a summer–autumn period of reproduction. These are phylogenetically more ancient, having originated in the warmer climatic conditions of the Tertiary Period; (ii) species with a winter–spring period of reproduction. These are younger, having originated under the conditions of decreasing temperature regime which took place during the Pleistocene; and (iii) species with year-round reproduction, primarily abyssal species. These taxa are phylogenetically the youngest, their evolutionary origin being connected to the rather recent transformation of Baikal into an ultra-deep-water lake.

Several major objections can be raised against this hypothesis. First, the representatives of the summer-reproducing genera *Hyaallelopsis*, *Micruropus* and *Gmelinoides* are not primitive, but are morphologically advanced forms. Bazikalova has subsequently acknowledged this fact. Secondly, the reproduction of many shallow-water species of the winter complex begins in September–October, at which time water temperatures exceed 6°C. This is warmer than the *c.* 3–4°C seen during May to June, when reproduction of species in the summer complex takes place. Thirdly, it would seem logical to expect that species with winter reproduction would be more cold-loving than those with summer reproduction. However, a study of thermal preferences of littoral Baikalian amphipods (Timofeev, unpublished) has shown that the winter-reproducing *Eulimnogammarus verrucosus* (preferred temperature 5–13°C) and *E. vittatus* (Dyb., 1874) (preferred temperature 9–13°C) are no more cold-loving than the summer-reproducing *E. cyaneus* (preferred temperature 5–13°C) and *Micruropus wohlii* (Dyb., 1874) (preferred temperature *c.* 11°C). Among the investigated species having a summer reproduction period, only for *Gmelinoides fasciatus* is the preferred range of temperature rather high (10–19°C).

Thus, the factors determining the timing of amphipod reproduction remain unknown. It is likely that not only temperature but also photoperiod is involved. However, the ecological implications of differentiation by season of reproduction are clear: it prevents the simultaneous output and synchronous development of the young of different species, and thus acts to reduce potential

interspecific competition, which might be expected to be especially intense among the similar-sized early life stages.

C. Segregation in Terms of Substrate Layer

Studies have revealed several examples of closely related forms, such as congeneric species, inhabiting different “floors”, such as benthic, suprabenthic and various layers within the bottom sediment. The various species occupying these different layers have diverged in body shape to different ecomorphs, as is seen in members of the genus *Plesiogammarus* (Figure 3). The initial members of this lineage, *P. zeinkowiczii* (Dyb., 1874) and *P. longicornis* Sow., 1915, are nectobenthic, while the final member, *P. brevis* Bazikalova, 1975, with two subspecies, is a burrower, tunnelling in the silt to a depth of 3 cm (Takhteev, 1997). The morphological changes associated with these different habitats include (Figure 3, left to right) a trend of reduction in the length of antenna I, the substitution of the plumose setae on uropods III by simple ones, and then the shortening of this pair of limbs and the gradual reduction of the eyes from large, dark structures of *P. zeinkowiczii* to the white and dotted structures seen in *P. brevis*.

Among the nectobenthic amphipods three ecomorphs can be distinguished:

- (i) permanent inhabitants of the near-bottom water layer. All representatives of the genera *Garjajewia*, *Paragarjajewia* and *Leptostenus*, most members of the genus *Poekilogammarus*, and also probably *Abyssogammarus*, are in this category. Characteristic features of this group include a weak, elongated body, long, thin and fragile extremities, and uropods with plentiful plumose setae. The shape of these animals most closely resembles that of the marine planktobionts;

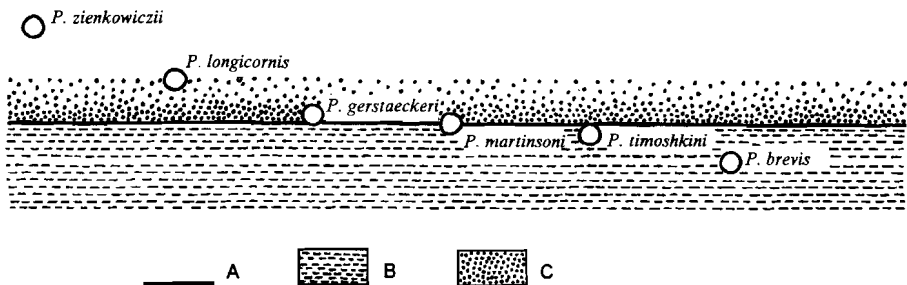


Fig. 3. Schematic representation of the partitioning of benthopelagic and benthic strata by several species of *Plesiogammarus*. A, Substrate surface; B, overlying sediment layer; C, pelogenic layer. Based on Takhteev (1997).

- (ii) species which are capable of walking on the bottom and of swimming significant distances. This group includes *Plesiogammarus zeinkowiczii* and species of the genus *Acanthogammarus*. Characteristics features are a large body size, strong cuticle and widely outstretched extremities;
- (iii) "plaice" species, which rest on their side but are capable of swimming significant distances. Representatives include members of the genera *Ceratogammarus* and *Parapallasea*. The body of these species exhibits a strong lateral flattening and their legs are not elongated.

Another version of layer differentiation is the transition of benthic amphipods to a nectobenthic lifestyle and, as a final stage of this process, to a pelagic lifestyle. Within Lake Baikal, the pelagic environment has been mastered by only one species, *Macrohectopus branickii* (Dyb., 1874), which belongs to the endemic family Macrohectopodidae Sow., 1915. Vinogradov (1988) assigns this species to the lifeform of "gnat-like, poorly mobile" crustaceans. It is probable that the transition to a pelagic lifestyle was made through the first group of nectobenthic animals mentioned above. The most recent view is that *Macrohectopus* originated from a form close to the common stem of the benthic genus *Pallasea* and the nectobenthic genus *Poekilogammarus* (Tachteew, 1995). Molecular investigations are necessary to confirm or refute this scenario.

D. Differentiation by Substrate

Partitioning of substrate has led to the evolution of several stenotopic groups of benthic amphipods: psammophiles (members of the genus *Crypturopus* and many species of *Micruropus*), pelophiles (series of species from the genera *Plesiogammarus*, *Macropereiopis* and *Homocerisca*); lithophiles (*Hyalellopsis* and many *Eulimnogammarus* species) and phytophiles [e.g. *Micruropus vortex vortex* (Dyb., 1874), which lives on the alga *Ulothrix zonata*].

One distinct group of amphipods is spongiophiles, and are found only on Baikal sponges of the family Lubomirskiidae. For the sponge *Lubomirskia baikalensis* (Pallas), the following species are characteristic: *Brandtia (Spinacanthus) parasitica* (Dyb., 1874), *Eulimnogammarus (Eurybiogammarus) violaceus* (Dyb., 1874) and *Poekilogammarus (Onychogammarus) erinaceus* Tachteew, 1992 (Kamaltynov *et al.*, 1993).

