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Distribution and some biological features of *Arctodiaptomus (Rhabdodiaptomus) bacillifer* (Koelbel, 1885) (Copepoda, Calanoida) in Kazakhstan

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Abstract

Based on the males and females' morphology and own long-term data, the freshwater diaptomid copepod *Arctodiaptomus (Rhabdodiaptomus) bacillifer* (Koelbel, 1885) presence was confirmed at three localities of Kazakhstan: the ultra-fresh mountain lakes Markakol (Eastern Kazakhstan) and Upper Kolsay, and a small lake located in the floodplain of the Aksu River (Southeastern Kazakhstan). *A. (R.) bacillifer* is known from various regions of the world not only as an inhabitant of ultra-fresh and fresh waters, with a total dissolved solids of 0.08–0.81 g/dm^3, but also in salt waterbodies (up to 58.1 g/dm^3). The reasons for the contradictory information on the distribution and biology of *A. (R.) bacillifer* in Kazakhstan and other regions are discussed. A comparative analysis of the key identifying features of its morphologically close congeners *A. (R.) bacillifer, A. (R.) acutilobatus* (Sars, 1903), and *A. (R.) salinus* (Daday, 1885), which are often mistakenly identified, is provided. The necessity of critical analysis of data on the wide distribution of *A. (R.) bacillifer* in mineralized waterbodies of different regions of the world is emphasized, since *A. (R.) bacillifer*, in addition to *A. (R.) acutilobatus, A. (R.) salinus*, is mixed with other species of the subgenus, in particular, with "alpinus" and "rectispinosus". The absence of *A. (R.) bacillifer* in the optimal gradient of water mineralization is likely caused by competitive relationships with other species of calanoid crustaceans, most often with *Acanthodiaptomus denticornis* (Wierzejski, 1887) and *Arctodiaptomus (Rhabdodiaptomus) spinosus* (Daday, 1891).

Key words: Balkhash-Alakol water basin, morphologically close species, total dissolved solids, distribution

Introduction

In the world fauna, 75 species of the genus *Arctodiaptomus* (Kiefer, 1932) (WoRMS) are known. This information is far from complete, since the description of new species for science continues (Inaotombi, Sarma, 2024), and the taxonomic status of previously described species is also being clarified. There is a significant lack of knowledge regarding the distribution and biology of already known species of Calanoida.

One of such poorly studied species of Calanoida is *Arctodiaptomus (Rhabdodiaptomus) bacillifer* (Koelbel, 1885). It is reliably known from Hungary (Forró, 1989), Austria (Gaviria, 1998), Turkey (Ustaoðlu, 2004), Romania, Yugoslavia, Slovakia, Bulgaria, Poland, the North Caucasus (Reddy, 1994), and Armenia (Meshkova, 1975; Sergeeva *et al*., 2017; Malin *et al*., 2021). Some authors classify it as a cold-water stenothermic species (Rylov, 1930; Meshkova, 1975), preferring ultra-fresh and fresh, mainly cold-water, mountain lakes (Bossone, Tonolli, 1954; Tonolli, 1954; Ferrari, 1971; Vundtsetel, 1977; Seefried, Czygan, 1978; Ayuushsuren, 2012; Shaburova , 2014; Sergeeva *et al*., 2017; Afonina, Tashlykova, 2018; Ermolaeva, Fetter, 2021; Kirova , Oydup, 2022). In addition, *Arctodiaptomus (R.) bacillifer* is indicated for both fresh (Sobakina *et al*., 2009; Ermolaeva, Fetter, 2021; Ermolaeva, Burmistrova, 2017), brackish (Akbulut, 1998; Flößner *et al*., 2005), and salt lakes (Dobrokhotova, 1979; Stuge *et al*., 2007, 2009; Tashlykova *et al*., 2020; Afonina, Tashlykova, 2020; Zsuga *et al*., 2021).

