Arthropoda Selecta 12 (3–4): 171–182

Littoral Cladocera (Crustacea: Branchiopoda) from the Altai mountain lakes, with remarks on the taxonomy of *Chydorus sphaericus* (O.F. Müller, 1776)

Литоральные Cladocera (Crustacea: Branchiopoda) горных озер Алтая с таксономическими заметками о *Chydorus sphaericus* (O.F. Müller, 1776)

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KEY WORDS: faunistics, Cladocera, *Chydorus sphaericus*, Altai, mountain lakes, littoral zone.
КЛЮЧЕВЫЕ СЛОВА: фаунистика, Cladocera , *Chydorus sphaericus*, Алтай, горные озера, литоральная зона.

ABSTRACT: The faunistic data on Cladocera (Crustacea) of the Altai Mountains are summarized from published and the author's records. The latter include data on 18 lakes situated between 450 and 2700 m a.s.l. Of 22 species of littoral cladocerans, which are mostly eurytopic and widely distributed, five are recorded for the region for the first time. Cluster analysis revealed three groups of habitats that differ in their cladoceran species composition. A detailed investigation of the population of *Chydorus* cf. *sphaericus* from Lake Verhnii Kuyguk (2250 m a.s.l.) and its comparison with the type material of the species revealed substantial morphological differences. Nevertheless, the absence of males and gamogenetic females made it impossible to come to an unambiguous conclusion regarding the taxonomic status of the Altaian *Chydorus*.

РЕЗЮМЕ: Фаунистические данные по ветвистоусым ракообразным горных озер Алтая обобщены по литературным источникам и собственным сборам проб. Последние были проведены на 18 озерах, расположенных на высоте 450–2700 м над ур.м. Из 22 собранных видов, большинство из которых оказались эвритопными и широко распространенными, пять были отмечены для данного региона впервые. Кластерный анализ выявил три группы водоемов, различающихся по видовому составу кладоцер. При сравнении популяции *Chydorus* cf. *sphaericus* из озера Верхний Куйгук (2250 м над ур.м.) с описанием типового материала были обнаружены существенные отличия. Вследствие отсутствия самцов и гамогенетических самок таксономический статус алтайской популяции *Chydorus* остается неопределенным.

Introduction

The cladoceran fauna of the Altai mountain region remained to be scarcely investigated. The only specific faunistic survey on Cladocera was made by Sars and published in two papers [Sars, 1903a, b]. There were also a few studies on zooplankton, some of which contained occasional records of littoral species [Rylov, 1949; Shipunova, 1991; Zuykova, 1998; Vesnina et al., 1999; Popov et al., 2003]. All the species so far recorded from the Altai Mountains are widely distributed, occurring in lowlands as well, and a sole species — the recently described *Alona werestschagini* Sinev, 1999 — has a disjunct arctic-alpine range. To date, according to published data, the cladoceran fauna of the region numbered 32 species (Table 1).

The lakes under consideration are oligotrophic and have low bioproductivity and comparatively poor species richness [Alekin, 1935; Smirnov, 1935; Shipunova, 1980, 1991; Popov et al., 2003]. Nevertheless, the latter appears to be higher than was known before, because the littoral zone, generally having a higher diversity of Cladocera [Smirnov, 1971], remained poorly investigated. Thus, the present study is aimed at the littoral cladoceran fauna of the region.

The sample from Lake Verhnii Kuyguk (2250 m a.s.l.) contained an abundant population of *Chydorus* cf. *sphaericus*, which was sufficient for taxonomical study. The taxonomy of *Chydorus sphaericus* (O.F. Müller, 1776) is not fully clarified up to now. Frey [1980, 1985] redescribed *C. sphaericus* s.str. from Denmark and proposed that the former taxon *Chydorus sphaericus* is a species complex with an unknown number of species. Afterwards D. Frey described two new species of this complex from North America [Frey, 1980, 1985], but in the eastern hemisphere only a few European populations have been analyzed [Duigan & Murray, 1987; Duigan, 1992; Røen, 1987]. Here, the morphology and size-frequency distribution of the population sampled in Altai was investigated in detail in order to define its taxonomic status.

Table 1. Published records on Cladocera from Altai mountain lakes and species, collected during this study.
Таблица 1. Литературные данные по Cladocera горных озер Алтая и виды, собранные во время данного исследования.

	Our data	Sars [1903]	Rylov [1949]	Shipunova [1991]	Zuykova [1998]	Sinev [1999]	Vesnina et al. [1999]	Popov et al. [2003]
Acroperus harpae	•							•
Alona affinis	•	•	•		•		•	•
Alona costata								•
*Alona guttata**	•							
Alona quadrangularis				•			•	
Alona rectangula		•						
Alona werestschagini	•					•		
Alonella excisa	•		•					
*Alonella nana**	•							
Bosmina longirostris	•	•	•		•		•	•
Bosmina longispina	•	•	•					
Ceriodaphnia affinis					•			•
Ceriodaphnia quadrangula	•	•			•		•	•
Ceriodaphnia reticulata	•						•	
*Ceriodaphnia rotunda**	•							
*Ceriodaphnia pulchella**	•							
Chydorus ovalis				•				
Chydorus sphaericus	•	•		•	•		•	•
Daphnia cucullata				•			•	•
Daphnia hyalina					•			
Daphnia longispina	•	•					•	•
Daphnia pulex		•		•				•
Diaphanosoma brachyurum	•		•	•	•		•	
Graptoleberis testudinaria	•				•			•
Eurycercus lamellatus	•	•		•				
Leptodora kindtii		•					•	
Macrothrix hirsuticornis		•		•				
*Macrothrix groenlandica**	•							
Macrothrix sp.					•			
Moina macrocopa							•	
Pleuroxus striatus								•
Pleuroxus truncatus	•							•
Pleuroxus uncinatus		•						
Polyphemus pediculus	•			•	•		•	•
Scapholeberis microcephala							•	
Scapholeberis mucronata	•	•		•	•			•
Sida cristallina			•		•			•
Simocephalus vetulus	•	•	•		•			•

*species recorded for the first time.