In the phytophile and spongiophile taxa, differentiation by substrate has been combined with trophic differentiation. Underwater observations have revealed that representatives of the genus *Pallasea* (*P. cancellus* and others) feed on the algae that they inhabit, and that the spongiophile *Brandtia parasitica* eats the tissue of the sponge on which it lives. It is also believed that the phytophile amphipods eat aquatic vegetation, although detailed studies are needed to confirm this. It has been suggested that the relationship between the sponge *Lubomirskia* and members of its consortium (which include the above-

named amphipods) is primarily trophic (stenophagic) and that stenotopy is incidental (Kamaltynov *et al.*, 1993). The same may also be true of certain phytophilic species.

In nectobenthic forms, differentiation by substrate is expressed poorly or is absent. For example, within the genus *Poekilogammarus*, the majority of species is characterized by a nectobenthic lifestyle, and only *P. crassimanus* (stones, frequently with sponges), *P. erinaceus* (only sponges) and *P. longipes* (black sand-silt substrates with detritus) are benthic forms (Tachteew, 1995).

E. Trophic Differentiation

Many species of amphipods are euryphagic and opportunistic generalists (see Morino *et al.*, this volume). However, one group has become specialized necrophages and has evolved morphological adaptations to search actively for the bodies of dead animals. This group includes species of the genera *Ommatogammarus* and *Polyacanthisca* (Tachteew, 1995). Scavengers are usually characterized by a compact, streamlined body, biting mouthparts, moderate to short pereopods with tenacious claws, and well-developed pleopods and uropods III bearing plumose setae.

In other species, notably members of the genus *Odontogammarus*, these adaptations are still at an early stage (Tachteew, 1999). In such taxa the pleopods and uropods are not well developed, but the mandible possesses a strongly developed molar edge and lacinia, and the maxilliped has a long palp. However, the body is not streamlined, but is slightly elongated, and whereas the claws of pereopods III–V are rather strong, those of pereopods VI and VII (or occasionally only pair VII) are greatly reduced and are unable to serve as organs of attachment. Based on these anatomical features, the *Odontogammarus* species can be placed in the trophic category of facultative scavengers.

Some parasitic species are highly specialized. For example, the members of the parasitic genus *Pachyschesis* (see below) are specialized for devouring the ova of their hosts (Tachteew and Mekhanikova, 1993).

F. Transition to Marsupial Parasitism

The genus *Pachyschesis* originated through a transition to marsupial parasitism and is presently placed in the same family as the Caspian genus *Iphigenella* (Bousfield, 1977). However, more recent studies have questioned this classification (*Pachyschesis* has evolved within Lake Baikal completely independently of the Caspian genera). It is therefore proposed to place this group in a newly erected endemic and monotypic family, the Pachyschesiidae (Tachteew, unpubl.). This grouping unites 17 supposed species, only four of which have been described.

These animals live in the gill cavity and marsupium of large nectobenthic amphipods. Many of the parasite species are host specific (Takhteev, unpubl.), an adaptation which may be viewed as an extreme version of differentiation by substrate. The basic morphological features of *Pachyschesis* include dwarf males, a thick spherical body in females, with an abundance of lipid inclusions, short legs with strong and tenacious claws, and poorly developed mouthparts.

G. Appearance of Giant Forms

The phenomenon of gigantism is present in many groups of Baikalian fauna and flora. Within the amphipods of the lake gigantism is displayed by many species of the genera *Acanthogammarus*, *Garjajewia*, *Abyssogammarus*, *Parapallasea* and *Ceratogammarus*, and also by *Plesiogammarus zienkowiezii* and several other amphipod species. Perhaps the most striking example is that of *Acanthogammarus grewingkii* (Dyb., 1874), in which body length can reach 6 cm in females and 9 cm in males.

Several theories have been proposed to explain the occurrence of gigantism in Baikal amphipods. However, until recently, few of these explanations were convincing or were based on actual material. Vereschagin (1940) believed that the gigantism of certain Baikal fauna and the great differences between the lake's fauna and that of other lakes in East Siberia was due to the presence of heavy isotopes of oxygen and some "unique dissolved substance" (which he does not name) in the abyssal waters of the lake. These assumptions have proved to be completely unfounded. Vereschagin (1940) also dismissed the possibility of dissolved gasses being involved in the presence of giant forms, and considered the composition and concentration of dissolved gasses in Baikal to be unremarkable, and typical of lakes in general.

An alternative explanation was provided by Bazikalova (1948a), who posited that the intralacustrine origin of giant (and dwarf) amphipods took place as an evolutionary response to predation pressure, especially that from fishes of the family Cottidae. By this logic, giant forms were difficult for the cottids to handle, whereas the small size of the dwarf forms enabled them to hide easily from predators within interstices in the rocky substrate of the Baikal littoral. This explanation is also unsatisfactory. Sideleva and Mechanikova (1990) investigated food specialization in six abyssal species of cottoid fishes. From stomach content analyses of 175 fish specimens they identified 18 amphipod species. Examination of this list reveals that 15 of the 18 species exceed 20 mm body length when mature, and that 12 of them exceed 30 mm. It is thus apparent that larger sized amphipods are favoured food items for cottoid fishes, and are actively selected over smaller individuals and species.

The most recent explanation for gigantism in Baikal invertebrates is that of Chapelle and Peck (1999), who compared Baikal and oceanic waters from polar to tropical zones, and obtained a positive correlation between the

number of giant species present and the degree of oxygen saturation in the water. The authors consider that in the highly oxygenated waters of Baikal and the polar seas, the haemolymph of large species is well able to supply sufficient oxygen to all sites of the body. Conversely, in waters with a low dissolved oxygen concentration, such as the tropical seas, normal interchange of gases is possible only for small species. Here, natural selection exerts pressure on the large forms and does not affect small ones. While this finding is undoubtedly important, in my opinion, gigantism among the amphipods of Lake Baikal cannot be explained exclusively in terms of oxygen availability. This question demands further study.

H. Appearance of Dwarf Forms (Hypomorphosis)

Dwarf forms have also appeared in various phyletic lineages. Examples include *Micruropus pusillus* Baz, 1962 (body length 1.5–2 mm), some other species of *Micruropus*, species of *Homocerisca*, and *Plesiogammarus martinsoni impransus* Takhteev, 1997 and *P. timoshkini* Takhteev, 1997. Both of the latter forms have evolved in the abyssal zone of northern Baikal, which is characterized by the most oligotrophic conditions throughout the lake (Takhteev, 1997).

Dwarf males are known in several ecologically diverse species, all of which exhibit some degree of hypomorphosis, e.g. the pelagic *Macrohectopus branickii*, some burrowing species of *Micruropus* and the parasitic genus *Pachyschesis* (Figure 4). Bekman (1958) proposed that the development of dwarf males facilitates an economy of resources, and thus a higher output of progeny. Studies of marsupial parasites of the genus *Pachyschesis* (Tachteev and Mekhanikova, 1993) lend strong support to this hypothesis: for this group, the habitat in the marsupium of the host means that not only food resources (eggs of the host) but also space are limiting factors.

