MORPHOLOGY OF MANDIBLE AND LATERALIA IN SIX ENDEMIC AMPHIPODS (AMPHIPODA, GAMMARIDEA) FROM LAKE BAIKAL, IN RELATION TO FEEDING

BY

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ABSTRACT

The morphology of the mandible and stomach lateralia in some Lake Baikal amphipods has been investigated in regard to their food preference. Six species of endemic amphipods with different life styles (so-called “life forms”) have been studied by means of light and scanning electron microscopy. The modifications of the mandible are attributed to the food resources used. The position of the incisor and lacinia mobilis, their width and length, the structure of the triturative area of the molar, the wearing of incisor and lacinia mobilis between two molts, and the relative length of the stomach depend on the type of food. None of the species studied revealed complete reduction of any part of the mandible. The most specialized species are the oophage *Pachyschesis bazikalovae* G. Karaman, 1976, the necrophage *Ommatogammarus albinus* (Dybowsky, 1874), and a species biting holes in sponges with a siliceous skeleton, *Eulimnogammarus violaceus* (Dybowsky, 1874). The morphology of the lateralia seems not to be connected with the food type, but is probably important from a phylogenetic point of view.

RéSUMÉ

La morphologie de la mandibule et des pièces latérales de l’estomac de certains amphipodes du lac Baïkal a été étudiée en relation avec leurs préférences alimentaires. Six espèces d’amphipodes endémiques ayant des modes de vie différents (désignés par le terme “life forms”) ont été examinées au microscope électronique à balayage et au microscope optique. On a montré que les modifications de la mandibule sont déterminées par le type d’aliments utilisés. La position du processus incisif et de la lacinia mobilis, la largeur et la longueur de ces pièces, la structure de la surface broyeuse du processus molaire, l’usure subie par le processus incisif et la lacinia mobilis pendant l’intermue, ainsi que la longueur relative de l’estomac dépendent du type de nourriture. Parmi les espèces examinées, aucune n’a subi la réduction totale d’une partie ou d’une autre de la mandibule. Les espèces les plus spécialisées sont l’oophage *Pachyschesis bazikalovae* G. Karaman, 1976, le nécrophage *Ommatogammarus albinus* (Dybowsky, 1874) et une espèce inquiline *Eulimnogammarus violaceus* (Dybowsky, 1874) qui vit dans des cavités qu’elle creuse dans des éponges à squelette siliceux. La

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morphologie des pièces latérales de l’estomac ne semble pas liée au type de nourriture, mais est probablement importante du point de vue phylogénétique.

INTRODUCTION

The morphology of the mouthparts of amphipods is closely connected with their feeding habits (Sainte-Marie, 1984; Moore & Rainbow, 1989; Coleman, 1991a, b; Steele & Steele, 1993; Watling, 1993). The structure of the digestive tract, in contrast, is more conservative (Johnston et al., 2004). However, the size and structure of the stomach in some groups of amphipods (fig. 1A) reflect their feeding strategy (Agrawal, 1964; Coleman, 1992).

In most amphipods, all parts of the mandible are well developed (fig. 1B). This type of mandible is called a basic gammaridean type (Barnard, 1969). A high specialization of the mouth apparatus depending on a particular type of food consumed is observed in some families of Amphipoda: either reduction, or overgrowth of some parts, or even atrophication of the mouth apparatus as a whole (De Broyer & Thurston, 1987; Watling, 1993; Bellan-Santini, 1999). The majority of the mandible modifications found are attributed to predation or to carrion feeding (Sainte-Marie, 1984; Coleman, 1989; Steele & Steele, 1993; Dauby et al., 2001; Legezinska, 2008). However, there are aberrations from the basic scheme of the structure in herbivorous amphipods (Agrawal, 1964). Subtle differences in the structure of some parts of the mandible are also attributed to feeding habits. For example, the reduction of molar size and increase of densely set short spinules on

![Fig. 1. Schematic structure of: A, the stomach; and, B, the mandible of the basic type of amphipod.](image_url)
the triturative area of *Talorchestia* species II (family Talitridae) are adaptations to the grinding of siliceous diatom valves (Johnston et al., 2004).