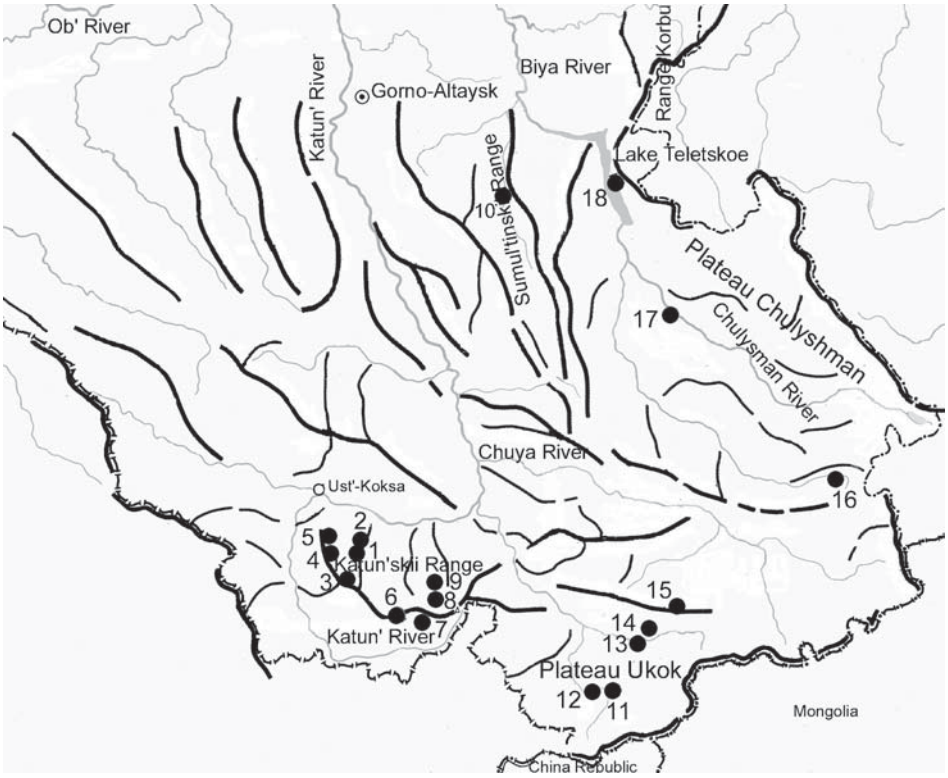


Fig. 1. Map of the Altaian ranges with marked sampling localities.
Рис. 1. Карта горных хребтов Алтая с отмеченными местами сбора проб.

Materials and Methods

Qualitative samples were taken in the littoral zone of 18 lakes in Mountain Altai (Fig. 1).

LIST OF LOCALITIES

Katunskii Range.

1. Verhnii Kuyguk: 49º58′N, 86º53′E; 2250 m a.s.l.; a large barrier lake connected with the Lower Kuyguk by a stream. It is situated on the border of the alpine and subalpine zones.

2. Nizhnii Kuyguk: 49º 58′N, 86º53′E; 2200 m a.s.l.; it is smaller and shallower than the previous one. It is the source of the River Kuyguk.

3. Verhnee Mul'tinskoe: 49º55′N, 86º51′E; 1770 m a.s.l.; a lake of complex origin: the southern part is barrier and the northern portion is ice-scoured. It is situated on the border of the alpine and subalpine zones.

4. Srednee Mul'tinskoe: 49º59′N, 86º51′E; 1640 m a.s.l.; a subalpine lake, the only one in Katunskii Range with vegetation in the littoral zone (*Carex* sp.).

5. Nizhnee Mul'tinskoe: 50º00′N, 86º51′E; 1640 m a.s.l.; a large subalpine lake with stony banks, a source of the River Mul'ta.

6. Kucherlinskoe: 49º50′N, 86º26′E; 1780 m a.s.l.; a large, two kilometer-long lake in the forested belt.

7. Svyatoe: 49º50′N, 86º28′E; 2400 m a.s.l.; a small rounded tarn situated directly under a glacier. The water is of low transparency due to the high content of glacial silt.

8. Akkayukskoe # 4: 49º52′N, 86º32′E; 2500 m a.s.l.; a small tarn under Akkayuk glacier in the treeless belt. The water with a high content of glacier silt. The numbers to this and the following lake are given after Alekin [1935].

9. Akkayukskoe # 5: 49º50′N, 86º28′E; 2400 m a.s.l.; a very shallow tarn in the treeless belt with significant in- and outflow and comparatively transparent water.

Sumul'tinskii Range.

10. Uymen': 1600 m a.s.l. A large subalpine lake situated near Gorno-Altaysk.

Plateau Ukok.

11. Ukok: 49º15′N, 87º23′E; 2420 m a.s.l.; sampled near the inflow of the river Kara-Bulak. A large lake in the system of the Argut River.

12. An isolated pond near the West edge of Lake Ukok: 49º15′N, 87º23′E; 2420 m a.s.l.

13. Unnamed lake with its outflow into Lake Chembak-Kul: 49º25′N, 88º08′E; 2700 m a.s.l.

14. Chembak-Kul': 49º26′N, 88º09′E; 2640 m a.s.l. A large lake in the system of the Argut River.

15. Unnamed lake in the Kypchil valley, in the system of the Argut River: 49º25′N, 88º08′E; 2050 m a.s.l.

16. Dlinnoe (Shaldan-Kol): 50º13′N, 89º15′E; 2270 m a.s.l; in the Chuya River basin.

Plateau Chulyshman.

17. A lake in the basin of the River Chulyshman: 50º35′N, 88º15′E; 1500 m a.s.l.

Range Korbu.

18. Teletskoe: 51º35′N, 87º30′E; 450 m a.s.l. A large subalpine lake, the best studied water body in Mountain Altai.

The sampling in localities 1–16 was conducted in August, 2000; in localities 17, 18 — in August 1999. The lakes of Katunskii Range were sampled by the author, N 10 by M. Afonina, ## 11–16 by A.S. Golubtsov, # 17 by N.V. Levina, # 18 by P.V. Matekin.