I. Occupation of the Shallow Gulf Habitats of the Lake

The temperature and chemical conditions in the shallow-water gulfs (sors) differ greatly from those in the open waters of the lake. The sor habitats are protected from the influence of the open lake and are inhabited mainly by Euro-Siberian fauna (Kozhov, 1972; Sideleva; Kozhova *et al.*, this volume), including the Palaeoartic gammarid *Gammarus lacustris*. Few Baikal species live in the sors, and the amphipod fauna of these habitats comprise the most eurytopic species and those with high intraspecific variability (e.g. *Gmelinoides fasciatus*). It has been shown that species with high variability and intraspecific diversity are evolutionary the most stable (Severtsov, 1990), and such polymorphic Baikal species which show these characters are capable of extending their range beyond Baikal proper. For example, the Yenisey River is home to more than 10 species of Baikal amphipods (Bazikalova, 1945),

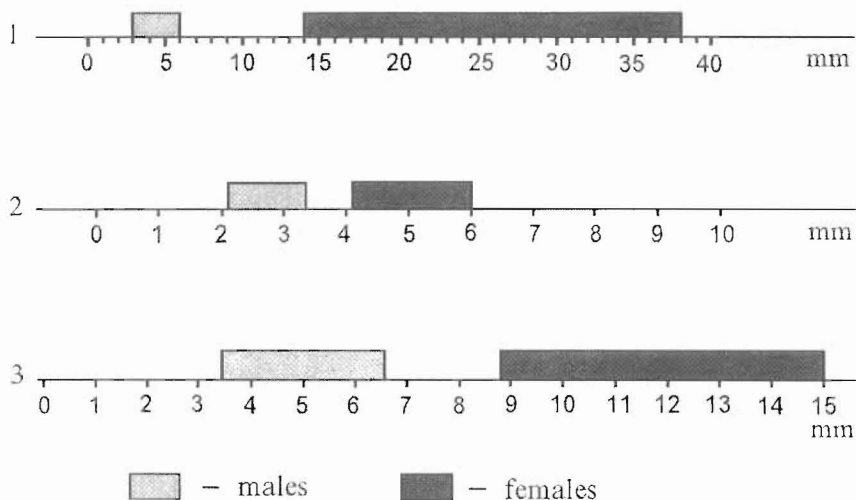


Fig. 4. Adult body size (length) in several species of Baikal amphipods in which dwarf males are present. 1, *Macrohectopus branickii*, a pelagic species; 2, *Micropurus ciliodorsalis* Sow., 1915, a burrowing psammophile; 3, *Pachyschesis acanthogammarii* Takhteev, sp. n., a parasitic species. Based on data given in Bekman (1958), Timoshkin *et al.* (1995) and Tachteev and Mekhanikova (1993).

including *E. cyaneus*, *E. viridis*, *G. fasciatus* and *M. wohlii*. *Eulimnogammarus viridis* has also been reported from Lakes Taymyr, Khantayskoye and Norilsk in the north of Siberia (Grese, 1957; Vershinin, 1960; Vershinin *et al.*, 1967). These examples provide the very few exceptions to the general rule of discrete distributions of Baikalian and Siberian faunas.

However, in those localities where the habitat is intermediate between sor-like and typically Baikalian, several Baikalian species can be found. Nevertheless, they are here most often represented by derived types, such as subspecies and varieties. For example, the nominotypical form of *Eulimnogammarus verrucosus verrucosus* inhabits the stony littoral zone of the open coast of Baikal, whereas in the intermediate habitat of the Chivyrkuy Gulf an unusual subspecies, *E. verrucosus olicacanthus* Baz., 1945, occurs. Similarly, *Poekilogammarus megonychus perpolitus* subsp. n. (Takhteev, 2000) inhabits the open waters of Baikal, but in Chivyrkuy Gulf and in the warmer and shallow waters of the southern half of Maloe More Strait is replaced by *P. megonychus megonychus* Sow., 1915.

The tendency for specially adapted forms to inhabit the sor zone is especially evident in the middle part of Chivyrkuy Gulf, where there are shallow-water bays that warm up during the summer (e.g. Zmeinaya Bay and Ongokonskaya Bay). The shallow waters of Zmeinaya Bay (<4 m depth) reach 20°C in August, and here Baikalian amphipod taxa are represented mostly by known

subspecies (*E. verrucosus oligacanthus*, *P. megonychus megonychus*) and by (presumed) new subspecies such as *E. lividus* subsp. n. and *Micruropus wohlii* subsp. n. (Tachteev, unpubl.). The high incidence of unique subspecies within the sor habitats can best be understood in terms of ongoing "classical" Darwinian microevolution taking place in representatives of diverse genera, presumably as an adaptation to the unique conditions of the sor habitat.

J. Geographical Differentiation

Several examples of geographical differentiation (allopatric speciation) are known among the Baikalian amphipods. The clearest examples are those at the shoal near the Ushkany Islands, where several local endemic forms have arisen under conditions of insular isolation. Typical examples include *Brandtia* (*Spinacanthus*) *insularis* (Dorogostajsky, 1930), *Hyalellopsis insularis* (Baz., 1936), *Micruropus macroconus tenuis* Baz., 1962, *M. pupilla* Baz., 1962 and *M. ushkani* Baz., 1945.

As noted earlier, allopatric speciation was for a long time the only evolutionary mechanism considered possible by Russian biologists, and this mechanism still dominates evolutionary thought world-wide. However, the author believes that allopatric speciation has not played a major role in the diversification and speciation of the Baikalian amphipod fauna. Instead, the major factor influencing the formation of the faunal differences among the separate regions of Baikal (Selenga region, Chivyrkuy Gulf, Olkhonskiye Vorota Strait, etc.) is not spatial isolation, but the ecological conditions unique to each of these regions.

Allopatric speciation requires that populations be physically separated, but analyses of the distribution of pelophylic species have concluded that within Lake Baikal there are no impassable barriers preventing species dispersal (Mekhanikova and Takhteev, 1991). In particular, studies in the northern basin of the lake found seven pelophylic species and one subspecies restricted to that basin. Throughout the lake, at depths greater than 25 m the substrate is dominated by silts, yet the thresholds between separate lake basins (northern, middle and southern) are located much deeper, at 250–500 m depth. The silt layer is thus continuous through all three basins and there are no barriers to the dispersal of pelophylic species. The restriction of these taxa to the northern basin cannot, therefore, be due to geographical isolation.