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According to F. Kiefer (1978) and E.V. Borutskiy *et al*. (1991), the findings of *A. (R.) bacillifer* in many water bodies in Europe and Asia requires confirmation, since it is often confused with *A. (R.) alpinus* (Stella, 1984) and *A. (R.) acutilobatus* (Sars, 1903). This problem fully applies to Kazakhstan, since there are no photographs or drawings in faunistic works confirming the species identification.

This study aims to clarify data on the distribution of *A. (R.) bacillifer* in the waterbodies of Kazakhstan based on our long-term data, description of the morphology of males and females and critical analysis of published information.

Study site description

Kazakhstan is situated in four distinct natural zones: forest-steppe, steppe, semi-desert, and desert. The last two zones account for 60% of the territory. The Tien Shan, Dzungarian Alatau, Saur Tarbagatai and Altai mountains are located in the south, southeast and northeast of the country. The climate is sharply continental over most of the territory, with a maximum annual air temperature difference of up to 99.0 °C (Salnikov *et al*., 2018). The average annual air temperature is +5.5 °C. In the extreme south, it reaches +15.8 °C. The average annual precipitation varies from 100–200 mm in deserts and semi-deserts to 350–650 mm in the steppe zone and up to 900–1200 mm in mountainous areas. Most of the precipitation falls in spring and early summer. The driest months are July and August. In mountainous areas, precipitation falls all year round.

The most significant waterbodies in Kazakhstan are the Caspian and Aral Seas, the Balkhash, Alakol, Zaisan, Teniz, and Markakol Lakes, and the Bukhtarma, Kapchagay, and Shardara reservoirs. The flatlands' climatic features result in many endorheic lakes of varying sizes. All major rivers—Irtysh, Ile, Syr Darya, and Ural—are transboundary.

Total dissolved solids (TDS) in water vary widely, from 0.1–0.2 g/dm^3 in mountainous areas to 300.0 g/dm^3 in the steppe endorheic lakes of Northern Kazakhstan (Krupa, 2012). Waterbodies with TDS from 0.6–0.8 to 1.2–3.5 g/dm^3 predominate. The maximum water temperature reaches 26.0–28.0°C in the lowland waterbodies of Southern and Southeastern Kazakhstan, to 23.0–24.0°C in the north of the country, and 10.0–18.0°C in mountainous areas.

Materials and methods

The study of *A. (R.) bacillifer* distribution was carried out based on the analysis of 3800 zooplankton samples we collected in 2000–2024. The zooplankton samples are stored in the collection fund of the Institute of Zoology (Almaty, the Republic of Kazakhstan), which made it possible to conduct their re-analysis in questionable cases.
A total of 160 waterbodies from various regions of Kazakhstan were surveyed, including the Caspian and Aral Seas, all large lakes and reservoirs (except for Bukhtarma), the Syr Darya, Ile, and Irtysh rivers (Fig. 1). In each waterbody, zooplankton samples were collected using a grid of conditional stations, with one station per 1.5–2.5 km^2 of water surface. Zooplankton samples were collected using a Juday plankton net with an inlet diameter of 12 cm by pulling it from the bottom to the surface. The filtered water was poured into 250 mL plastic containers. The samples were fixed with 40% formalin to a final concentration of 4%.

In the laboratory, the sample was concentrated to a particular volume, depending on the abundance of organisms. Then, each sample was examined at several dilutions (250, 125, 50 mL), each time collecting three subsamples using a 1 mL pipette. Finally, the sample, with a 20–25 mL volume, was examined as a whole. The step-by-step processing procedure allows for a more accurate account of the species composition and the abundance of age stages. The results obtained were recalculated per 1 m^3. Adult males and females of *A. (R.) bacillifer* were dissected using an MBS-10 microscope. Temporary preparations were made and photos of key identifying features (Borutskiy *et al*., 1991; Reddy, 1994) were taken using a SopTop microscope with a digital camera.