Table 2. Occurrence of Cladocera in the investigated lakes.
Таблица 2. Встречаемость кладоцер в исследованных озерах.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Occ.*
Acroperus harpae			p	p	p						p	p		p	p	p		p	50.0
Alona affinis				p	a					p	p				p	p		p	38.9
Alona guttata												a			p	p			16.7
Alona werestschagini	p	p	p	p	a	p				p	p		a			p		p	61.1
Alonella excisa															p	p	p		16.7
Alonella nana											p		p	p	p	p			27.8
Bosmina longirostris											p		p						11.1
Bosmina longispina											p			p	p	p		p	27.8
Ceriodaphnia pulchella															p			p	11.1
Ceriodaphnia quadrangula																		p	5.6
Ceriodaphnia reticulata																	p		5.6
Ceriodaphnia rotunda																	p		5.6
Chydorus sphaericus	a	p	p	p	p			p		a	p	p	p	p		a	p		72.2
Daphnia longispina				p							p	a		p					22.2
Diaphanosoma brachyurum																		p	5.6
Eurycercus lamellatus										p	p	p		p	p	a	p	a	44.4
Graptoleberis testudinaria																		p	5.6
Macrothrix groenlandica	p	p				a												p	22.2
Pleuroxus truncatus															p	p			11.1
Polyphemus pediculus																	p	p	11.1
Scapholeberis mucronata				p											p	p			16.7
Simocephalus vetulus											p				p	p			16.7
Total species number	3	3	3	6	4	2	0	1	0	4	10	5	4	6	11	12	6	11	

p — present; a — abundant
Occ.* — occurrence, %

Data on the geology and hydrochemistry of the Altaian lakes, including those listed above, are given by Alekin [1935], Lepneva [1937], Popov et al. [2003]. These lakes are of three types by genesis: shallow tarns with a granite bed, large and deep alpine barrier lakes, and ice-scoured subalpine lakes. They are situated in the treeless alpine belt and in the forested subalpine belt, in a remote area, unexposed to direct anthropogenic impact.

All the localities were sampled during the warmest season — in August, when the water temperature varied within 5–12°C. The bottom substrate of all the lakes was rocky, with gravel and a thin layer of sediments consisting mainly of glacial silt. Of the lakes of Katunskii Range, only Srednee Mul'tinskoe had littoral vegetation. The lakes of Plateau Ukok and Teletskoe had fairly well-developed vegetation (described in Popov et al. [2003]).

Samples were collected with a hand plankton net (diameter 25 cm, mesh size 50 μm). Each lake was sampled in two — five inshore locations. Samples were preserved in 4% formalin or 70% ethanol. The occurrence of Cladocera in the samples is given in Table 2. The species represented by more than 20 specimens in a sample are shown in Table 2 as abundant (a), fewer than that as present (p). Samples from localities 7 and 9 contained no cladocerans.

Drawings were made by means of camera lucida. To study the fine morphology of *Chydorus,* some specimens were lyophilized, mounted on stubs, coated with silver and examined under a scanning electron microscope (Hitachi S 405-A at Biological Faculty of Lomonosov Moscow State University). About 150 parthenogenetic females, both juveniles and adults, were measured to reveal the size-frequency population structure.

Cluster analysis was applied to differentiate lakes regarding their cladoceran species composition. The lakes containing no Cladocera (localities 7 and 9 in the list above) were excluded from the analysis. Localities 1 and 2 had an identical species composition and were united. The data were examined using the Sørensen similarity index [Sørensen, 1948]:

$$D(X, Y) = 2a / (2a + b + c);$$

where a = the number of shared species for the lakes X and Y, b and c = the number of species recorded only in each of the lakes.A successive cluster analysis by the method of average adjunction was applied to the matrix of similarity indexes. The similarity between groups was calculated as a mean from the values of similarity between all possible pairs of lakes from these groups. All calculations were performed using the statistical packages on ecology "EKOS", worked out by A. Azovsky (Moscow State University).

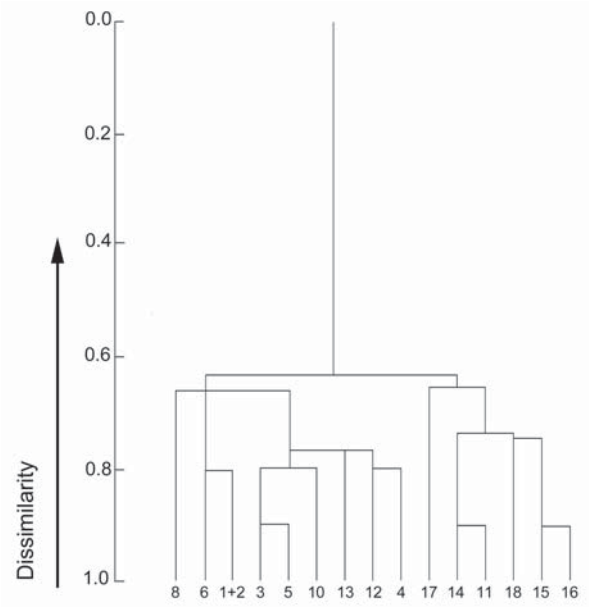


Fig. 2. Clustering of the lakes according to the cladoceran species composition.

Рис. 2. Распределение озер по кластерам в соответствии с видовым составом кладоцер.

Results

Species composition

Altogether, 22 cladoceran species were found. Five species: *Alona guttata* Sars, 1862, *Alonella nana* (Baird, 1850), *Ceriodaphnia pulchella* Sars, 1862, *C. rotunda* Sars, 1862, *Macrothrix groenlandica* Lilljeborg, 1900 have been recorded for this region for the first time. On the other hand, 15 species, recorded by the previous researchers, also from the pelagic zone, were absent in our collection (Table 1).

Two species, *Chydorus* cf. *sphaericus* and *Alona werestschagini,* occurred in more than a half of the localities. Five species, *Ceriodaphnia quadrangula* (O. F. Müller, 1785), *C. reticulata* (Jurine, 1820)*, C. rotunda* Sars, 1862*, Diaphanosoma brachyurum* (Lievin, 1848)*, Graptoleberis testudinaria* (Fisher, 1851)*,* were encountered only in one locality each. Representatives of the family Chydoridae predominated both qualitatively and quantitatively (Table 2).

Cluster analysis revealed two compact clusters, each of them containing lakes inhabited by 3 or more species (Fig. 2). Some lakes, inhabited by 1–3 species, were not clustered due to the low number of species and they are assumed to be similar in their environmental conditions to those lacking any cladocerans. Hence, we regard the latter as belonging to a first group and the clustered lakes as belonging to a second and a third groups respectively.