Mashiko *et al.* (1997a, b) found population-specific genetic differences within the littoral amphipod *Eulimnogammarus cyaneus* and concluded that "intralacustrine speciation by localised topographic changes played a substantial role in the steady increase of indigenous species in ancient lakes." It should be noted that, despite the genetic differences between populations, morphologically they all belong to a single species. At the same time, in the Angara River, which drains from Lake Baikal, there are two morphologically

distinct subspecies of *E. cyaneus*. The upper section of the Angara River is late Pleistocene in age, i.e. less than 15 000 years old (Popova *et al.*, 1989). Hence, the habitat conditions in the Angara River, even during its geologically short existence, have exerted a more substantial influence on the morphology of *E. cyaneus* than the numerous geological events connected to the formation of modern Baikal and the genetic divergence in *E. cyaneus* populations around the shoreline of the lake proper (see Mashiko, this volume). This supports the thesis that spatial isolation has played an insignificant role in the speciation of amphipods in Lake Baikal.

Speciation related to bathymetric and substrate differentiation is most often interpreted as being allopatric, but in relation to the amphipods, this view is incorrect. The majority of amphipod species is highly mobile and capable of extensive migrations. Furthermore, many benthic species (at least 25) make daily nocturnal migrations into the water column (Bessolitsyna, 1999; Takhteev and Bessolitsyna, 1999). These vertical migrations are made by both adult animals and young, and during the summer period the density of amphipod aggregations in the water column can reach 250 individuals m^{-3} . (To emphasize the point made in the paragraph above, *E. cyaneus* is one of the most common species in the nocturnal migratory complex of amphipods.) Carried by currents, migrants can come to rest a significant distance away from the place where they left the substrate. For example, consider that average speeds of horizontal currents in open Baikal during the ice-free period are c. $1.5\text{--}6\text{ cm s}^{-1}$ and during storms they can reach $10\text{--}18\text{ cm s}^{-1}$ (Shimaraev *et al.*, 1994). Simple calculations reveal that amphipods remaining in the water column at a current speed of 6 cm s^{-1} for only 5 h in a single night will travel in excess of 1 km. That such transportation of amphipods occurs is evinced by individuals of the benthic littoral-inhabiting *Micruropus wohlii* being found in the surface layers of open Baikal, where depths exceeded 400 m. Therefore, the complete isolation of populations in separate habitats or depth zones is exceedingly unlikely.

Bathymetric and habitat segregation are sometimes included under the umbrella of parapatric speciation (Martens, 1997). In the present author's opinion, this term is applicable only to poorly mobile aquatic animals, such as molluscs, where movement to an adjacent habitat patch is difficult. However, for mobile organisms, such as the amphipods, the patchy distribution of suitable habitat presents no barrier to the mixing of different populations. For such groups speciation can only be considered meaningfully when viewed as an allopatric or a sympatric mechanism. It would be more informative and interesting to examine the genetic mechanisms that result in speciation under these conditions – a metapopulation scenario, with essentially sympatric populations.

IV. PARALLEL (NOMOGENETIC) DEVELOPMENT OF THE BAIKALIAN AND MARINE MALOCOSTRACAN FAUNAS

The term "nomogenesis" was coined by the Russian scientist L.S. Berg to define an evolutionary process which proceeded on the basis of laws, as opposed to the widely accepted view of evolution as a causal process (tychogenesis), as characterized by the theory of Darwinian evolution (Berg, 1922; there are three English editions, including Berg, 1969).

The key theses of Berg's theory can be expressed as follows:

- (i) Evolution is not a casual, but a law-governed process whose direction is as predetermined as the direction of individual development of each organism (ontogenesis).
- (ii) Natural selection is not the main evolutionary factor, but acts only to eliminate those forms unsuited to the specific conditions of a given environment.
- (iii) The diversity of organisms arises under the influence of internal laws, which are inherent in the given group of a fauna or a flora (i.e. phylogenetic development is predetermined, just as the individual development of an organism is predetermined by its genetic programme).
- (iv) Many characters of an organism will be formed independently of natural selection, but can be supported or eliminated by it.
- (v) Parallelisms (evolutionary development in the same directions) are not a casual phenomenon in nature, but are completely normal and governed by laws.
- (vi) If parallelisms can be demonstrated within a certain group of animals or plants, it is possible to discern an evolutionary law for this group and to predict its future course.

The theory of nomogenesis certainly contains several incorrect hypotheses. However, its summary dismissal, most often by supporters of Darwinism and a synthetic theory of evolution, was premature and entailed the rejection of several reasonable ideas. For example, in Russia the ideas of nomogenesis have been applied only in the works of a rather small group of scientists, yet these studies have resulted in major advances in the development of a general theory of systems (Urmantsev, 1988).

Unfortunately, page limitations prevent deeper discussion here on the philosophy and logic of the theory of nomogenesis. One should at least note that it offers a seemingly high potential for developing a general evolutionary law for specific animal groups, such as the amphipods. Therefore, attention should be paid to any cases of parallel occurrence of the same morphological attributes seen in organisms inhabiting different water bodies, irrespective of whether or not these are environmentally similar.

Evolutionary parallels can be divided into three categories: ecological, phylogenetic and nomogenetic. However, the first and second categories are

but special cases of the third; they can be explained either by similar living conditions (first category) or by the close phyletic relationship of the organisms (second category). In contrast, nomogenetic parallels *per se* cannot be explained in terms of either reason. They reflect system laws ("refrains" *sensu* Meyen, 1978), according to which there is ordering of the diversity in nature. Thus, similar morphological characters can arise in amphipods which are related only distantly, or which live in completely different conditions.

How can nomogenetic similarities be distinguished from ecological ones? In the case of an ecological parallelism (convergence), correlation of an aggregate of morphological attributes is observed. Similar living conditions stimulate morphological changes in a given direction and this process is reflected in the concept of the life form. Some examples of ecologically caused evolutionary parallels between the faunas of amphipods of Lake Baikal and the sea are given in Table 1.

Table 1
Ecological parallels seen between Baikal amphipods and marine crustaceans

Ecological group	Lake Baikal	Marine habitats
Nectobenthic scavengers; compact active swimmers with a streamlined body	Genera <i>Ommatogammarus</i> , <i>Polyacanthisca</i> , partly <i>Odontogammarus</i>	<i>Hirondella gigas</i> Birst. et Vinogr., many species of the family Lysianassidae, etc.
Gnat-like pelagobionts	<i>Macrohectopus branickii</i>	Families Vitjazianidae, Hyperiopsideae (partly); genera <i>Eusirogenes</i> , <i>Pareusirogenes</i> , <i>Eurisella</i> , etc.
Burrowing psammophiles with a thick compact body	Genus <i>Crypturopus</i>	Genus <i>Niphargoides</i>
Burrowing pelophyles with a compact body	Genera <i>Micruropus</i> and <i>Macropereiopus</i>	Genus <i>Pontoporeia</i>
Burrowing amphipods with an elongate body and reduced uropods III	<i>Plesiogammaris brevis</i> (with two subspecies) and <i>P. timoshkinii</i>	Family Corophiidae; suborder Ingolfiellidae (extreme case)
Parasites of gill cavities and marsupial chambers of Malacostraca; poorly mobile crustaceans with tenacious claws	Genus <i>Pachyschesis</i>	Many Isopoda (e.g. Bopyridae); to a lesser extent the Amphipoda (e.g. the Caspian <i>Cardiophilus baeri</i> Sars, 1896)

Data are taken partly from Birstein and Romanova (1968), Osadchikh (1977), Ginetsinskaya and Dobrovol'skiy (1978), Müller (1989), Belyajev (1989), Vinogradov (1992), Tachteev (1995), Tachteev (1995) and Takhteev (1997).

