Acanthodiaptomus tibetanus (Daday, 1908) (Calanoida, Diaptomidae) – a biogeographic relict in the water bodies of Baikal Rift Zone

I F Krivenkova¹⁴, O G Pen'kova², N V Makarkina² and N G Sheveleva³

¹Institute of Natural Resources, Ecology and Cryology Siberian Branch of RAS, 16a, Nedorezova Street, Chita, 672014, Russian Federation
²Irkutsk State University, 1, Karl Marx Street, Irkutsk, 664003, Russian Federation
³Limnological Institute Siberian Branch of RAS, 3, Ulan-Batorskaya, Irkutsk, 664033, Russian Federation
⁴E-mail: krivenkova_iren@list.ru

Abstract. A detailed morphological description of the copepod Acanthodiaptomus tibetanus and its geographic distribution on the territory of Irkutsk Region, Buryat Republic, Zabaikalsky Region and Republic of Sakha (Yakutia) within the limits of Baikal Rift Zone is presented for the first time. The authors provided information on the paleogeographic conditions of the territory these crustaceans inhabited and characterized their habitats in brief. An overview of the personal data and available literature on the geographic distribution of A. tibetanus is given. One of the major results obtained under this study was elucidation of the distribution patterns of A. tibetanus. In order to understand current distribution patterns of organisms, A. tibetanus in particular, in different basins, we carried out a historical analysis of the relief formation taking into account climatic aspects involved in these transformations.

1. Introduction
Baikal rift zone (BRZ) started to evolve in the Neogene. It stretched for over 1800 km from Lake Khovsgol in the north of Mongolia across Baikal to northern Zabaikalye and southwestern termination of Yakutia (Republic of Sakha). Geomorphologists define the BRZ as a system of deep, linear elongated depressions stretching from the south-west to the north-east amidst high mountain ridges.

Lakes in the Baikal rift zone shelter relict flora and fauna [1]. Under repeated climatic changes, representatives of the flora and fauna were preserved as relict populations in refugia of this area. Relics of the pre-Pleistocene fauna that survived in these refugia may be termed “biogeographic relicts” [2]. The cladocerans Daphnia dentifera Forbes, 1893, Daphnia turbinata Sars, 1903 are the example of biogeographic relics in mountain bodies of water in the south of Eastern Siberia, lakes of the Baikal rift zone in particular: Tunka, Mysk-Chara depressions and Vitimsk plateau [3, 4]. This group also includes some copepods: A. tibetanus (Daday, 1908), Arctodiaptomus paulseni (Sars, 1903) [5, 6].

This study was focused on morphology and habitat area of A. tibetanus in water bodies of the Baikal rift zone.

2. Material and Methods
Samples to study the morphology of the copepod *A. tibetanus* were collected from twelve lakes in the BRZ and rivers north-west of Baikal (Figure 1) using a Juday net with a filtering sieve cone (mesh size 100 µm). The samples were fixed in 96% alcohol or 40% formaldehyde. Mature male and female specimens were picked up from samples for morphological analysis. Body length was measured from tip of rostrum to end of caudal rami. In this study, we used an optical microscope OLYMPUS BX 41 and a scanning electron microscope Quanta 200.

![Legend (Symbols)](image)

Legend (Symbols)
Are designated by figures:
- Lakes •
- 1. Ilheir
- 2. Stupa
- 3. Polovinskoe
- 4. Devochanda
- 5. Goltsvoe
- 6. Maloe Leprindo
- 7. Bolshoye Leprindo
- 8. Leprindokan
- 9. Bolshoy Namarakit
- 10. Dovochan
- 11. Nichatka
- 12. Tocco
- River ▲
- 13. Gramma

Figure 1. Schematic map showing localities where of *A. tibetanus* were found.

### 3. Results

According to scientific publications, for the first time *A. tibetanus* (Daday, 1908) was registered in mountain water bodies of southern Tibet and named after it. The species was found in the European part of Russia – northern Urals beyond the Arctic Circle, lake on the bank of the Kara River [9], water bodies in the north-eastern part of Bolshaya Zemlya tundra [10].

The first finding of the species in the Scandinavian countries, Lake Pilgujaur (Petsamo district, former Northern Finland) was reported by Kiefer (1978) [11]. Later the species was found in Sweden [12], Norway [13–15]. In Asia the species was encountered in Tibetan lakes and reported later [17–19].

The first records of finding *A. tibetanus* in lakes of Muysk-Chara Valley were published by Shulga [20]. Tomilov [21]. In late XX – early XXI century the researchers surveyed almost all deep lakes in Muysk-Chara depression, Vitim plateau and Stanovoy Range. As they reported, the dominant
zooplankton species was *A. tibetanus* [21–26]. Besides, *A. tibetanus* was found in the mouth part of the Gramna river (northwestern Baikal) [27] (table 1).