The first group contains water bodies (## 1, 2, 6, 7, 8, 9 in the list above) with the poorest species composition of 0–3 species situated at high altitudes (1770–2500 m a.s.l.) in Katunskii Range, both tarns and barrier lakes. The species encountered here are: *Chydorus* cf. *sphaericus, Alona werestschagini* and *Macrothrix groenlandica*.

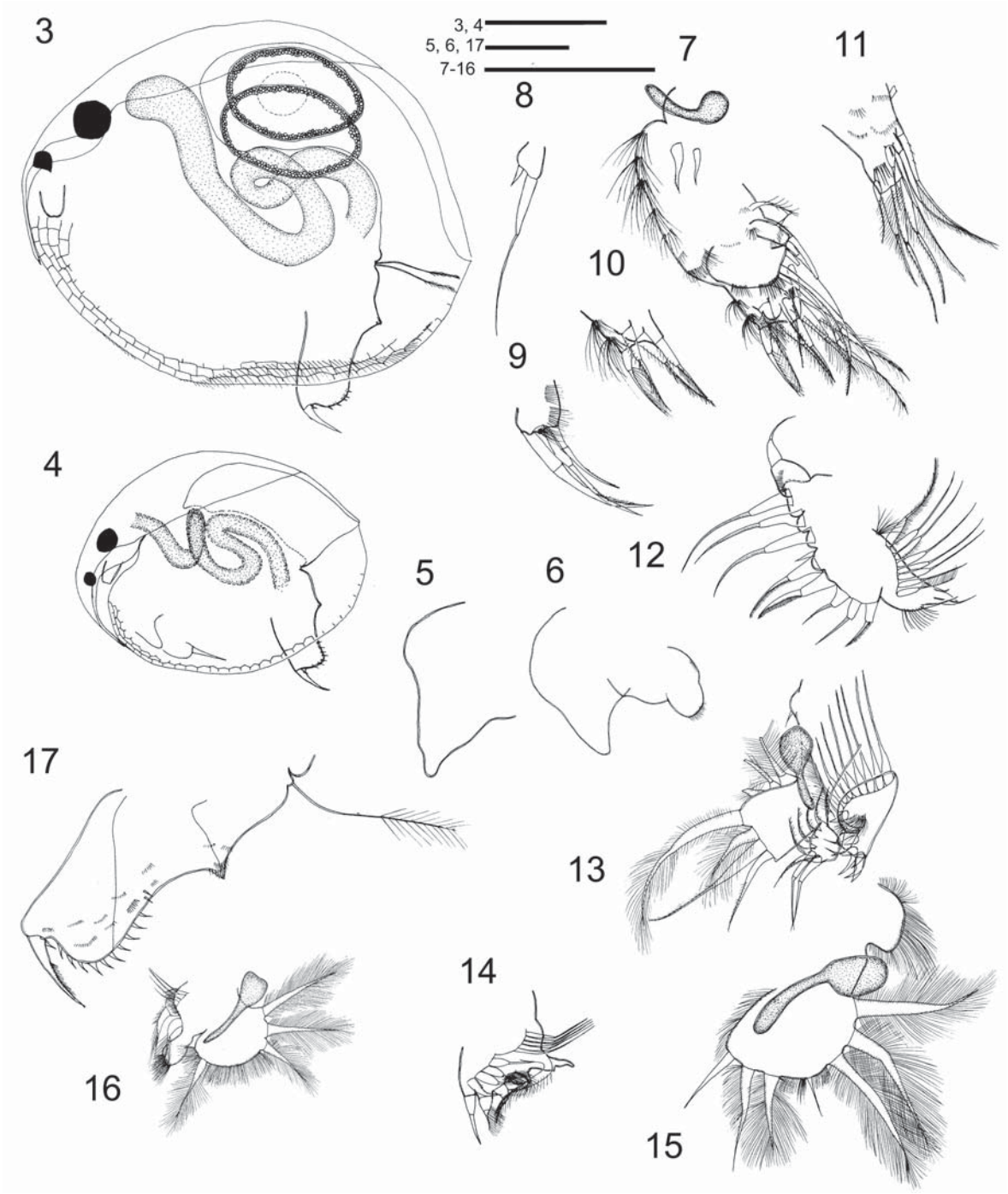
The second group contains alpine barrier lakes (## 3, 4, 5, 10, 12,13), situated between 1600 m and 2700 m a.s.l. within different ranges. Each lake was inhabited by 3–6 species, and 10 species *in toto* were encountered here: *Chydorus* cf. *sphaericus, Alona werestschagini, Acroperus harpae* (Baird, 1834)*, Alona affinis* (Leydig, 1860)*, Eurycercus lamellatus* (O.F. Müller, 1785)*, Daphnia longispina* O.F. Müller, 1776*, Alona guttata* Sars, 1862, *Alonella nana* (Baird, 1850)*, Bosmina longirostris* (O.F. Müller, 1785)*,* and *Scapholeberis mucronata* (O.F. Müller, 1785).

Lakes of the third group were situated within a wide range of altitudes (450–2650 m), both in the alpine and subalpine belts (## 11, 14, 15, 16, 17, 18). They were characterized by high species richness: 6-12 species in each lake and 22 species in sum, including those ones occurring in the lakes of the two previous groups. Species found only in lakes of the third group are as follows: *Alonella excisa* (Fisher, 1854)*, Bosmina longispina* Leydig, 1860*, Pleuroxus truncatus* (O.F. Müller, 1785)*, Polyphemus pediculus* (Linne, 1761)*, Simocephalus vetulus* (O.F. Müller, 1776)*, Ceriodaphnia pulchella, C. quadrangula, C. reticulata, C. rotunda, Graptoleberis testudinaria*, *Diaphanosoma brachyurum*.

Taxonomic remarks on some species

Alona werestschagini, previously included in *Alona guttata* has been recently described as a separate species [Sinev, 1999]. This is the second record of the species from Altai after its original description, where the author records it from Lake Teletskoe. *A. werestschagini* proved to be one of the commonest cladocerans in the lakes of Mountain Altai after *Chydorus* cf. *sphaericus*, being found in 10 of 18 water bodies (Table 2). The Altaian *A. werestschagini* mostly corresponds to the species description. The only exception is that the marginal denticles of the postabdomen are not grouped as in the type specimens from Tien Shan but are mostly single like in *A. guttata*. In the lakes of the third group *A. werestschagini* coexisted with *A. guttata*, but they were easily distinguished by difference in body size. *A. werestschagini* has a disjunct range, being found only in the Arctic region and in Tien Shan and Altai mountains [Sinev, 1999].