In purely nomogenetic parallelisms, similar morphological features arise in animals of different lifeforms. These similar features are most often unique or are correlated with only a few other features in the morphology of the animal; the probability of the independent concurrence of a large set of attributes (not correlated with each other) is extremely insignificant. The nomogenetic similarity of organisms may be viewed as nature arriving at identical constructive "decisions" as the solution to different adaptive problems. In amphipods, examples of nomogenetic similarities can be found in the cuticular armature of the body surface, and the remainder of this chapter focuses on these examples.

The similarity in gross morphology between the Baikalian and Caspian amphipod faunas has long been recognized (Bazikalova, 1940) and has led to some Baikalian genera being placed within Caspian families (e.g. Bousfield, 1977). However, if in this case one assumes a common genesis of the fauna in both basins, then must one not similarly explain the equally striking similarity of armature of representatives of the Baikalian gammarid genus *Acanthogammarus* (family Acanthogammaridae; Bousfield, 1977), Titicacan amphipods of the genus *Hyalella* (family Orchestriidae) and even those members of the family Epimeriidae from the waters of the Antarctic Ocean (see Martens, 1997, Figure 3)?

An even more interesting case of nomogenetic similarity in the structure of the cuticular armature of the body is shown by the two pairs of species illustrated in Figure 5. In the Atlantic species *Laetmatophilus armatus* the metasomal segments are supplied by precisely the same vertically positioned teeth as seen in representatives of the Baikalian subgenus *Propachygammarus*, and also *Acanthogammarus maximus* (Garjajew, 1901) (the present author's unpublished revision of *A. maximus* places it within *Propachygammarus*, which is elevated to the rank of genus). The *Propachygammarus* taxa are ecologically diverse; *P. bicornis* is an endemic of the Olkhonskiye Vorota Strait and lives at shallow depths (35–40 cm) among clumps of aquatic vegetation, whereas *P. dryshenkoi* (Garj., 1901) and *P. lamellispinus* Baz., 1945 are mostly deep-water forms found on silt substrates. In the two species depicted in Figure 5a and b the antennae are arranged differently, and one can thus infer that they also function differently. These two species clearly belong to different life forms and no single adaptive interpretation can explain the formation of similar armature of segments of their bodies.

In the marine species *Pereionotus testudo*, the dorsal and marginal rows of eminences on the body are remarkably similar to those seen in Baikalian amphipods of the genus *Brandtia* (*sensu* Bazikalova, 1948) (Figure 5c, d). Species of this genus are usually found on stones and on sponges and are weakly mobile. However, they also show some similar characters of armature to some Baikalian species of the genus *Hyalellopsis*, which inhabit a wide spectrum of substrate types, from stones to silts (Bazikalova, 1945). In contrast, the marine amphipod species which occur on sponges sometimes have a completely smooth body [e.g. *Perrierella audouiniana* (Bate, 1857) or *Aristias*

neglectus Hansen, 1887; Lincoln, 1979, pp. 46–47, 60–61]. These examples comprise species with different lifestyles but similar armatures, and species with similar lifestyles but different armatures, and here also, an adaptive interpretation for the similarities seen in the body armature of these species is not obvious.

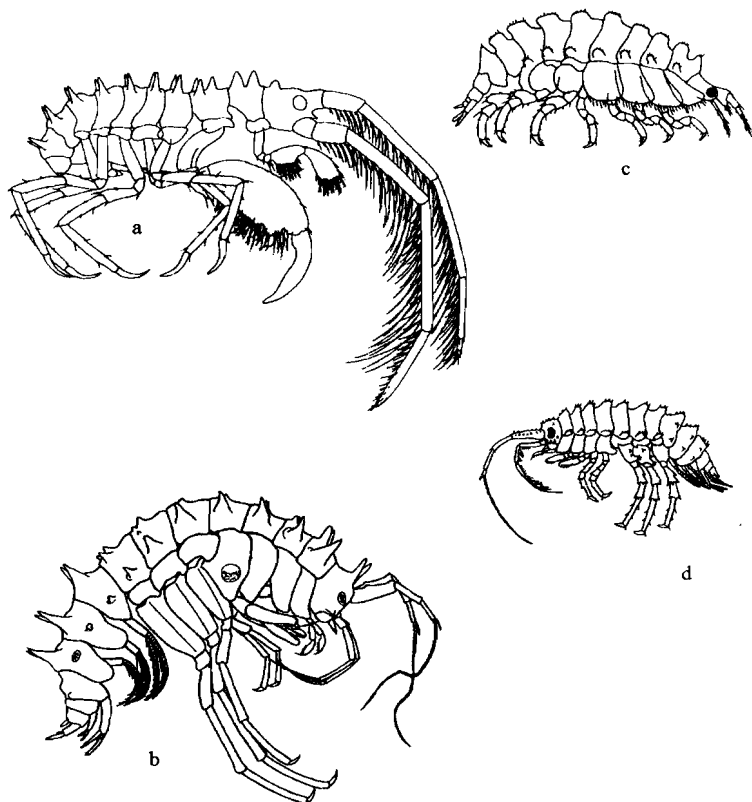


Fig. 5. Nomogenetical similarities in the character of the body armature of Baikol amphipods and marine malacostracan taxa. Similarities are evident between the dorsal row of eminences (a, b), and in the dorsal and lateral rows (c, d), despite the vast taxonomic and ecological differences between these component species pairs. (a) *Laetmatophilus armatus* (Norman, 1869) (family Podoceridae): a marine species, found in the north-east Atlantic, north and west Norway, the Bay of Biscay and the Mediterranean Sea, at depths of 35–900 m. Figure and data adapted from Lincoln (1979). (b) *Pallasea (Propachygammarus) bicornis* Dorogostajsky, 1930: a Baikol endemic, found only in the Olkhonskiye Vorota Strait at depths of 35–40 m; probably a phytophile. (c) *Pereionotus testudo* (Montague, 1808) (family Phliantidae): a marine species, found in the Mediterranean and Red Seas, and along the Atlantic coast of Europe, in the intertidal–shallow subtidal zone. Figure and data adapted from Lincoln (1979). (d) *Brandtia (Spinacanthus) parasitica* (Dybowsky, 1874): a Baikol endemic; a spongiophage, found only on sponges, at depths of 1–60 m. Figure adapted from Kamal'tynov *et al.* (1993).