**Table 1.** Geographic and morphometric parameters of lakes and river.

| Locality                          | Lake, river name | Latitude, longitude | Elevation above sea level (m) | Depth (max) (m) | Surface area (km²) | Data       |
|-----------------------------------|------------------|---------------------|-------------------------------|-----------------|--------------------|------------|
| East Sayan Tunka depression       | Ilchir           | 51°58’ N, 100°59’ E | 1963                          | 12              | 3.1                | personal data|
|                                   | Stupa            | 51°39’ N, 100°53’ E | 2007                          | 7               | 0.5                | personal data|
| Vitim plateau                     | Polovinskoe      | 57°01’ N, 116°30’ E  | 1400                          | 21              | 0.319              | personal data|
| Stanovoy highlands                | Devochanda       | 56°48’ N, 116°10’ E  | 1174                          | 23              | 0.188              | [7]        |
|                                   | Goltsvoe         | 57°24’ N, 118°15’ E  | 1100                          | 25              | 0.126              | [7]        |
| Muysk-Chara depression            | Maloye           | 56°36’ N, 117°22’ E  | 986                           | 67              | 6.05               | personal data|
|                                   | Leprindo         | 56°37’ N, 117°31’ E  | 983                           | 65              | 18.1               | [8]        |
|                                   | Leprindokan      | 56°32’ N, 117°29’ E  | 1048                          | 32              | 12.1               | [8]        |
|                                   | Bolsyoy          | 56°14’ N, 116°57’ E  | 987                           | 35              | 11.8               | [8]        |
|                                   | Namarakit        | 57°26’ N, 117°33’ E  | 1104.8                        | 48.5            | 4.0                | [7]        |
| Patomsk highlands                 | Nichatka         | 57°45’ N, 117°65’ E  | 554                           | 117             | 40.5               | [8]        |
| Tokkinsk depression               | Tocco            | 57°11’ N, 119°41’ E  | 1360.3                        | 42              | 0.7                | [7]        |
| Baikalsky Ridge northwestern Baikal | River Granna   | 55°54’ N, 108°55’ E  | -                             | -               | -                  | personal data|

Records of finding *A. tibetanus* in lake Kutaramakan (Putorana Plateau) and Kureysk reservoir) are doubtful [28, 29], since morphology of mature specimens we examined showed differences between them and the species described by Kiefer (1978) [11].

In 1998-1999 and 2020, studies were carried out in water bodies of Tunka depression [5]. For the first time *A. tibetanus* was registered in the lakes in the south of Eastern Siberia: Ilchir and Bezmyannyoe. The zooplankton community was dominated by this species population. A thorough morphological examination using SEM allowed us to prove that *A. tibetanus* inhabiting water bodies of the area under study was identical to the species from a lake in southern Tibet and lakes of Muysk-Chara depression. A detailed description and illustrations of mature specimens of this population are given below.

Material. Zooplankton samples from Lake Bolshoe Leprindo (24.06.2000) and Lake Ilchir (29.09.2020).

Order Calanoida Sars, 1903
Family Diaptomidae Sars, 1903
Genus *Acanthodiaptomus* Kiefer, 1932
*Acanthodiaptomus tibetanus* (Daday, 1908)

Brief diagnosis. Female (figure 2). Lobes of last thoracic segment asymmetrical, left lobe larger than right, pointed, armed with a large distal sensory spine (figure 2a). Abdomen three-segmented, widened anteriorly. Inner margin of caudal rami bearing fine hair-like setulae, half-length of the distal portion. Antennule of female long, extending beyond caudal rami (figure 2a). Rostrum of female moderately developed with long processes (figure 2c). Second endopodite segment P2 without Schmeil'sche Lobus. Coxopodite of fifth pair of legs with a short spine (figure 2c), first exopodite
segment elongated with parallel sides, flat without projections (figure 2d). Second exopodite segment with a stout spiniform process bearing minute spinules (figure 2d, f). Third exopodite segment with strong spines, inner spine almost reaching end of second segment. Endopodite one-segmented, half the length of first exopodite, armed with two chitinous processes, one of them stout, 3 times longer than second one. Distal surface of endopodite covered by small cuticular processes (figure 2g). Female size 1.4–1.5 mm

**Figure 2.** Female structure of *A. tibetanus*

Male (figure 3). Abdomen symmetrical. Geniculating antennule on apical segment with a tooth-like process typical for the genus and relatively long conical process (figure 3c, b). Segment 13 of geniculating antennule with a long spine reaching almost middle of segment 16 armed with one short spine (figure 3b). The right fifth leg with short and broad coxopodite and basipodite, the latter broadened distally (figure 3d). First segment of exopodite short, broad with acutely tapering distal angle projecting outward. Second segment of exopodite wide in the proximal portion and abruptly narrowed beyond base of lateral spine 2. Lateral spine stout, slightly curved, attached to prominence in proximal part. Prehensile claw long, falciform, swollen at base. Right leg endopodite very short, barely reaching the distal margin of first exopodite. Left leg coxopodite and basipodite large. First
exopodite short, second exopodite with a long outer projection and a globular outgrowth covered with numerous fine cuticular processes on its caudal side, and 8–10 relatively large cuticular spinulae, flat on the dorsal side (figure 3f). Inner outgrowth relatively short with 1–2 cuticular spinulae at the apical margin, inner side bearing hair-like setulae along the full length (figure 3e, f). Endopodite one-segmented, massive, reaching middle of exopodite 2. Male size 1.3–1.25 mm.