The amphipod fauna of Lake Baikal is characterized by its high species diversity: 348 endemic species and subspecies from 41 genera and 6 families (Takhteev, 2000). Amphipods are one of the most species-rich groups of invertebrates, inhabiting all biotopes and depths of the lake, including the maximal depths. There are very few specialized forms in the Baikal amphipod fauna (Takhteev & Mekhanikova, 1993), and most species are omnivorous (Bazikalova, 1954; Bekman, 1962; Morino et al., 2000; Mekhanikova, 2001, 2006). However, an analysis of the ratio of carbon isotopes $^{13}C/^{12}C$ of twenty benthic species of amphipods showed that the isotopic composition of food consumed by those varies within wide ranges, which indicates their different feeding strategies (Melnik et al., 1996).

The structure of Baikal amphipod organs responsible for the capture and processing of food in relation to their food preferences, has not been studied previously. Six species of endemic amphipods of different life forms\(^2\) were selected for this work (fig. 2). *Brandtia parasitica* (Dybowsky, 1874) lives exclusively on Baikal sponges of the family Lubomirskiidae. For a long time it has been considered a parasitic species, feeding on sponge tissue (Lomonosov & Chekanovsky, 1869; Kamaltynov, 1999). However, recently it has been established that this is an omnivorous species (Mekhanikova, 2001). Another symbiont, *Eulimnogammarus violaceus* (Dybowsky, 1874) inhabits sponges by carving out holes in their bodies. Morino et al. (2000) believe that it feeds upon sponge tissue. *Brandtia latissima lata* (Dybowsky, 1874), a typical inhabitant of the stony littoral zone, is a polyphage (Mekhanikova, 2006). *Acanthogammarus grewingkii* (Dybowsky, 1874), one of the most common species of the deep zone of Lake Baikal, is also a polyphage; age dependent changes in its feeding were studied in detail by Bazikalova (1954). *Pachyschesis bazikalovae* G. Karaman, 1976 inhabits the gill cavity of a large nectobenthic amphipod, *Garjajewia cabanisii* (Dybowsky, 1874) and feeds upon its eggs (Takhteev & Mekhanikova, 1993). *Ommatogammarus albinus* (Dybowsky, 1874) feeds on carrion and is usually caught with a baited trap containing rotting fish or meat (Dybowsky, 1874; Bazikalova, 1945; Takhteev, 2000).

The morphology of the mandible corpus and some detailed structures of the lateralia of the stomach have now been studied for the first time in Baikal

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\(^2\) The term “life forms” has been coined by Takhteev (2000). It encompasses life history, habitat, and morphological adaptations. Its classification is rather complicated, but it gives a more complete view on a particular species. E.g., “lithophilic, armoured, walking” or “lithophilic, smooth, swimming”, etc. This system of life forms had previously been elaborated for marine amphipods (Kamenskaya, 1984; Vinogradov, 1988, 1990).
amphipods of different life forms. The relationship between their feeding habits and the morphology of the organs responsible for the capture and processing of the food is discussed in this paper.

**MATERIAL AND METHODS**

Amphipods were sampled with dredges, trawls, baited traps, nets, and by divers in different areas of Lake Baikal during the years 1988-2009. The amphipods were fixed with 4% formalin and stored in 75% ethanol. Analyses of gut contents and food preferences were performed on 392 specimens. Between 10 and 16 specimens
of each species were dissected to determine the length of the stomach, while 15 to 30 (or more) specimens were used for studies of the morphology of the mandibles and lateralia.

Amphipods were dissected with microscissors under a stereoscopic microscope MBS-10, and sex and body length were also determined. Temporary preparations of food components were prepared in water or a mixture of water and glycerin, and examined under an Ergaval compound microscope. Permanent preparations of mandibles and lateralia were prepared in Fora-Berlese liquid and examined under compound light microscopes Axiostar Plus and Axiovert 2000. For scanning electron microscopy, the mandibles were dehydrated in an ethanol series, dried, glued onto aluminum stubs with carbonic adhesive tape, coated with gold in vacuum (Balzers SCD 004), and examined under a scanning electron microscope Philips SEM 525M.