Another example of parallelism is seen in the sharp, rear-directed teeth on the back edges of metasomal segments, which have arisen independently in the Baikalian genus *Pallasea* (nominative subgenus), the North Atlantic species *Gitanopsis bispinosa* (Boeck, 1871) (family Amphilochidae; Lincoln, 1979, Figure 73), the boreal-Atlantic *Melita gladiosa* Bate, 1862 (family Melitidae; Lincoln, 1979, Figure 141) and the circumpolar Antarctic *Gnathiphimedia sexdentata* (Schellenberg, 1926) (family Acanthozomatidae; Sieg and Wegele, 1990, Figure 277). It should be noted that the latter species inhabits depths greater than 700 m (Sieg and Wegele, 1990, p. 138), whereas the Baikalian *Pallasea* are phytophilic species inhabiting shallow waters.

Many other examples could be given, such as that of amphipods with a variety of lifestyles, but in which only one dorsal row of eminences is formed as flat keels, cut off in front and pointed behind. Among the Baikalian forms this is seen in *Carinogammarus waggii* (Dyb., 1874) (Bazikalova, 1945; Figure 2) and among marine forms in representatives of the families Atylidae, Epimeriidae (= Paramphithoidae), Gammarellidae (= Calliopiidae), Eusiridae, Gammara-canthidae, etc. (Lincoln, 1979; Bousfield, 1989; Sieg and Wegele, 1990; Bousfield and Kendall, 1994).

These examples of similarity may be considered as demonstrations of nomogenesis (directed development) in the evolution of amphipods. It is hoped that detailed karyological, genetic and physiological research will clarify the taxonomy of the Baikalian amphipods and help to reveal the evolutionary mechanisms, and perhaps even allow an understanding of the parallelisms seen between this and other faunas.

ACKNOWLEDGEMENTS

The author thanks all colleagues from whose discussions and correspondence the ideas of this article were born: Prof. Ya.I. Starobogatov, Drs O.A. Timoshkin, I.V. Mekhanikova, V.R. Alekseev, V.N. Ryabova, E.L. Bousfield and H.-G. Andres, Prof. I. Zerbst-Boroffka, employees of Laboratory of the Marine Research of the Zoological Institute RAS (St Petersburg) and the Chair of Invertebrate Zoology, Irkutsk State University. Thanks also to Dr A. Rossiter for his kindness and for improving the style and content of this article. This work was supported by the Russian Foundation for Basic Research (RFFI), grant 96-04-49766.

REFERENCES

- Bazikalova, A.J. (1940). Caspian elements in the fauna of Baikal. *Trudy Baik. Limnol. Inst. SO AN SSSR* 10, 357-367 (in Russian with French summary).

- Bazikalova, A.J. (1941). Materials on the study of the amphipods of Baikal. II. Reproduction. *Izvestiya Acad. Sci. USSR, Biol.* **3**, 407–426 (in Russian with French summary).
- Bazikalova, A.J. (1945). The amphipods of Lake Baikal. *Trudy Baikal Limnol. Inst. SO AN SSSR* **11**, 1–440 (in Russian with French summary).
- Bazikalova, A.J. (1948a). Adaptive importance of the sizes of Baikalian amphipods. *Doklady Akad. Nauk SSSR* **61**, 569–572 (in Russian).
- Bazikalova, A.J. (1948b). Notes on amphipods of Baikal. *Trudy Baikal Limnol. Inst. SO AN SSSR* **12**, 20–32 (in Russian).
- Bazikalova, A.J. (1951). On the growth of some amphipods from Baikal and Angara. *Trudy Baikal Limnol. Inst. SO AN SSSR* **13**, 206–216 (in Russian).
- Bazikalova, A.J. (1954). Some data on the biology of *Acanthogammarus (Brachyuropus) grewingki* (Dyb.). *Trudy Baikal Limnol. Inst. SO AN SSSR* **14**, 312–326 (in Russian).
- Bazikalova, A.J. (1962). The systematics, ecology and distribution of the genera *Micruropus* Stebbing and *Pseudomicruropus* nov. gen. (Amphipoda, Gammaridae). *Trudy Limnol. Inst. SO AN SSSR* **22**, 3–140 (in Russian).
- Bazikalova, A.J. (1971). Benthic fauna. In: *Limnologiya prideltovykh prostranstv Baikala. Selenginskiy rayon*, pp. 95–114. Nauka, Leningrad (in Russian).
- Bazikalova, A.J. (1975). On the systematics of Baikal amphipods (the genera *Carinogammarus* Stebbing, *Eucarinogammarus* Sowinsky, *Echiuropus* (Sow.) and *Asprogammarus* gen. n.). In: *Novoye o faune Baikala*, Part 1, pp. 31–81. Nauka, Novosibirsk (in Russian).
- Bazikalova, A.J., Birstein, Ya. A. and Taliev, D.N. (1946a). Osmotic pressure of the cavity liquid of sideswimmers of Lake Baikal. *Doklady Akad. Nauk SSSR* **53**, 293–295 (in Russian).
- Bazikalova, A.J., Birstein, Ya.A. and Taliev, D.N. (1946b). The osmoregulatory abilities of sideswimmers from Lake Baikal. *Doklady Akad. Nauk SSSR* **53**, 381–384 (in Russian).
- Bekman, M.Y. (1958). Dwarf males in Baikal endemics. *Doklady Akad. Nauk SSSR* **120**, 208–211 (in Russian).
- Bekman, M.Y. (1959). Some patterns in the distribution and productivity of mass species of the zoobenthos in the Maloye More Strait. *Trudy Baikal Limnol. Inst. SO AN SSSR* **17**, 342–381 (in Russian).
- Bekman, M.Y. (1962). Ecology and production of *Micruropus possolskii* Sow. and *Gmelinoides fasciatus* Stebb. *Trudy Limnol. Inst. SO AN SSSR* **22**, 141–155 (in Russian).
- Bekman, M.Y. (1983a). Amphipods. In: *Ecology of Southern Baikal* (Ed. by G.I. Galuzii), pp. 128–143. Nauka, Irkutsk (in Russian).
- Bekman, M.Y. (1983b). Benthos of sites near river mouths. In: *Limnologiya Severnogo Baikala* (Ed. by G.I. Galuzii and V.T. Bogdanov), pp. 103–108. Nauka, Novosibirsk (in Russian).
- Bekman, M.Y. (1984). The deep-living amphipod fauna. In: *Sistematika i evolutsiya bespozvonochnykh Baikala* (Ed. by A.A. Linevich), pp. 114–123. Nauka, Novosibirsk (in Russian).
- Bekman, M.Y. and Bazikalova, A.J. (1951). Biology and production potentials of some Baikalian and Siberian sideswimmers. In: *Problemy gidrobiologii vnutrennikh vod*, Part 1, pp. 61–67. Nauka, Leningrad (in Russian).
- Belyajev, G.M. (1989). *The Deep-water Oceanic Troughs and Their Fauna*. Nauka, Moscow (in Russian).
- Berg, L.S. (1922). *Nomogenesis, or Evolution Determined by Laws*. State Publishing House, St Petersburg (in Russian).