**Figure 3.** Male structure of *A. tibetanus*

4. Discussion

During the last glaciation period in the Late Pleistocene, the northward flow of Siberian rivers was changed by interference of a continental glacier that resulted in origination of pre-glacial and ice-dammed lakes in the north. Glaciation on the territory of Altai, Sayan Mountains and Eastern Siberia was semi-superficial \[30, 31\]. It seems likely that populations mixed and some species isolated in refugia of Altai and Sayan at that time. Many refugia were located in the mountain areas which were sources of endemic forms on their own \[32\]. The species complex of cladocerans and copepods inhabiting water bodies of Altai-Sayan mountain region, including Mongolia and Baikal rift zone owes its peculiarity to the presence of *A. tibetanus*, *A. (S.) paulseni*, *D. dentifera*. The population of rare cladoceran and copepod species experienced severe bottleneck events during glaciations of the territory of Siberia \[3\]. After glacier retreat the population presumably grew in size to some extent, however, the area of these species was restricted to Altai-Sayan region. *A. tibetanus* was able to survive glaciations in periglacial mountain deep water bodies. Rift depressions (Lake Nitchatka) and inter-montane basins (Tunka, Muysk-Chara, Tokkin) might provide refugia for them. Isolation of *A.
A. tibetanus was associated with the post-glacial period in early Holocene and took place in already existing hydrological network under large-scale fall of the water level in the Pleistocene lakes caused by decrease of river runoff. At present, these relict bodies of water still harbor highly flexible or specialized Tertiary hydrobionts. Only psychrophilic species survived in deep lakes until the Holocene warming and outlasted environmental changes when climate altered between glacial and interglacial cycles [33]. However, existence of the Pleistocene hydrobiont refugia in southern Siberia and southern Asia remains insufficiently studied. There are some records of their occurrence in the Tibetan foothills and highlands. A. A. Tumilov thought that the lakes located in the basin of the Vitim and Olyokma rivers (Zabaikalye) existed even before the glaciation or were later connected with other large basins. The territory with diverse landscapes served the hotspot for specific hydrofauna formation [21].

5. Summary
In the Quaternary period (2.58 million years ago) A. tibetanus became isolated within some water bodies-refugia due to separation of aquatic fauna in ancient lakes. This psychrophilic species was able to tolerate temperature fluctuations during large climatic cycles in this environment. Obviously, A. tibetanus is a representative of relict ancient fauna surviving in refugia during several glacial periods. It may be assumed that A. tibetanus was common in the northern part of Eurasia in the pre-Pleistocene epoch. During Pleistocene the dispersal of this crustacean was occasionally limited to small refugia. Similar models of post-glacial expansion dated late Pleistocene were characteristic of the genus Polyphemus [34] and D. galeata population from North America and Japan [35].

Acknowledgments
Samples were collected on an expedition funded by the Russian Foundation for Basic Research, projects №. 20-54-44017.