RESULTS

**Brandtia (Brandtia) latissima lata** (Dybowsky, 1874) (fig. 3A-F)

All parts of the mandible are well developed. The incisor and lacinia mobilis are directed backwards. The left mandible incisor bears 5 teeth, and the lacinia mobilis is slightly smaller with 4 teeth (fig. 3A). The right mandible incisor bears 5 teeth, and the lacinia mobilis is in the shape of a short plate with teeth of different length (fig. 3B). Both mandibles are topped by a “crown” on the toothed edges. The teeth of the incisor and lacinia mobilis in some specimens that were ready for moulting, are slightly truncated, in the others they are extremely dulled (fig. 3E). Different wearing levels of the teeth of the mandible in different individuals of the species are likely to be attributed to different food types consumed. The molar is massive, with rows of teeth (fig. 3C) and a large triturative area.

The stomach length makes up 19.3 ± 0.5% of the body length. The lateralia are with long, thin spines, without secondary spinules on the surface (fig. 3D).

The gut content of *B. latissima lata* is diverse and consists of both vegetable and animal matter. The main vegetable components are lower plants and macrophytes, sometimes pine spores. Among lower plants there are various benthic (fig. 3F) and planktonic diatoms, and green and blue-green filamentous algae. Diatoms were found in the form of fragments, valves, and even of intact colonies (e.g.,

3) “Crown” — the teeth of the incisor and lacinia mobilis are of yellow colour in omnivorous and in spongicolous species, and together look like a golden crown on the tooth.
Fig. 3. *Brandtia latissima lata* (Dybowsky, 1874). A, incisor and lacinia mobilis of left mandible; B, incisor and lacinia mobilis of right mandible; C, molar; D, lateralia; E, incisor and lacinia mobilis of left mandible (before moult); F, benthic diatoms in stomach. Scale bars: 100 μm.
Gomphonema). The food of animal origin was represented by oligochaetes, rotifers, entomostracans (harpacticoids, ostracods, and cyclopoids) and malacostracans (amphipods). Entomostracans were found intact and in fragments, whereas the amphipods occurred in fragments only (cuticle fragments, extremities, antennae, and mouthparts). Detritus, mineral particles, and sponge spicules were common components of the gut contents (Mekhanikova, 2006).

**Brandtia (Spinacanthus) parasitica** (Dybowsky, 1874) (fig. 4A-F)

All parts of the mandible are well developed. The incisors and lacinia mobilis are directed backwards. The left incisor bears 6 teeth. The lacinia mobilis with 4 teeth is slightly shorter than the incisor (fig. 4A). The right incisor is provided with 4 teeth. Sometimes there is an additional fifth, short tooth. The second tooth is the longest. The lacinia mobilis is in the shape of a short plate with teeth (fig. 4B). Both mandibles are topped by a “crown”. The molar is massive, with rows of teeth (fig. 4C, D) and a large grinding area.

The stomach length amounts to $16.7 \pm 0.2\%$ of the body length. The lateralia bear short, thick spines, wide at the base, with fine spinules in the distal and middle parts (fig. 4E).

*B. parasitica* feeds upon vegetable and animal organisms, dwelling on sponges and settling from the water column. Vegetable food components are represented by planktonic (fig. 4F) and benthic diatoms, chrysophycean and filamentous algae, macrophytes, unidentified vegetable remains, and spores of higher plants. Animal organisms are represented by entomostracans and malacostracans, oligochaetes, rotifers, and ciliates. Sponge spicules and their fragments get into the gut of *B. parasitica* together with the food consumed. Sponge tissues have not been found in the gut of any of the specimens studied. A planktonic diatom, *Aulacoseira baicalensis* (K. Meyer) Simonsen, is the major food component in *B. parasitica* in spring during its massive growth. Fragments of diatom valves are more often encountered in the food, although intact cells are also found, even in juveniles (Mekhanikova, 2001).