- Berg, L.S. (1969). *Nomogenesis, or Evolution Determined by Laws*. MIT Press, Massachusetts.
- Bessolitsyna, I.A. (1999). The change of structure of gammarid migratory complexes under the influence of anthropogenic factors. In: *Problemy ekologii i prirodopolizovaniya Baikalskogo regiona* (Ed. by S.B. Kuzmin), pp. 36–39. Irkutsk State Technical University Publishers, Irkutsk (in Russian).
- Birstein, Y.A. and Romanova, N.N. (1968). Order sideswimmers: Amphipoda. In: *Atlas bespozvonochnykh Kaspiyskogo morya*, pp. 241–289. Pischevaya Promyshlennost Publishers, Moscow (in Russian).
- Bousfield, E.L. (1977). A new look at the systematics of gammaroidean amphipods of the world. *Crustaceana* **4**, Suppl., 282–316.
- Bousfield, E.L. (1989). Revised morphological relationships within the amphipod genera *Pontoporeia* and *Gammaracanthus* and the “glacial relict” significance of their postglacial distributions. *Can. J. Fish. Aquat. Sci.* **46**, 1714–1725.
- Bousfield, E.L. and Kendall, J.A. (1994). The amphipod superfamily Dexaminoidea on the North American Pacific coast; families Atylidae and Dexaminidae: systematics and distributional ecology. *Amphipacifica* **3**, 3–66.
- Brauer, R.W., Bekman, M. Yu., Keyser, D.L., Nesbitt, S.G., Sidelew, G.N. and Wright, S.L. (1980a). Adaptation to high hydrostatic pressures of abyssal gammarids from Lake Baikal in eastern Siberia. *Comp. Biochem. Physiol.* **65A**, 109–128.
- Brauer, R.W., Keyser, D., Nesbitt, D.L., Wright, S.L., Bekman, M.Y. and Sidelov, G.N. (1980b). Reaction of gammarids from Baikal to hydrostatic pressure. *J. Evol. Biochem. Physiol.* **16**, 545–550 (in Russian with English summary).
- Chapelle, G. and Peck, L.S. (1999). Polar gigantism dictated by oxygen availability. *Nature* **399**, 114–115.
- Gavrilov, G.B. (1949). On the problem of the time of reproduction in amphipods and isopods in Lake Baikal. *Doklady Akad. Nauk SSSR* **64**, 739–742 (in Russian).
- Ginetsinskaya, T.A. and Dobrovolskiy, A.A. (1978). *Special Parasitology. Parasitic Worms, Molluscs and Arthropods*. Vysshaya Schkola Publishers, Moscow (in Russian).
- Grese, V.N. (1957). General features of the hydrobiology of Taymyr Lake. *Trudy Vsesoyuznogo Gidrobiol. Obshestva* **8**, 183–218 (in Russian).
- Kamaltynov, R.M., Chernykh, V.I., Sluginina, Z.V. and Karabanov, E.B. (1993). The consortium of the sponge *Lubomirskia baicalensis* in Lake Baikal, East Siberia. *Hydrobiologia* **271**, 179–189.
- Kozhov, M.M. (1972). *Characteristic Features of the Natural History of Baikal*. Vostochno-Sibirskoye knizhn. Izd-voi Publishers, Irkutsk (in Russian).
- Lincoln, R.J. (1979). *British Marine Amphipoda: Gammaridea*. British Museum (Natural History), London.
- Martens, K. (1997). Speciation in ancient lakes. *Trends Ecol. Evol.* **12**, 177–182.
- Mashiko, K., Kamaltynov, R.M., Sherbakov, D.Y. and Morino H. (1997a). Genetic separation of gammarid (*Eulimnogammarus cyaneus*) populations by localized topographic changes in ancient Lake Baikal. *Arch. Hydrobiol.* **139**, 379–387.
- Mashiko, K., Kamaltynov, R.M., Sherbakov, D.Y. and Morino H. (1997b). Speciation of gammarids in ancient Lake Baikal. In: *Animal Community, Environment and Phylogeny in Lake Baikal* (Ed. by N. Miyazaki), pp. 51–56. Otsuchi Marine Research Center, Ocean Research Institute, University of Tokyo, Tokyo.
- Mekhanikova, I.V. and Takhteev, V.V. (1991). The amphipod fauna of Northern Baikal. In: *Morfologiya i evolutsiya bespozvonochnykh* (Ed. by A.A. Linevich and E.L. Afanasyeva), pp. 199–210. Nauka, Novosibirsk (in Russian).

- Melnik, N.G., Timoshkin, O.A., Sideleva, V.G., Pushkin, S.V. and Mamylov, V.S. (1993). Hydroacoustic measurement of the density of the Baikal macrozooplankter *Macrohectopus branickii*. *Limnol. Oceanogr.* **38**, 425–434.
- Melnik, N.G., Timoshkin, O.A. and Sideleva, V.G. (1995). Distribution of *M. branickii* and some characteristics of its ecology. In: *Guide and Key to Pelagic Animals of Baikal (with Ecological Notes)* (Ed. by O.A. Timoshkin), pp. 511–522. Nauka, Novosibirsk (in Russian).
- Meyen, S.V. (1978). The basic aspects of the typology of organisms. *J. Gen. Biol.* **39**, 495–508 (in Russian with English summary).
- Müller, H.-G. (1989). Asseln als Parasiten mariner Krebse und Fische. *Microcosmos* **78**, 42–45.
- Nikolayeva, E.P. (1964). Materials on the feeding of a pelagic Baikalian sideswimmer. In: *Sbornik kratkikh soobscheniy i dokladov o nauchnoy rabote po biologii I pochvovedeniyu (Irkutskiy Universitet)*, pp. 31–35. Vostochno-Sibirskoye knizhn. Izd-voi Publishers, Irkutsk (in Russian).
- Nikolayeva, E.P. (1967). Some data on the reproduction biology of pelagic Baikalian sideswimmer *Macrohectopus branickii* (Dyb.). *Izvestiya Biologo-geograficheskogo nauchno-issledovatel'skogo instituta pri Irkutskom gosudarstvennom universitete* **20**, 28–33 (in Russian).
- Ogarkov, O.B., Kamaltynov, R.M., Belikov, S.I. and Sherbakov, D.Y. (1997). The analysis of phylogenetical relations of Baikalian endemic amphipods (Crustacea, Amphipoda) on the basis of comparison of nuclear sequences of a mitochondrial gene CO III fragment. *Molek. Biol.* **31**, 32–37 (in Russian).
- Osadchikh, V.F. (1977). Finding of the crustacean *Cardiophilus baeri* in a marsupium of corophiids (Amphipoda, Gammaridae). *Zool. Zh.* **56**, 156–158 (in Russian with English summary).
- Popova, S.M., Mats, V.D. and Chernyaeva, G.P. (1989). *Paleolimnological Reconstructions: The Baikal Rift Zone* (Ed. by N.A. Logachev). Nauka, Novosibirsk (in Russian).
- Rudstam, L.G., Melnik, N.G., Timoshkin, O.A., Hansson, S., Pushkin, S.V. and Nemov, V. (1992). Diel dynamics of an aggregation of *Macrohectopus branickii* (Dyb.) (Amphipoda, Gammaridae) in the Barguzin Bay, Lake Baikal, Russia. *J. Great Lakes Res.* **18**, 286–297.
- Salemaa, H. and Kamaltynov, R. (1994). Chromosomal relationships of the endemic Amphipoda (Crustacea) in the ancient lakes Ohrid and Baikal. In: *Genetics and Evolution of Aquatic Organisms* (Ed. by A.R. Beaumont), pp. 405–414. Chapman and Hall, London.
- Severtsov, A.S. (1990). Intraspecific variety as a cause of evolutionary stability. *J. Gen. Biol.* **51**, 579–589 (in Russian with English summary).
- Shimaraev, M.N., Verbolov, V.I., Granin, N.G. and Sherstyankin, P.P. (1994). *Physical Limnology of Lake Baikal: A Review*. Baikal International Center for Ecological Research, Irkutsk.
- Sideleva, V.G. and Mechanikova, I.V. (1990). Feeding preference and evolution of the cottoid fishes of Lake Baikal. *Proc. Zool. Inst. Leningrad* **222**, 144–161 (in Russian with English summary).
- Sieg, J. and Wegele J.W. (eds) (1990). *Fauna der Antarktis*. Paul Parey Verlag, Berlin.
- Tachteev, V.V. (1995). On the ecology of a rare species of Baikal amphipods *Polyacanthisca calceolata* in the context of the problem of parallel geneses of the abyssal Baikal and oceanic faunae. *Zool. Zh.* **74**, 141–143 (in Russian with English summary).