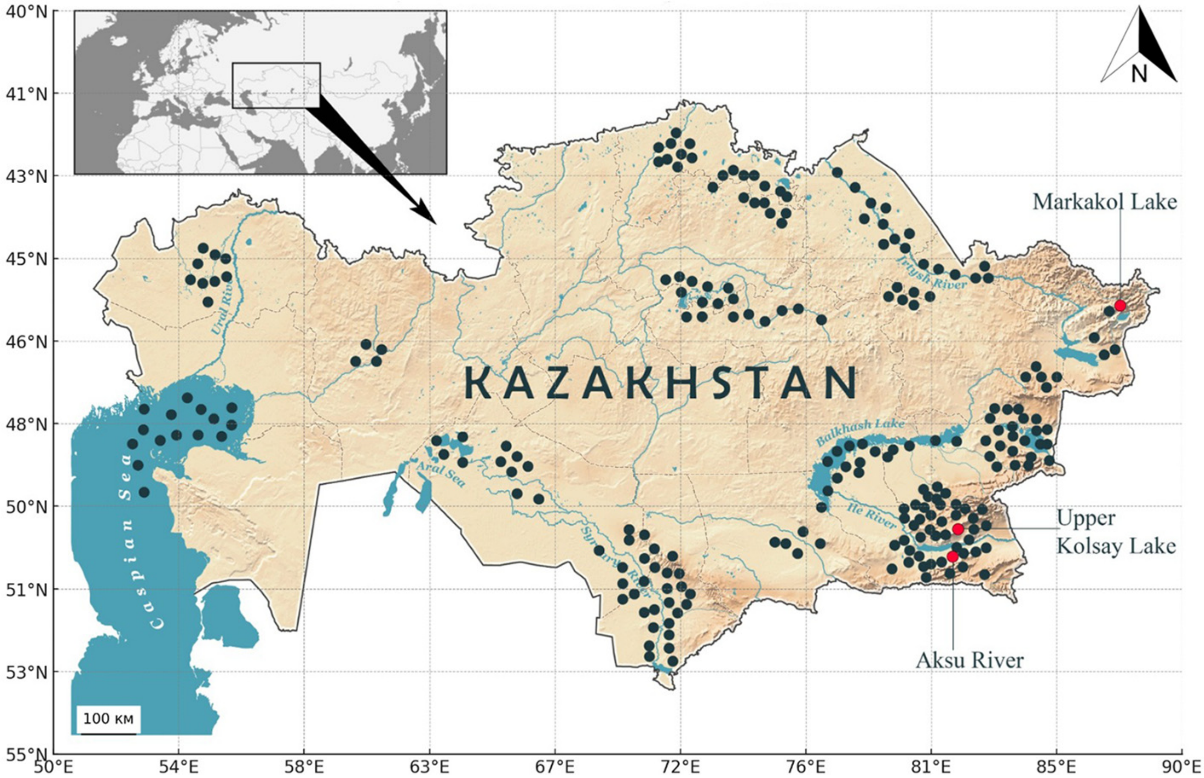

FIGURE 1. Map-scheme of zooplankton sampling in water bodies of Kazakhstan. Red circles are locations of *A. (R.) bacillifer* detection. The map was made by T. Bannikov (Institute of Zoology).

Lakes description

We found *A. (R.) bacillifer* in three lakes: Markakol (Eastern Kazakhstan), Upper Kolsay (Southeastern Kazakhstan), and an unnamed lake in the Aksu River floodplain (Southeastern Kazakhstan).

The deep-water Markakol Lake (Fig. 2A) is located in the Kazakh part of the Altai between the Kurchum and Azutau ridges at an altitude of 1445 m. The banks are covered with deciduous forests and shrubs, and are rocky in places. Fifty rivers flow into it, the largest of which are Topolevka, Tikhushka, Elovka, Karabulak. The Kalzhir River, a right tributary of the Irtysh, flows out. The lake is moderately warm: the surface layers of water do not warm up above 20.0°C in summer. The water is characterised by a low total dissolved solids content (Table 1).

FIGURE 2. The Markakol (A) and Upper Kolsay (B) Lakes. Photos by E.G. Krupa.