**Acanthogammarus growingkii** (Dybowsky, 1874) (fig. 5A-G)

All mandible parts are well developed. The mandible corpus is thick and strongly chitinized. The incisors and lacinia mobilis are directed backwards. The left incisor bears 5 teeth and sometimes a very short additional sixth tooth. The lacinia mobilis bears 4 teeth, the first one being the longest (fig. 5A, C). The right
Fig. 4. *Brandtia parasitica* (Dybowski, 1874). A, incisor and lacinia mobilis of left mandible; B, incisor and lacinia mobilis of right mandible; C and D, molar; E, lateralia; F, planktonic diatoms in stomach. Scale bars: 100 μm in A-C, E, and F; 10 μm in D.
Incisor is equipped with 5 teeth, the second being the longest. The lacinia mobilis is bifurcated, with 2 teeth (fig. 5B, D). Some specimens have 1-2 short additional teeth at the base of the short tooth. Both mandibles are topped by a “crown”. The teeth of the incisor and lacinia mobilis are worn during the inter-moult period. The molar is massive, with rows of teeth.
The stomach length amounts to 11.5 ± 0.3% of the body length. The lateralia have sharp, smooth spines, without secondary spinules. The spine width at the base is two times the width in the distal part (fig. 5F).

*A. grewingkii* consumes different types of food, from detritus to invertebrates and, if possible, carrion. Its main food components are amphipods, entomostracans, and detritus (Bazikalova, 1954). Diatoms play an important role in feeding, especially in years of their mass development. In June, when they settle in abundance onto the bottom, this omnivorous species feeds almost exclusively on diatoms (fig. 5G). At this time of the year, the alimentary canal of *A. grewingkii* is filled with a green-gray substance: semi-digested diatom cells with a large number of intact valves and their fragments. The food of *A. grewingkii* consists of the following dominant species: *Aulacoseira baicalensis* (in volume), *Stephanodiscus meyerii* Genkal & Popovskaya (in valve number), *Cyclorella*, and *Aulacoseira islandica* (O. Müller & Simonsen). *Acanthogammarus grewingkii* breaks chains of planktonic diatoms and swallows them without grinding (fig. 5G), but a great portion of these diatoms are ground with molar processes as well, which causes wearing of rows of teeth on their surface (fig. 5E). The chains of *A. baicalensis* consist of 2-3 cells (4-6 valves), more rarely of 4 cells (8 valves). Besides diatoms, we encountered sponge spicules, setae of crustaceans, fragments of amphipods, and entire entomostracan crustaceans in the gut as well.

**Eulimnogammarus (Eurybiogammarus) violaceus** (Dybowski, 1874)  
(fig. 6A-G)

The mandible corpus is massive, the incisor and lacinia mobilis are strongly chitinized. The teeth are worn for the period between two moults (fig. 6C, D). In the samples of this species it has been impossible to find two specimens with similar mandibles. The incisor and lacinia mobilis are directed downwards and slightly forwards. The left incisor in a specimen after moultng bears 7-8 sharp teeth, the second being the largest. The lacinia mobilis bears 7-8 teeth, the first being the longest (fig. 6A). The left incisor looks like a spatula in specimens during the intermoult, sometimes a terminal tooth remains. The incisors have numerous cracks and fissures on their surface. At the beginning of moultng, the lacinia mobilis is also provided with rather truncated teeth and numerous cracks. The right incisor bears smooth teeth. The lacinia mobilis has a long, hook-like, sharp tooth, and one tooth is in the shape of a plate with several teeth (fig. 6B). The right lacinia mobilis is worn during the intermoult and looks like a spatula (“fish tail”) (fig. 6D). Incisors of both mandibles are topped with a massive “crown” (not only on the toothed edges). The molar is provided with ridges and cone-shaped elevations (fig. 6E, F).
Fig. 6. *Eulimnogammarus violaceus* (Dybowsky, 1874). A, incisor and lacinia mobilis of left mandible (after moult); B, incisor and lacinia mobilis of right mandible (after moult); C, incisor and lacinia mobilis of left mandible (before moult); D, incisor and lacinia mobilis of right mandible (before moult); E, molar (after moult); F, molar (before moult); G, lateralia. Scale bars: 100 μm in A-E, and G; 10 μm in F.
The stomach length amounts to 17.2 ± 0.7% of the body length. The very long and thin spines of the lateralia are hooked at the edges. Secondary spinules are located along the entire length of the spines (fig. 6G).