Macrothrix groenlandica differs from the closely related *M. hirsuticornis* Norman & Brady, 1867 in the presence of prominence on the headshield and additional large spines on the second antennae [Negrea, 1983; Smirnov, 1992]. The great variability of these diagnostic traits caused doubts of the validity of the taxon [Usai & Margaritora, 1987], but in the absence of detailed investigation the problem remains as yet unsolved. For this reason we follow the last revision of the family Macrothricidae [Smirnov, 1992], considering these species as separate. Published records of *M. hirsuticornis* from Mountain Altai are assumed to be misidentifications of *M. groenlandica*. This species was recorded



Figs. 3–17. *Chydorus* cf. *sphaericus* from Lake Verhnii Kuyguk, parthenogenetic female: 3 — mature female; 4 — I-instar female; 5–6 — labrum; 7–11 — limb I and its fragments; 12 — limb II; 13 — limb III; 14–15 — limb IV; 16 — limb V; 17 — postabdomen. Scales: 100 μm for 3, 4; 50 μm for 5–17.

Рис. 3–17. *Chydorus* cf. *sphaericus* из озера Верхний Куйгук, партеногенетическая самка: 3 — взрослая самка; 4 — самка первого возраста; 5–6 — лябрум; 7–11 — нога I и ее фрагменты; 12 — нога II; 13 — нога III; 14–15 — нога IV; 16 — нога V; 17 — постабдомен. Масштаб: 100 μm для 3, 4; 50 μm для 5–17.

only from the Arctic region (Greenland, Iceland, North Europe) and mountains in Europe (Alps, Carpates, Pyreneans, Caucauses) [Negrea, 1983; Smirnov, 1992].

Bosmina longispina Leydig, 1860 was recorded from Mountain Altai by Sars [1903a, b] under the name *B. obtusirostris*, which is considered now as a synonym of the former species [Lieder, 1996]. Hence, the records of *B. obtusirostris* are given in Table 1 as *B. longispina.*

Sars [1903a, b] recorded six varieties of *Daphnia longispina* from Altai, all of which as well as the general

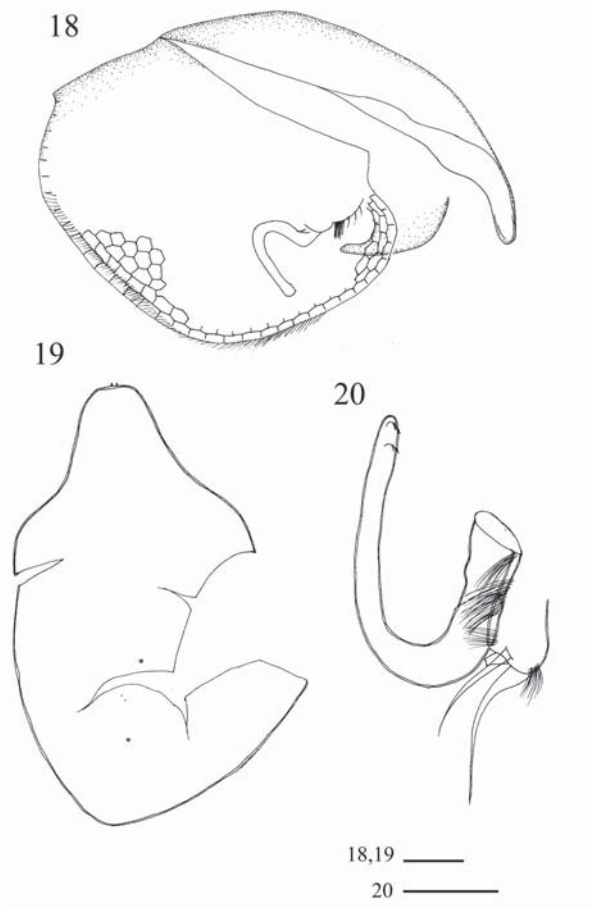
taxonomy of the species needs detailed reexamination as well.

Ceriodaphnia affinis Lilljeborg, 1901 has been synonymized with *C. dubia* Richard, 1894 [Berner, 1986], the validity of that synonymy needs to be acertained by further research.

Comparison of Altaian *Chydorus* cf. *sphaericus* with the known European populations of the *C. sphaericus* species complex

The morphology of *Chydorus* cf. *sphaericus* from Lake Verhnii Kuyguk, a population consisting of only parthenogenetic females, is illustrated by Figs. 3–17; 21–32. The size-frequency distribution is given in Fig. 33.

In spite of the observed differences (see below), *Chydorus* from Lake Verhnii Kuyguk belongs to the *C. sphaericus* species complex sensu Frey [1980], which is proved by the following characters: presence of polygons in shell reticulation with wavy margins and of elongated labral keel; absence of dimples in shell sculpture and line, connecting setules of ventral shell margin; similarity in morphology of thoracic limbs, postabdominal claw and shape of male copulatory hook typical of *C. sphaericus* species complex.



Figs. 18–20. *Chydorus* cf. *sphaericus*, male exuvium from Lake Srednee Mul'tinskoe: 18 — exuvium; 19 — separated head shield; 20 — copulatory hook. Scales: 50 μm for 18, 19; 20 μm for 20.

Рис. 18–20. *Chydorus* cf. *sphaericus*, экзувий самца из озера Среднее Мультинское: 18 — экзувий; 19 — отделенный головной щит; 20 — копулятивный крюк. Масштаб: 50 μm для 18, 19; 20 μm для 20.

There are only two well-described populations of the *C. sphaericus* species complex from the eastern hemisphere: one from Denmark [Frey, 1980, 1985; Duigan & Murray, 1987] and one from Ireland (morphotype 1) [Duigan & Murray, 1987; Duigan, 1992]. Morphological comparison of the Altaian *Chydorus* with the published descriptions of these populations is presented in Table 3. Comparison of the population size structures is presented in Table 4. There are no significant differences between the Danish and Irish populations, but the Altaian *Chydorus* is somewhat different from these two. Each juvenile instar is larger and reproduction starts at a larger size than in European populations. This could possibly be correlated with slower growth rates and longer periods between instars associated with lower water temperatures in the Altaian lakes, as such increase in size was shown for Cladocera at low temperatures [Frey & Hann, 1985]. Nevertheless, the maximum size of mature females does not differ significantly among all three populations.