TABLE 1. Hydrophysical variables of waterbodies in Kazakhstan inhabited by *A. (R.) bacillifer*

Waterbody	*Region	Altitude above sea level, m	Area, km^2	Depth max, m	Water temperature, °C	TDS, g/dm^3
Markakol	EK	1445	455.0	27.0	19.5	0.08
Upper Kolsay	SEK	2642	0.2	25.0	10.5	0.11
floodplain lake of the Aksu River	SEK	381	0.04	2.0	25.0	0.45

*Note – EK – East Kazakhstan, SEK – South-East Kazakhstan.

Upper Kolsay (Fig. 2B) is located in the Kungey Alatau Mountains. It is one of three lakes located in the eponymous gorge at altitudes from 1829 to 3170 m above sea level. All the lakes (according to their altitude, Upper, Middle and Lower Kolsay) are connected by the river of the same name, canyon-type, deep-water, with a sharp increase in depth, ultra-fresh. Upper Kolsay is the smallest in area. It is located near the upper boundary of the spruce belt. It is fed by the river of the same name, springs, and precipitation.

The floodplain lake (no name) belongs to the Aksu River basin. It is fed by the Aksu River, which begins in the glaciers of the Dzungarian Alatau at an altitude of 3700–3800 above sea level. It is 316 km long. It is 316 km long and flows into the eastern part of the Balkhash Lake. In the mountainous part, the water is ultra-fresh since glaciers and precipitation feed the river. Downstream, before flowing into Balkhash Lake, the TDS of the water increases to 0.40–0.45 g/dm^3.