The guts of only two out of 34 dissected animals were filled with sponge tissues. The gut of 11 specimens contained fragments of sponges, and the guts in 21 specimens contained no sponge tissues at all. Besides sponge tissues, some diatoms were found in the gut (Navicula, Ceratoneis, Cocconeis, Gomphonema, and Aulacoseira baicalensis: intact cells and valve fragments), brown or green, uniform, unidentified substance, a rotifer, oligochaete setae, and a fragment resembling an oligochaete.

**Ommatogammarus albinus** (Dybowsky, 1874) (fig. 7A-F)

The mandibles are highly specialized, with a wide incisor and a lacinia mobilis with almost the same width. The incisor and lacinia mobilis are directed downwards and slightly backwards. The left incisor is composed of 7 teeth located in one plane, and looks like a wide ridge (fig. 7A, C). The lacinia mobilis is also flat, with 6 teeth of almost similar length (fig. 7A, C). The right incisor bears 5-6 teeth located in the same plane, the second tooth being longer than the others (fig. 7B, D). The lacinia mobilis is falciform. Short and sharp teeth are located between extremely long teeth (fig. 7B, D). Wearing of the teeth of incisor and lacinia mobilis has not been observed for the intermoult period. The teeth of the mandible are without a “crown”. The molar is small, weak, and with a row of ridges (fig. 7E).

The stomach is long: 17.2 ± 0.3% of the body length. The spines of the lateralia are smooth, sharp, and straight, without spinules on the surface (fig. 7F).

Fat droplets (pale yellow, or sometimes orange) are always present in the gut of *O. albinus*, as well as a whitish, structureless substance (muscles of fishes and mammals). Sometimes the gut content is dark in colour, or it contains darker inclusions (it is obvious that in this case fish internal organs were consumed). Only in three specimens out of 26 the gut contents resembled detritus.

**Pachischesis bazikalovae** G. Karaman, 1976 (fig. 8A-G)

The mouthparts of *P. bazikalovae* are specialized for feeding on the host’s eggs. The incisor and lacinia mobilis are adapted for piercing eggs (fig. 8A, B), and are directed vertically downwards. The left incisor is provided with 5 teeth, each of which is located much lower than the previous one, the lacinia mobilis bears 3-4 teeth, the location of which is the same (fig. 8A). The right incisor bears 4 teeth.
located as on the left incisor (fig. 8B, C). The lacinia mobilis is bifurcated with two very long sharp teeth (fig. 8B, D). During the intermoult, the mandible teeth are not worn, their cusps being slightly truncated (fig. 8A, B). The mandible teeth are not “crowned”. The molar is reduced; pineal elevations are observed on its surface (fig. 8E, F).
Fig. 8. *Pachyschesis bazikalovae* G. Karaman, 1976. A, incisor and lacinia mobilis of left mandible (before moult); B, incisor and lacinia mobilis of right mandible (before moult); C, incisor of right mandible; D, lacinia mobilis of right mandible; E and F, molar; G, lateralia. Scale bars: 100 μm in A and B; 10 μm in C-F; 50 μm in G.

The stomach is short: only 7.6 ± 0.2% of the body length. The lateralia bear short, sharp spines, with secondary spinules on the surface (fig. 8G).

The guts of all specimens examined, except two females, were filled with an orange, lipid substance, but sometimes of lighter colour and then in a smaller
amount. *P. bazikalovae* inhabits the gill cavity of *Garjajewia cabanisii* and feeds exclusively on its eggs. The reproduction period of amphipod host is extended, thus the parasites do not experience shortage of food. Moreover, they periodically change host in search of food and sex partners (Takhteev & Mekhanikova, 1993).