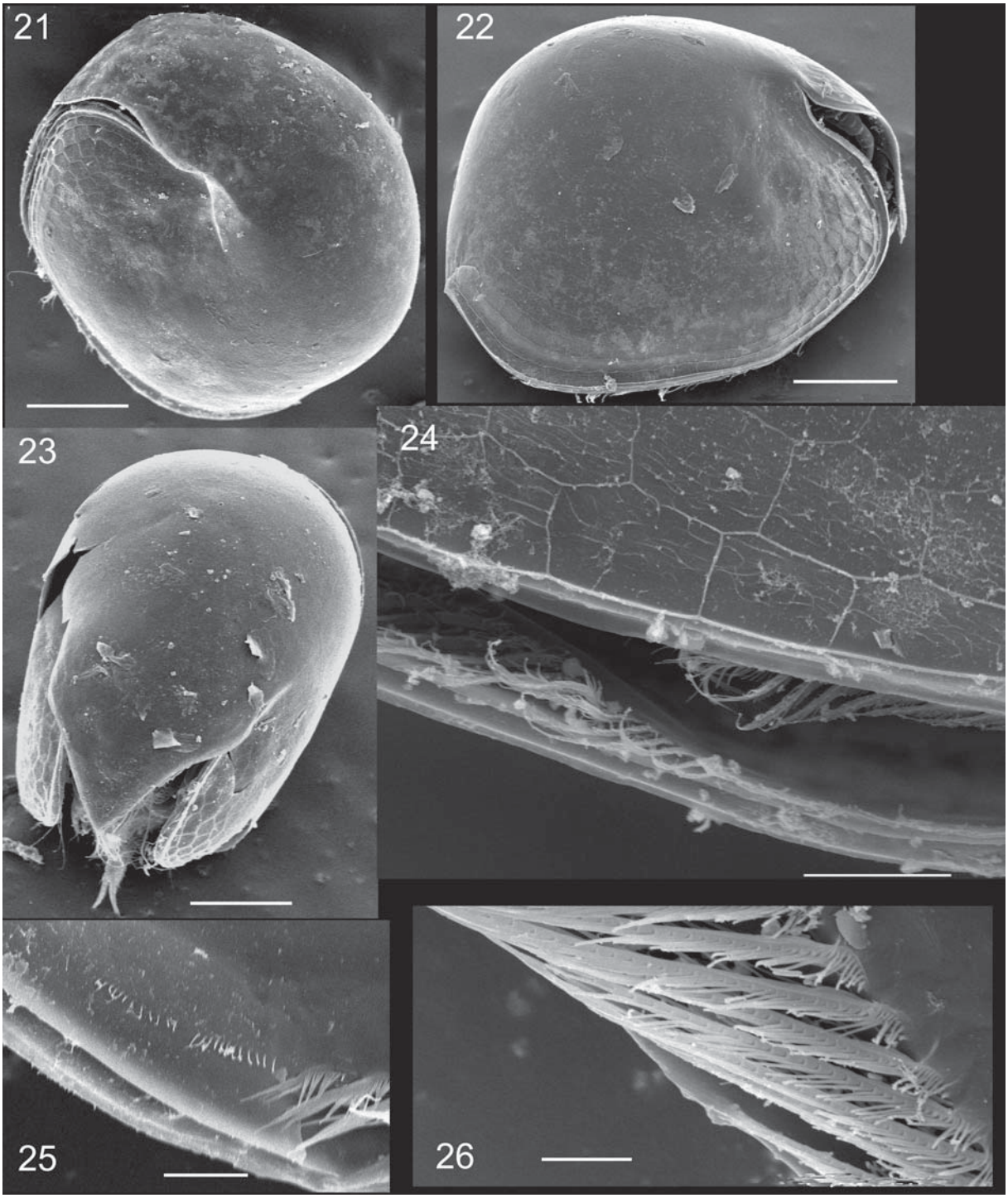
The only male specimen found, an exuvium consisting of a shell and first trunk limb from Lake Srednee Mul'tinskoe (Figs. 18–20), was also used for morphological comparison (Table 3).

Discussion

Occurrence and distribution of Cladocera in Mountain Altai

With the addition of the author's data, the known cladoceran fauna of Mountain Altai yields 37 species. It has no endemic taxa and it is similar to the faunas of other mountain water bodies in the temperate latitudes. Of the 22 species found, 19 are eurytopic and widely distributed all over the Palearctic or Holarctic regions. The cold-stenothermic species *Alona werestschagini* and *Macrothrix groenlandica* were encountered in the most of the lakes, but they do not occur in the lowland Altai where two closely related species —*Alona guttata* and *Macrothrix hirsuticornis* appear to occur instead [Vesnina et al., 1999]. The two former species have disjunct ranges, occurring in southern alpine and Arctic water bodies [Sinev, 1999; Smirnov, 1992]. Another probable cold-stenotermic species with a restricted range is *Chydorus* cf. *sphaericus* but its taxonomical status can be determined only by investigation of a gamogenetic population (see below).

The grouping of lakes provided by the cluster analysis does not correlate with altitude. Other factors have a greater influence on cladoceran distribution, as it has been pointed out by previous researchers [Smirnov, 1935; Shipunova, 1991]. Among them, low water temperatures and low organic content as well as the absence of littoral vegetation (macrophytes find no suitable substratum on rocky shores) restrict the range of most