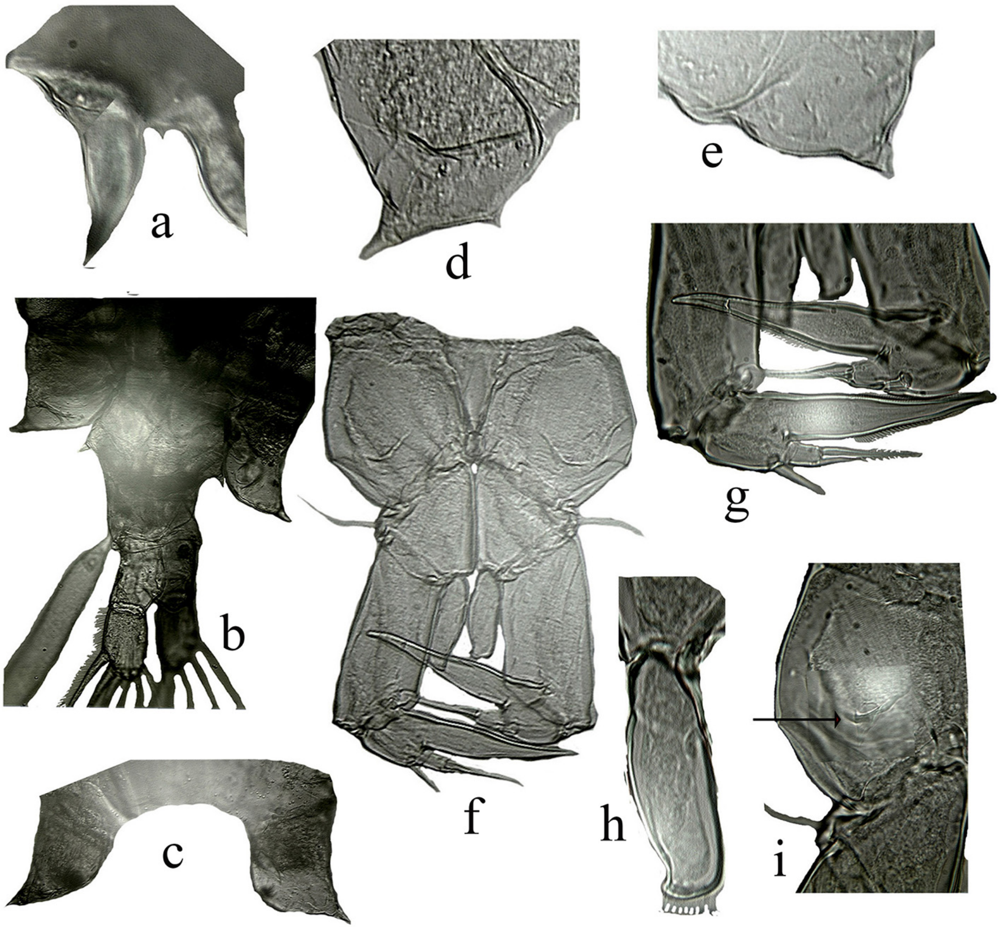

FIGURE 3. *Arctodiaptomus (Rhabdodiaptomus) bacillifer* (Koelbel, 1885), female, floodplain lake of the Aksu River (South-Eastern Kazakhstan): **(a)** rostrum; **(b)** pediger 5 and urosome with caudal rami; **(c)** wings of pediger 5; **(d,e)** spines on the pediger 5; **(f)** legs 5; **(g)** distal segments of legs 5; **(h)** endopodite of leg 5; **(i)** coxa and basis of the leg 5. Photo by E. Krupa.

Results

Description of *A. (R.) bacillifer* females and males

The morphology of females and males of *A. (R.) bacillifer* was described based on material collected in the floodplain lake of the Aksu River (Balkhash-Alakol basin, South-Eastern Kazakhstan) and partially in the Markakol Lake (Eastern Kazakhstan). A total of 5 females and 10 males from the floodplain lake and 3 females and 10 males from the Markakol Lake were examined. The zooplankton samples collected in the floodplain lake are stored at the Institute of Zoology of the Ministry of Science and Higher Education of the Republic of Kazakhstan, Almaty. The zooplankton samples collected in Lake Markakol are stored at the private institution "Institute of Hydrobiology and Ecology", Almaty region, Irgeli village.

The morphology of *A. (R.) bacillifer* females from the abovementioned localities were typical for the species (Fig. 3), so we do not provide a detailed description. The most critical taxonomic characters are as follows: the wings of pediger 5 are well developed and symmetrical; the spines of the somewhat asymmetrical genital somite are moderately developed; the endopodite of the fifth pair of legs does not quite reach the middle of the inner edge of the segment; the penultimate segment of the fifth pair of legs ends in a powerful hyaline spine. The length of females is 1.40–2.00 mm.

The morphology of *A. (R.) bacillifer* males, generally typical for the species, were characterised by some features (Fig. 4). The rostral spines are long. The process of the antepenultimate segment of the grasping antennule is rod-shaped, longer than the segment itself, but unlike the type description (Borutskiy *et al*., 1991), it is curved at the end; in individuals from the Markakol Lake, it is straight. The lateral spine of the distal segment of the right leg 5 is located approximately in the middle of the outer edge of the segment. The chitinous peg of the distal segment of the right leg 5 is located proximally. Its size and shape vary: in males from the floodplain lake of the Aksu River, it is pointed at the end, its size is comparatively small (Fig. 4m); in individuals from the Markakol Lake, the outgrowth is rounded and somewhat larger (Fig. 4r).