**DISCUSSION**

The mandible morphology of the six species of amphipods studied shows that these species have different feeding strategies (table I), although none of them showed complete reduction of any of the parts of the mandible. Mandibles in the three omnivorous species (*Acanthogammarus grewingkii*, *Brandtia latissima lata*, and *Brandtia parasitica*) are of a basic type. The mandible is increasingly modified when a new feeding strategy is adopted or there is adaptation to any specialized habitat (Watling, 1993). In Lake Baikal, alternative food sources are the eggs of large amphipods, and carcasses of vertebrates (fishes and seals), whereas sponges with a siliceous skeleton constitute a specialized habitat. Our investigations show that modification of the mandibles is indeed more expressed in the necrophage *Ommatogammarus albinus* and the parasitic *Pachischesis bazikalovae*, feeding on eggs of a large amphipod (table I). The wide incisor and lacinia mobilis of both mandibles of *O. albinus* function as a knife system, while the elongated incisors and laciniae mobiles of *P. bazikalovae* are adapted to pierce egg shells. The right lacinia mobilis of *P. bazikalovae* is the most modified: it looks like a long, two-pronged fork. Describing *Pachischesis*, Takhteev (2000) noted that “The transition to oophagy did not cause any transformation of the mouthparts.” This viewpoint can hardly be supported. The mandibles of *Eulimnogammarus violaceus*, a symbiont of Baikal sponges, must carve out holes, and thus experience a massive friction and wear when cracking the siliceous spicules. Therefore, between two moult, these teeth are completely worn, and numerous fissures are left on their surface. The mandibles of this species are adapted to crack those siliceous sponge skeletons, and they bear strong “crows” on both the incisor and lacinia mobilis (unlike polyphagic species, that bear “crows” only on the toothed edges). Morino et al. (2000) note that the mandibular corpus in *E. violaceus* is wider compared to the palp size. The distal part of the incisor is strongly developed and sponge fragments are found in the stomachs. According to our data, only in 6% of the specimens studied the guts were filled with sponge tissues, and in 32% these tissues were present in small amounts. The majority of the guts examined contained no sponge material. Therefore, it is still unclear whether those sponge tissues are to be considered as food, or that those pieces were bitten out while constructing a shelter, and next swallowed accidentally.
<table>
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<th>Species</th>
<th>Habitat</th>
<th>Depth in m</th>
<th>Life form</th>
<th>Body length, mm</th>
<th>Feeding type</th>
<th>Mandible</th>
<th>Stomach</th>
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<tr>
<td><em>Brandtia</em> (Brandtia) latissima lata (Dybowsky, 1874) (family Acanthogammaridae)</td>
<td>Lake Baikal</td>
<td>1-65 (usually at 2-40)</td>
<td>Walking, lithophilous, with armed body</td>
<td>Up to 18.7</td>
<td>Polyphage</td>
<td>Non-specialized; incisor directed backwards; molar with tooth rows</td>
<td>Relative stomach length 19.3%; lateralia spines long (∼56 μm), thin, without secondary spines</td>
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<td>Lake Baikal except the Selenga River shoal</td>
<td>1-60 (seldom at 200)</td>
<td>Epibiont of Baikal sponges</td>
<td>10-11.5</td>
<td>Polyphage</td>
<td>Non-specialized; incisor directed backwards; molar with tooth rows</td>
<td>Relative stomach length 16.7%; lateralia spines short (∼34 μm), thick, with secondary spines</td>
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<td><em>Acanthogammarus</em> growingkii (Dybowsky, 1874) (family Acanthogammaridae)</td>
<td>Lake Baikal</td>
<td>100-1380 (usually below 300-400)</td>
<td>Nectobenthic, straight swimmers</td>
<td>Up to 90</td>
<td>Polyphage</td>
<td>Non-specialized; incisor directed backwards; molar with tooth rows</td>
<td>Relative stomach length 11.5%; lateralia spines long (∼90 μm), thin, without secondary spines</td>
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<td>1.5-140</td>
<td>Symbiont biting</td>
<td>18-30</td>
<td>Biting</td>
<td>Specialized for biting out sponge tissues; incisor directed slightly forward; molar with rows of ridges and cone-shaped elevations</td>
<td>Relative stomach length 17.2%; lateralia spines long (~128 μm), thin, curved at the ends, with secondary spines</td>
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<td>holes in Baikal sponges</td>
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<td>Spongiophage?</td>
<td>Relative stomach</td>
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<td>except the (usually at holes in Baikal out sponge tissues; length 17.2%; (family Gammaridae)</td>
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<td><em>Ommatogammarus albinus</em></td>
<td>Open part of Lake Baikal, seldom Proval Bay</td>
<td>47-1641</td>
<td>Benthic-pelagic,</td>
<td>20-25</td>
<td>Obligate</td>
<td>Specialized; incisor directed slightly backwards; molar with rows of ridges</td>
<td>Relative stomach length 17.2%; lateralia spines long (~200 μm), without secondary spines</td>
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<td>necrophage</td>
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<td>(family Gammaridae)</td>
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<td>Southern Baikal, Maloye More, Barguzin Bay,</td>
<td>100-1050</td>
<td>Parasitic on</td>
<td>Female up to 13.8, males up to 8.4</td>
<td>Oophage</td>
<td>Specialized; incisor directed vertically downwards; molar with pineal elevations</td>
<td>Relative stomach length 7.6%; lateralia spines short (~25 μm), thick, with secondary spines</td>
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<td>(family Pachyschesiidae)</td>
<td>Sosnovsk Bankas, slope of Selenga River delta front</td>
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Note: Taxonomy and characterisation of life forms are after Takhteev (2000); distribution, habitat depth, and body length from Bazikalova (1945), Takhteev (2000), and Kamaltynov (2001).
Differences among polyphages, oligophages, and spongicolous *E. violaceus* have also been recorded in the structure of the triturative area of the molar. On the molar surface of all polyphages there are rows of teeth, which serve as a rasp, and in oligophages and *E. violaceus* there are rows of ridges and/or pineal elevations (table I).