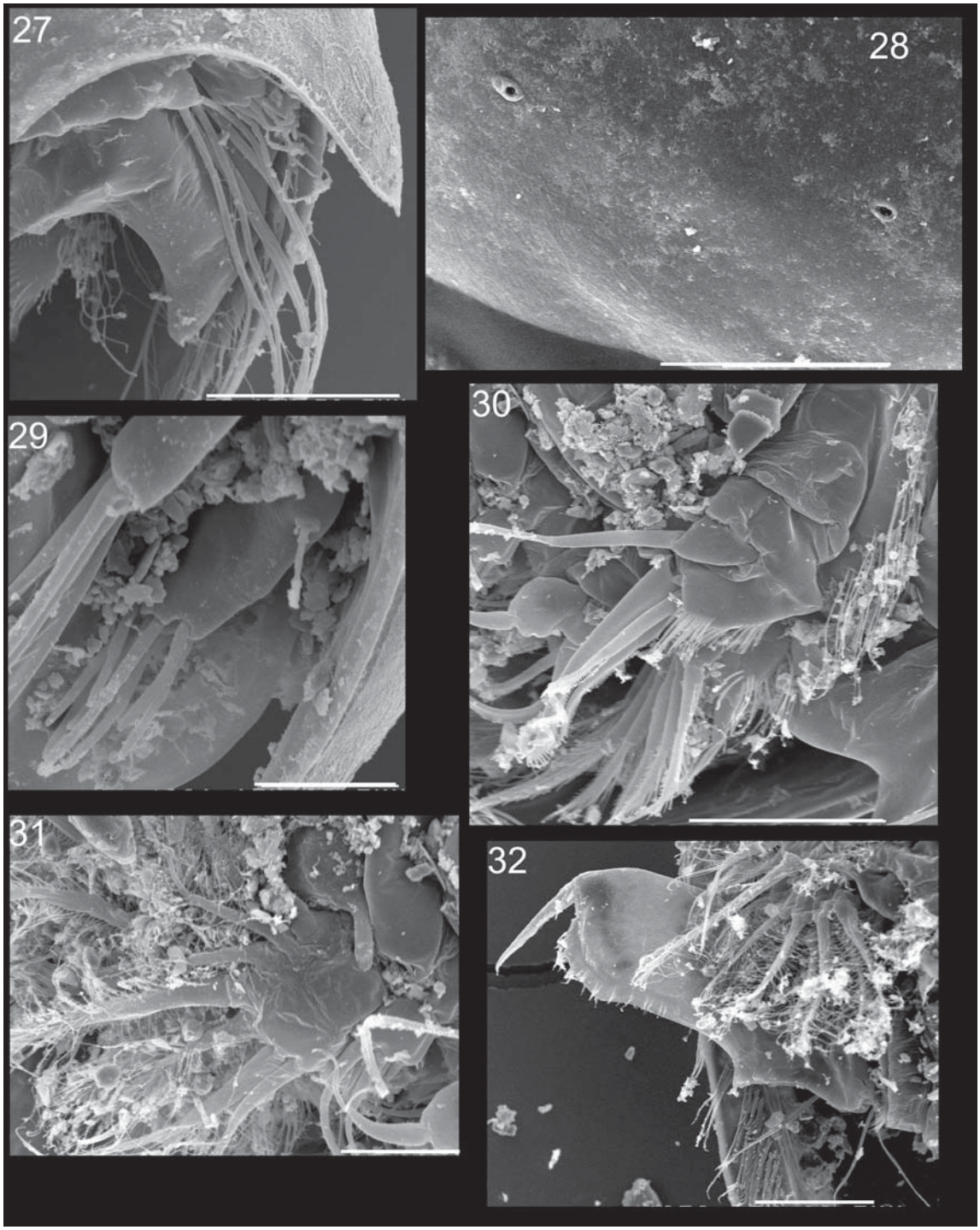


Figs. 21–26. *Chydorus* cf. *sphaericus* from Lake Verhnii Kuyguk, parthenogenetic female: 21 — dorsal view; 22 — lateral view; 23 — frontal view; 24 — reticulation of the shell margin; 25 — setation on the inner surface along the posterior margin; 26 — setation of the ventral margin. Scales: 100 мм for 21–23; 20 μm for 24; 10 μm for 25, 26.

Рис. 21–26. *Chydorus* cf. *sphaericus* из озера Верхний Куйгук, партеногенетическая самка: 21 — вид сверху; 22 — вид сбоку; 23 — вид спереди; 24 — ретикуляция края створки; 25 — щетинки на внутренней поверхности вдоль заднего края; 26 — щетинки брюшного края. Масштаб: 100 μm для 21–23; 20 μm для 24; 10 μm для 25, 26.

species. The importance of the latter factor is confirmed by the significant increase in the species number in the lakes of the third group, where littoral macrophytes are well developed.

Thus, the species richness of Cladocera in Mountain Altai changes from poor communities in the rocky littoral of high-mountain lakes to fairly diverse ones in the littoral with well-developed vegetation and better



Figs. 27–32. *Chydorus* cf. *sphaericus* from Lake Verhnii Kuyguk, parthenogenetic female: 27 — head in lateral view; 28 — head pores; 29 — antennule; 30 — limb I; 31 — limb III; 32 — postabdomen. Scales: 50 μm for 27, 28 30, 32; 20 μm for 29, 31.

Рис. 27–32. *Chydorus* cf. *sphaericus* из озера Верхний Куйгук, партеногенетическая самка: 27 — голова сбоку; 28 — головные поры; 29 — антеннула; 30 — нога I; 31 — нога III; 32 — постабдомен. Масштаб: 50 μm для 27, 28 30, 32; 20 μm для 29, 31.

food supply. The species inhabiting the lakes of the thirst two groups continue to occur in more favourable conditions of the lakes of the third group. This displays a high degree of similarity between all lakes in Mountain Altai. In the mean time, the mountain lakes were shown to have lower faunistic similarity with lowland lakes than between the latter of different regions in Altai [Vesnina et al., 1999]. In addition to this, we found a few species, which occur in the mountain lakes, but not in the lowland ones: *Alona werestschagini*, *Macrothrix groenlandica*,