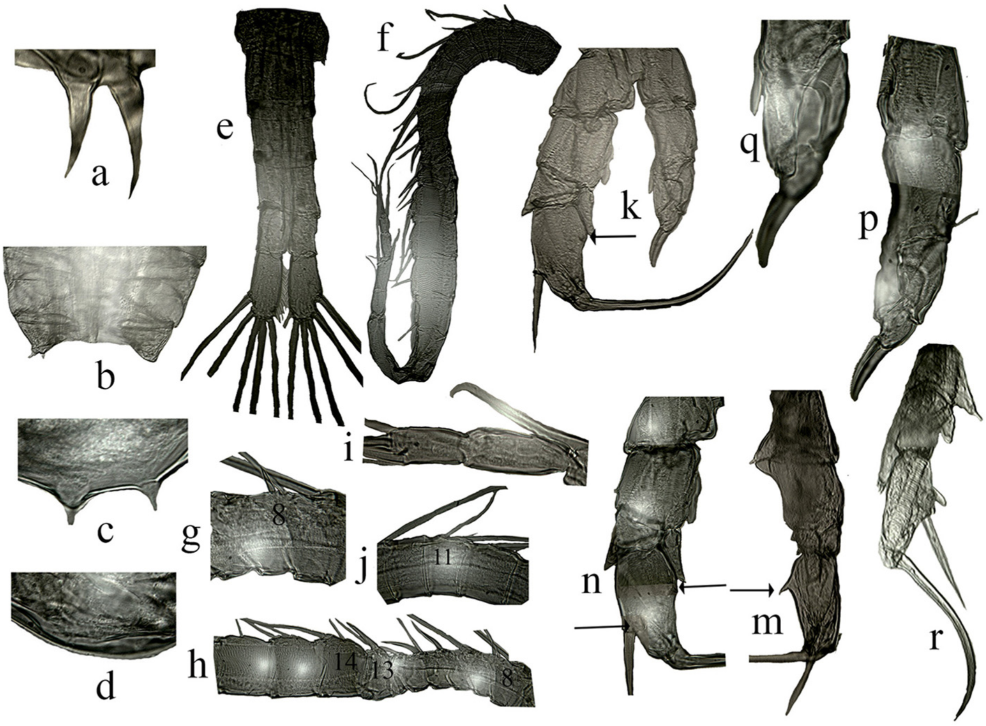

FIGURE 4. *Arctodiaptomus (Rhabdodiaptomus) bacillifer* (Koelbel, 1885), male. The floodplain lake of the Aksu river (South-Eastern Kazakhstan): **(a)** the rostral spines; **(b)** pediger 5; **(c,d)** wings of pediger 5; **(e)** urosome with caudal rami; **(f)** the right (grasping) antennule; **(g)** 8th segment of the right antennule; **(h)** 7–16th segments of the right antennule; **(i)** the process of the antepenultimate segment of the grasping antennule; **(j)** 10–12th segments of the left antennule; **(k)** legs 5, chitinous peg arrowed; **(m,n)** right leg 5, chitinous peg arrowed; **(p)** left leg 5; **(q)** distal segments of the left leg 5. The Markakol Lake (Western Kazakhstan): **(r)** right leg 5. Photo by E.G. Krupa.

Population abundance of *Arctodiaptomus (Rhabdodiaptomus*) *bacillifer*

The *A. (R.) bacillifer* population abundance in mountain lakes was low or moderate (Table 2). In the Markakol Lake, the population abundance of *A. (R.) bacillifer* decreased by about three times from summer to autumn. In summer, males dominate the sexually mature part of the population. In autumn, adult individuals of *A. (R.) bacillifer* were represented only by females. Another species of diaptomids appeared in the zooplankton – *Acanthodiaptomus denticornis* (Wierzejski, 1887), represented by all age stages. Of the four interconnected Kolsay lakes, *A. (R.) bacillifer* was recorded in very low density in Upper Kolsay (2642 m above sea level). *Acanthodiaptomus denticornis* was represented in the lower lakes in the zooplankton instead of this species.

TABLE 2. Abundance and structure of *A. (R.) bacillifer* populations in some Kazakhstan lakes

Lake	Year	Month	Abundance, thousands ind./m^3				Males/ Females
			Females	Females with eggs	Males	Total	
Markakol	2008	June	1.8±0.6	0.9±0.3	4.8±1.6	34.7±9.7	4.06±1.95
	2008	September	1.5±0.5	0.001±0.001	0.0	11.2±5.3	–
Upper Kolsay	2002	August	0.03±0.03	0.004±0.004	0.03±0.03	1.0±0.5	1.0±0.08