References
[1] Pleshanov A S and Takhteev V V 2008 Refugia in Baikalian Siberia as reserves of unique biodiversity Proc. Conf. Evolution of Life under Abiotic Changes on the Earth (Novosibirsk: SB RAS Press) pp 358–70
[2] Grandcolas P, Nattier R and Trewick S 2014 Trends in Ecology and Evolution 29 655–63
[3] Zuykova E I, Bochkarev N P and Kotov A A 2020 Zool. Zh. 99 1110–23
[4] Zuykova E I, Sheveleva N G and Kotov A A 2019 Zootaxa 4658 317–30
[5] Bondarenko N A, Sheveleva N G and Domysheva V M 2002 Japan. Soc. Limnol. 3 127–33
[6] Sheveleva N G, Arov I V, Shaburova N I, Evstigneeva T D and Itigilova M Ts 2009 Biota of Water Bodies of the Baikal Rift Zone ed. A S Pleshakov (Irkutsk: Irkutsk State University Press) pp 83–94
[7] Obyazov V A and Enikeev F I 2009 A Small Encyclopedia of Zabaikalye. Natural Heritage ed R F Geniutlin (Novosibirsk: Nauka) pp 81–2
Obyazov V A and Enikeev F I 2009 A Small Encyclopedia of Zabaikalye. Natural Heritage ed R F Geniutlin (Novosibirsk: Nauka) pp 297
Obyazov V A and Enikeev F I 2009 A Small Encyclopedia of Zabaikalye. Natural Heritage ed R F Geniutlin (Novosibirsk: Nauka) pp 367
[8] Alekseev S S, Matveev A N, Pichugin M Yu, Samusenok V P and Sheveleva N G 2000 Bull. Moscow Society of Naturalists Biol. Section 105 22–41
[9] Smirnov S S 1930 Zool. Anz. 87 159–70
[10] Vekhov N V 1985 Inform. Bull. Inland Waters Biol. 66 31–4
[11] Kiefer F 1978 Das Zooplankton der Binnengewässer Freilebenden Copepoda (Stuttgart: E. Schweizerbart’sche Verlagsbuchhandlung) p 343
[12] Nauwerck A 1980 Arh. Hydrobiologia 89 247–64
[13] Huru H, Schartau A K L, Halsvorsen G, Nost T and Walseng B 1996 Crustacea 69 868–77
[14] Walseng B and Halsvorsen G 1996 Limnofauna Norvegica. Katalog over Norsk
Ferskvannsfauna ed K Aagaard and D Dolmen (Tapir: Trondheim) pp 103–7

[15] Hessen D O and Walseng B 2008 Freshwater Biol. 53 2026–35
[16] Hessen D O, Jensen T C and Walseng B 2019 J. Front. Ecol. Evol. 7 74
[17] Shen C, Chen Y and Sung 1963 Acta Zoológ. Sin. 15 263–72
[18] Shen C and Sung T 1965 Acta Zoológ. Sin. 17 298–308
[19] Li H, Dumont H J, Han B P and Lin Q 2018 Crustacean 91 335–52
[20] Shulga E L 1953 The Bull. of Irkutsk State University (Irkutsk: Irkutsk Book Publ) VII 135–44
[21] Tomilov A A 1954 The Bull. of Irkutsk State University. Series Biology 11 5–86
[22] Sheveleva N G and Itigilova M Ts 1999 Zooplankton in the Kuanda-Chara lakes Proc. Conf. Sustainable Development: Problems of Protected Territories and Traditional Natural Resource Use in Baikal Region ed A B Ptitsyn (Ulan-Ude: Buryat Sci. Center SB RAS) pp 165–6
[23] Alekseev S S, Matveev A N, Pichugin M Yu, Samusenok V P and Sheveleva N G 2000 Bulletin of Moscow Society of Naturalists. Biological section 105 22–41
[24] Sheveleva N G 2006 Zooplankton Biota of the Vitim Reserve: Structure of Biota in Aquatic Ecosystems ed N M Pronin (Novosibirsk: Academic Publishers “Geo”) pp 57–78
Sheveleva N G 2006 Zooplankton Biota of the Vitim Reserve: Structure of Biota in Aquatic Ecosystems ed N M Pronin (Novosibirsk: Academic Publishers “Geo”) pp 127–38
[25] Krivenkova I F 2016 Zooplankton in lakes Maloye Leprindo and Bolshoye Leprindo. Uchenye Zapiski of Zabaikalsky State University. Series: Natural Sciences 11 81–5
[26] Sobakina I G and Solomonov N M 2013 Intern. J. Appl. & Fundam. Res. 8 180–2
[27] Levkovskaya L A 1981 Lakes of Pribaikalian part of Baikal-Amur Railway (Novosibirsk: Nauka) pp 146–56
[28] Dubovskaya O P, Kotov A A, Korovchinsky N M, Smirnov N N and Sinev A Yu 2010 Contemp. Probl. Ecol. 4 571–608
[29] Sheveleva N G 2007 First data on zooplankton of Kureysk Reservoir Ecosystems Biodiversity on the Putorana Plateau and Surrounding Areas ed A A Romanov (Moscow: Russian Agricultural Academy Press) pp 246–55
[30] Grosvald M G and Kotlyakov V M 1989 Great periglacial drainage system of northern Asia and its role in interregional correlations Scientific Digest Quaternary period. Paleography and Lithology (Kishinev: Shtiinsa) pp 5–13
[31] Volkov I A and Kaz’m in S P 2007 Geogr. Nat. Res. 4 7–10
[32] Kotov A A 2016 Zool. Zh. 95 748–68
[33] Takhteev V V et al 2008 Biota of water bodies in Baikal Rift Zone ed A S Pleshakov (Irkutsk: Irkutsk State University Press) pp 193–202
[34] Xu S, Hebert P D N, Kotov A A and Cristescu M E 2009 Mol. Ecol. 18 5161–79
[35] Ishida S and Taylor D J 2007 Mol. Ecol. 16 569–82