The modifications of the mandible are revealed not only by the reduction or, in contrast, by the extreme development of its separate parts, but also by the position of the mandible in the head (Watling, 1993). The incisors of Baikal omnivorous amphipods are directed backwards, in the oophage *P. bazikalovae* vertically downwards, in the necrophage *O. albinus* slightly backwards, and in the spongicolous *E. violaceus* slightly forward.

Variations in stomach structure depending on the type of food have been described for many marine species (Coleman, 1994). The lateralia of the Baikal species *E. violaceus* are equipped with long and very thin, serrated spines, which are hooked on the distal edges. In the other species studied, the lateralia spines are not hooked on the distal edges; in some they are smooth (*B. latissima lata, A. grewingkii, O. albinus*), and in others they have secondary spinules (*B. parasitica, P. bazikalovae*); in the latter species the lateralia bear triangular spines arranged in three rows, with remarkably sharp edges. Variations in the length of the spines of the lateralia were also recorded (table I).

It has previously been demonstrated in marine species, that the highest diversity of stomach size is characteristic of animals with a specialized type of feeding. For example, in the necrophage *Waldekia obesa* (Chevreux, 1905) (family Lysianassidae) the stomach length makes up about 34% of the body length, in *Andaniotes linearis* K. H. Barnard, 1932 (family Stegocephalidae), feeding on cnidarians, the length of the stomach is over 45% of the total body length. The stretching of the stomach in the first species is due to its adaptation to long intervals between food consumption, and in the other, due to consuming low-calory food. The stomach in marine detritophages is short, less than 10%, in carnivores it varies from 2-5 to 16-17% of the total body length (Coleman, 1991a, 1992). Such significant variations in the relative length of the stomach have not been registered in Baikal amphipods, although there is variation here, as well. The largest relative stomach length is encountered in the omnivorous *B. latissima lata* (19.3% of the body length), in the spongicolous *E. violaceus* (17.2%), and in the necrophage *O. albinus* (17.2%), the smallest relative stomach length occurs in the oophage *P. bazikalovae* (7.6%). Probably, this species is able to find enough food, at least during the major part of the year.

Baikal polyphagic amphipods consume any available organic material. It is shown in the case of the three omnivorous species studied, that larger and more mobile species have a broader spectrum of feeding. The similar food choice of
different species is attributed to the similarity of their mode of life and a shared habitat in the same biotopes. The differences in food composition in specimens of the same species from the same sample are explained rather by food availability, i.e., a patchiness in the distribution of vegetable and animal organisms in the biocenoses, than by food preference. Food composition also varies depending on season: in winter the percentage of animal matter in the feeding of polyphagic species increases (Mekhanikova, 2001, 2006; original data).