Discussion

Despite the extensive material from various regions of Kazakhstan, our confirmed findings of *A. (R.) bacillifer* in only three ultra-fresh and fresh lakes allows us to classify it as a rare species. In addition to these localities, *A. (R.) bacillifer* is also reported for three lakes in Central and Northern Kazakhstan: Toktamys (Stuge, 2010), Zharkol and Shoshkakol (Zsuga *et al*., 2021), with water TDS of 5.6, 2.0 and 6.0 g/dm^3, respectively. We believe that these data need to be verified. Classical manuals (Kiefer, 1978; Borutskiy *et al*., 1991) emphasise that *A. (R.) bacillifer* is often confused with *A. (R.) acutilobatus* and *A. (R.) alpinus*. We believe *A. (R.) bacillifer* is also erroneously identified as *A. (R.) salinus*, and vice versa. This is evidenced, in particular, by the discovery of *A. (R.) salinus* in the ultra-fresh Markakol Lake (Stuge, 2009) contradicts the present study's results (Fig. 4).

We believe that one of the reasons for the erroneous identification of the mentioned species is the variability of key morphological features: the location of the external spine and the size of the chitinous peg of the distal segment of the right leg 5. The most significant difficulties arise when separating *A. (R.) bacillifer* and *A. (R.) acutilobatus*, since the location of the external spine in males (typical forms) differs slightly: approximately in the middle of the outer edge in the first species and the distal part in the second (Fig. 5). If we take the drawings (Borutskiy *et al*., 1991) as a basis, then in the typical form of *A. (R.) acutilobatus,* the lateral spine is located slightly more distally, which does not provide apparent differences from *A. (R.) bacillifer* (approximately in the middle of the outer edge).

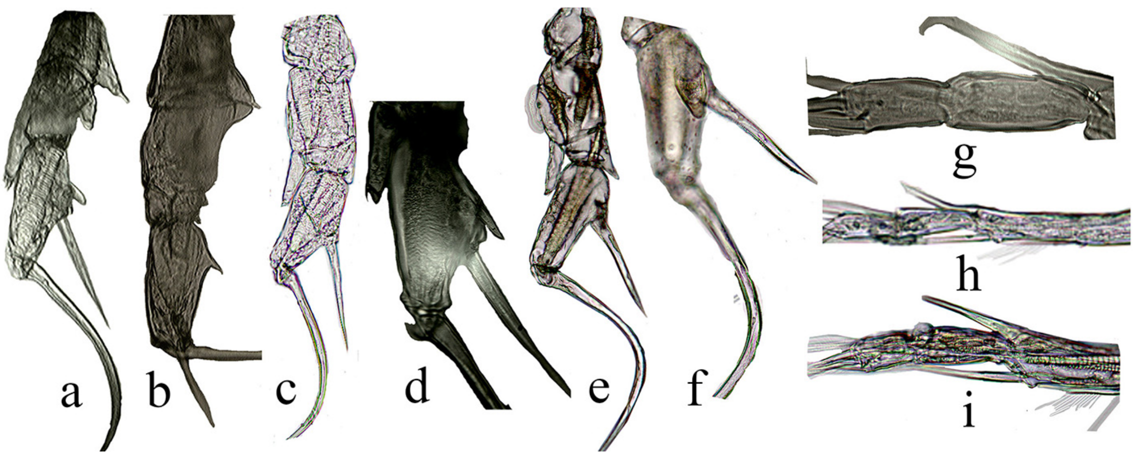

FIGURE 5. Comparative characteristics of key diagnostic features of males of *A. (R.) bacillifer* **(a, b, g)**, *A. (R.) acutilobatus* **(c, d, h)** and *A. (R.) salinus* **(e, f, i)** from Kazakhstan waterbodies. Photo by E. Krupa.