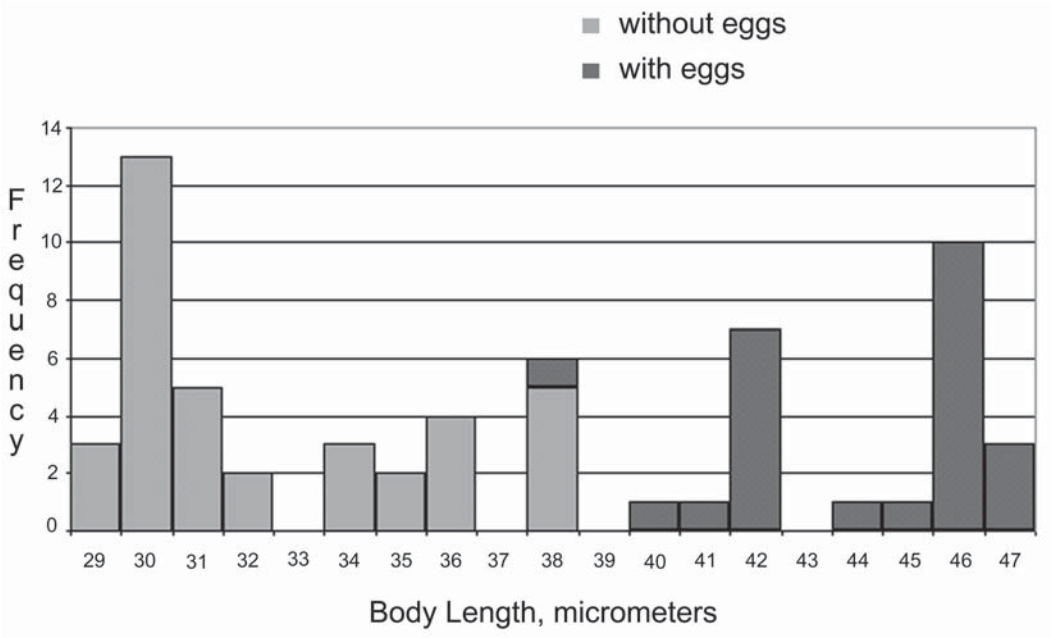


Fig. 33. Size-frequency distribution of the population of *Chydorus* cf. *sphaericus* from Lake Verhnii Kuyguk.
Рис. 33. Размерно-частотное распределение популяции *Chydorus* cf. *sphaericus* из озера Верхний Куйгук.

Table 3. Comparison of Altaian *Chydorus* cf. *sphaericus* with the European populations of the *C. sphaericus* species complex.
Таблица 3. Сравнение алтайского *Chydorus* cf. *sphaericus* с европейскими популяциями из видового комплекса *C. sphaericus*.

Character	*C. sphaericus* s.str. (Denmark)	*C. sphaericus*, morphotype I (Ireland)	*C.* cf. *sphaericus* (Altai)
Parthenogenetic females			
covers and reticulation pattern	1. 1–3 rows of dimple-like depressions along antero-ventral and posterior margins	1. no such depressions	1. no such depressions (Figs. 22, 24)
	2. fine tubercles anterior to head pores	2. fine tubercles anterior to head pores	2. no tubercles (Figs. 23, 28)
	3. reticulation pattern covers most of shell and headshield	3. reticulation pattern covers most of shell and headshield	3. reticulation pattern consists of 2–3 rows along anterior and ventral margins and at the end of rostrum (Figs. 3, 4, 21–24)
	4. distinct lines formed by reticulation pattern, connecting major pores	4. only remains of reticulation pattern between major pores	4. no reticulation pattern between major pores (Fig. 28)
body colouration	5. light-coloured	5. light-coloured	5. dark-coloured
postabdomen	6. marginal denticles straight, not increasing markedly in length distally	6. marginal denticles slightly curved, distal ones markedly stouter than proximal ones	6. marginal denticles slightly curved, distal ones markedly stouter than proximal ones (Figs. 17, 32)
Male			
copulatory hook	7. three curved rugae at tip	7. no description	7. two curved rugae at tip (Fig. 20)

and probably *Chydorus* cf. *sphaericus*. Therefore, Altai mountain lakes are not just extreme water bodies inhabited only by tolerant eurytopic species, but they represent a specific type of habitats.

It is interesting to note, that in some lakes with a low number of species, cladocerans sometimes had high population densities (Table 2). For example, *Alona werestschagini* was abundant in Lake Nizhnee Mul'tinskoe and Kucherlinskoe, though the zooplankton of these lakes had been shown to be extremely poor quantitatively [Smirnov, 1935]. As quantitative studies in the littoral zone have never been conducted in Mountain

Table 4. Comparison of the size population structure of Altaian *Chydorus* cf. *sphaericus* with the European populations from the *C. sphaericus* species complex. About 50 specimens of each of three age groups (I and II juvenile instars and mature females) were measured in each instance.
Таблица 4. Сравнение размерной структуры популяции алтайского *Chydorus* cf. *sphaericus* с европейскими популяциями из видового комплекса *C. sphaericus*. В каждом случае были измерены около 50 экземпляров в каждой из возрастных групп (I и II ювенильные стадии и взрослые самки).

Parameter	*C. sphaericus* s.str. (Denmark)	*C. sphaericus* morphotype I (Ireland)	*C.* cf. *sphaericus* (Altai)
Body length / distribution peak, μm			
I instar	23–29 / 25	22–28 / 26	29–32 / 30
II instar	29–33 / 31	30–32 / 31	34–36 / 35
The smallest females with eggs, μm	33	36	38
Maximum body length, μm	49	46	47

Altai, it was believed that cladocerans never occur in great numbers here. Such abundance of Cladocera in oligotrophic lakes might be explained by a much better nutrient supply in the littoral zone compared to the pelagic one.

Sampling made only once in each locality is unlikely to reveal all the species inhabiting a lake; thus, further findings are quite probable. Nevertheless, collecting during the warmest season, when the development of populations is maximal and where the littoral zone is of homogenous structure (mainly rocky substrate without macrophytes), seems to reveal most littoral cladoceran species occurring in the region.

Taxonomical status of *Chydorus* cf. *sphaericus* from Lake Kuyguk

Altaian *Chydorus* undoubtedly belongs to the *C. sphaericus* species complex sensu Frey [1980], but differs from *C. sphaericus* s.str. in a number of characters (Table 3). The variability of *C. sphaericus* s.l. is not investigated well enough to judge the "weight" of the characters. The significance of such characters as shell and head shield reticulation, armament of postabdomen and copulatory hook and size population structure was estimated by Frey as high. However, more material is needed for the reliable estimation of these characters. At the same time, reliable discrimination of taxa of the species complex is impossible without gamogenetic females and males. Our material lacked these (only fragments of one male exuvium were present), which made it impossible to come to an unambiguous conclusion regarding the taxonomical status of the Altaian *Chydorus*.

ACKNOWLEDGEMENTS. I am very grateful to Dr. A.Yu. Sinev for his supervision and confirmation of the species identifications, to Dr. N.M. Korovchinsky for valuable critique and corrections of an earlier draft, and Dr. N.N. Smirnov for correcting the English of this paper. Some samples were kindly provided by M. Afonina, A.S. Golubtsov, N.V. Levina, P.V. Matekin. This study was supported by grant from the Russian Foundation of Basic Research (RFFI # 03-04-48879).

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