During their mass development, diatoms play an important role in the feeding of amphipods (Carey & Boudrias, 1987; Quigley & Vanderploeg, 1991; Werner, 1997; Polterman, 2001). At that time of the year, even the marine necrophages and carnivores feed on diatoms (Carey & Boudrias, 1987). Many amphipods digest diatoms, bacteria, and fungi more effectively than any other organic food such as detritus, macroalgae, and higher plants, which serve them as a substratum (Kostalos & Seymour, 1976; Harrison, 1977; Zimmerman et al., 1979). Diatoms are a good food source: they are preferred and digested faster than green filamentous macroalgae (Giani & Laville, 1995). The selectivity in feeding of invertebrates is often attributed to different availabilities of the unicellular algae, due to their different adhesion to a substratum (Moore, 1977; Hudon, 1983). Most invertebrates prefer planktonic filamentous algae (Fragilaria, Melosira, and Diatoma), as well as attached bushy algae (Gomphonema, Cymbella, and Rhoicosphenia), and, to a lesser extent, they consume Cocconeis, Achnantes, and Amphora that are all firmly attached to the substratum (Moore, 1975, 1977; Hudon & Bourget, 1981). A similar selectivity for different diatoms has not been observed in the Baikal species studied. Both planktonic (solitary and colonial) and benthic (bushy and solitary attached) diatoms were present in different proportions in the food of the polyphages. Large attached diatoms (e.g., Didymosphenia) are likely to be actively consumed by amphipods, whereas small attached forms are swallowed together with the substratum on which they dwell. Amphipods break up diatoms that form filamentous colonies (Aulacoseira baicalensis) at their girdle band with the toothed incisor, and at the frustule openings with their molar teeth. In many cases, diatoms are reduced to such tiny pieces that it is impossible to identify their species or even genus.

Thus, according to the results found in the six species of Baikal endemic amphipods analysed in this paper, the relationship between their feeding habits and the structure of their mandible has been established. The following characteristics of amphipod mandibles and stomach are evidence of the varied composition of the food consumed (including diatoms with siliceous valves): the incisors and lacinia mobilis are directed backwards, there are dense rows of fine teeth on the triturative surface of the molar, the wearing of the incisor and lacinia mobilis between two molts is obvious, there is a “crown” present on the incisor, and they have a relatively long stomach. In species feeding on soft food (amphipod eggs
and rotten fish) the mandible teeth are without a “crown” and are not obviously worn during the period between two molts. The modifications of an oophage (P. bazikalovae) mandible are observed in the lengthening of the incisors that are also directed vertically downwards, and in the presence of pineal elevations on the molar surface instead of rows of teeth. The most pronounced mandible specialization is expressed in the necrophage, O. albinus: the incisors are wide, their teeth are located in one plane, and on the molar surface there are rows of ridges. As for the spines of the lateralia, their sizes and shapes and the presence or absence of secondary spinules on their surface are likely to be attributed, first of all, to phylogenetic characteristics, and only in some species they express food strategies (the oophage P. bazikalovae). An unusual form of the lateralia spines in E. violaceus, a Baikal symbiont biting out holes in sponges, is probably evidence for its separate taxonomic position.

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REFERENCES

AGRAWAL, V. P., 1964. The digestive system of some British amphipods — III. The alimentary canal. Proceedings of the National Academy of Sciences (India), (B, Biological) 34: 429-458.


— —, 1954. Some data on biology of Acanthogammarus (Brachyuropus) grewingki (Dyb.). Proceedings of Baikal Limnological Station, 14: 312-326. [In Russian.]


— —, 2006. Comparative studies on feeding of Baicalasellus angarensis (Dyb.) (Crustacea, Isopoda) and Branditia latissima (Dyb.) (Crustacea, Amphipoda) under conditions of their shared habitation in the littoral zone of southern Baikal. Proceedings of Biology and Soil Department of Irkutsk State University, 6: 83-93. (Irkutsk State University, Irkutsk). [In Russian.]


— —, 1990. Life forms of coastal White Sea amphipods (Crustacea, Amphipoda) from Velikaya Salma area. Biological Sciences, 8: 77-85. [In Russian.]