- Tachteev, V.V. (1995). The gammarid genus *Poekilogammarus* Stebbing, 1899, in Lake Baikal, Siberia (Crustacea Amphipoda Gammaridea). *Arthropoda Selecta* **4**, 7–64.
- Tachteev, V.V. and Mekhanikova, I.V. (1993). Some data on life history of the Baikal parasitic gammarids of the genus *Pachyschysis* (Amphipoda, Gammaridae). *Zool. Zh.* **72**, 18–28 (in Russian with English summary).
- Takhteev, V.V. (1999). Revision of the genus *Odontogammarus* (Crustacea, Amphipoda, Gammaridae) from Lake Baikal. *Zool. Zh.* **78**, 796–810 (in Russian with English summary).
- Takhteev, V.V. (2000). On the revision of a genus *Poekilogammarus* Stebbing, 1899. (Crustacea, Amphipoda, Gammaridae) from Lake Baikal. *Zool. Zh.* **79**, in press (in Russian with English summary).
- Takhteev, V.V. (1997). The gammarid genus *Plesiogammarus* Stebbing, 1899, in Lake Baikal, Siberia (Crustacea Amphipoda Gammaridea). *Arthropoda Selecta* **6**, 31–54.
- Takhteev, V.V. and Bessolitsyna, I.A. (1999). Some scientific problems of baikalugia and their importance for ecological education. In: *Ecology, Education, Health*, Part 1, pp. 20–26. Irkutsk State University Publishers, Irkutsk (in Russian).
- Takhteev, V.V. and Mekhanikova, I.V. (1996). Distribution of the endemic nectobenthic amphipods in the Lake Baikal. *Bull. Moscow Soc. Nat. Biol. Ser.* **101**, 39–48 (in Russian with English summary).
- Timofeev, M.A., Stom, D.I., Gil, T.A. and Naumova, E.Y. (1997). Ascertainment of the temperature preference of amphipods and their reaction to high temperatures. *Chelovek. Sreda. Vselennaya* **1**, 75–77. Irkutsk State Technical University Publishers, Irkutsk (in Russian).
- Timoshkin, O.A., Mekhanikova, I.V. and Shubenkov, S.G. (1995). Morphological peculiarities of *M. branickii*. In: *Guide and Key to Pelagic Animals of Baikal (with Ecological Notes)* (Ed. by O.A. Timoshkin), pp. 485–511. Nauka, Novosibirsk (in Russian).
- Urmantsev, Y.A. (1988). The general theory of systems: a condition, application and prospects of the development. In: *Systema. Simmetriya. Garmoniya*, pp. 38–130. Mysl Publishers, Moscow (in Russian).
- Vereschagin, G.J. (1940). The origin and history of Baikal and its flora and fauna. *Trudy Baikal Limnol. Inst. SO AN SSSR* **10**, 73–239 (in Russian with French summary).
- Vershinin, N.V. (1960). On the question of the genesis of relict fauna in the Norilsk lakes group. *Doklady Akad. Nauk SSSR* **64**, 739–742 (in Russian).
- Vershinin, N.V., Sychyova, A.V. and Syrygina, F.F. (1967). On the invertebrate fauna of Khantayskoye Lake. *Trudy Krasnoyarskogo otdeleniya Sibirskogo NII Rybnogo Khosyaystva* **9**, 214–230 (in Russian).
- Vilisova, I.K. (1962). On the ecology of a Baikalian pelagic sideswimmer *Macrohectopus branickii* (Dyb.). *Trudy Limnol. Inst. SO AN SSSR* **22**, 156–171 (in Russian).
- Vinogradov, G.M. (1988). System of life forms of pelagic sideswimmers. *Doklady Akad. Nauk SSSR* **298**, 1509–1512 (in Russian).
- Vinogradov, G.M. (1992). The probable ways of the gammarid (Amphipoda: Crustacea) invasion in the pelagic zone: analysis of the life forms. *J. Gen. Biol.* **53**, 328–339 (in Russian with English summary).
- Weinberg, I.V. and Kamaltnov, R.M. (1998a). Zoobenthos communities at a stony beach of Lake Baikal. 1. *Zool. Zh.* **77**, 158–165 (in Russian with English summary).

- Weinberg, I.V. and Kamaltynov, R.M. (1998b). Zoobenthos communities at a stony beach of Lake Baikal. 2. *Zool. Zh.* **77**, 259–265 (in Russian with English summary).
- Zerbst-Boroffka, I., Grospietsch, T., Mekhanikova, I. and Knopse, M. (1998). Osmotic and ionic adjustment in abyssal gammarids after acclimation to different water depths in Lake Baikal. *Zoology* **101**, 71.
- Zerbst-Boroffka, I., Grospietsch, T. and Mekhanikova, I. (1999). Osmotische und ionale Anpassung von abyssalen Amphipoden an verschiedene Wassertiefen im Baikal. In: *Crustaceologen Tagung*, p. 58. Humbolt Universität Publishers, Berlin.