Individual differences in the size of the chitinous peg on the distal segment of the right leg 5 may be another reason for the erroneous identification of the species listed above. In our material, the size of the chitinous peg in *A. (R.) bacillifer* varied, but was generally smaller than in *A. (R.) acutilobatus* (Fig. 5). *Arctodiaptomus (R.) salinus* is clearly distinguished from *A. (R.) acutilobatus* and *A. (R.) bacillifer* by the proximal position of the external spine and a large, usually rounded, chitinous peg on the distal segment of the right leg 5.

According to (Borutskiy *et al*., 1991; Reddy, 1994), the length of the process of the antepenultimate segment of the grasping antennule in *A. (R.) salinus* and *A. (R.) acutilobatus* varies; in *A. (R.) bacillifer,* this process is usually longer than the segment itself, which we also noted in individuals from Kazakhstan. Variability is also manifested in the process form: it was bent at the end in individuals of *A. (R.) bacillifer* from the floodplain lake of the Aksu River, and straight at the end in males from the Markakol Lake. In males of *A. (R.) acutilobatus*, described by us from a small steppe pond in Central Kazakhstan, this process was pointed at the end (Fig. 5h), which is not noted in classical manuals (Borutskiy *et al*., 1991; Reddy, 1994); its length was approximately equal to the length of the segment itself.

Thus, the absence of clearly interpreted key defining features and individual variability, which remains unstudied, leads to errors in identifying the above-listed species of the subgenus *Rhabdodiaptomus*. Accordingly, their ranges and ecological preferences remain unestablished. Below is a key to identify the three species of the subgenus *Rhabdodiaptomus* discussed above based on male morphology (Table 3). It should be emphasised that we do not consider the key taxonomic characters of *A. (R.) bacillifer propior* Kiefer, 1952 and *A. (R.) acutilobatus curdicus* (Brehm, 1938), known locally and differing from the typical forms by the extremely distal position of the lateral spine of the distal segment of the right leg 5 (Borutskiy *et al*., 1991).

TABLE 3. Species identification key for *A. (R.) bacillifer, A. (R.) acutilobatus* and *A. (R.) salinus* (typical forms, by males)

1(2)	The lateral spine of the distal segment of the right leg 5 is located proximal to the middle of the outer edge. The chitinous process is large, its length is more than half the maximum width of this segment……*A. (R) salinus.*
2(1)	The lateral spine of the distal segment of the right leg 5 is located approximately in the middle or slightly distal to the outer margin. The length of the chitinous process of the right leg 5 is less than half the maximum width of this segment.
3(4)	The lateral spine of the distal segment of the right leg 5 is located approximately in the middle of the outer margin. The chitinous process of the right leg 5 is small, its length being approximately one third of the maximum width of this segment........................….. *A. (R.) bacillifer.*
4(3)	The lateral spine of the distal segment of the right leg 5 is located distal to the outer edge. The chitinous process of the right leg 5 is of medium size, its length being slightly less than half the maximum width of this segment.…………………. *A. (R.) acutilobatus.*

An additional feature is the size of the endopodite of leg 5 in females. In *A. (R.) salinus*, the endopodite is significantly longer than the middle of the inner edge of the distal segment of the exopodite (approximately two-thirds of the length); in *A. (R.) bacillifer*, it is equal to half the length of the segment (reaches the middle of the inner edge); in *A. (R.) acutilobatus*, the endopodite is slightly longer than the middle of the inner edge.

Conflicting data on the distribution and, accordingly, ecological characteristics of *A. (R.) bacillifer* concern is not only in Kazakhstan, but also in other regions. This species is indicated for both ultra-fresh and fresh waters, with TDS of 0.08–0.81 g/dm^3 (Meshkova, 1953; Bossone, Tonolli, 1954; Ayuushsuren, 2012; Shaburova, 2014; Sergeeva *et al*., 2017; Ermolaeva, Fetter, 2021), and waterbodies with an increased content of total dissolved solids (4.1–14.6 g/dm^3) (Forró, 1989; Tashlykova *et al*., 2020; Ermolaeva, Fetter, 2021; Kirova, Oydup, 2022). According to (Afonina, Tashlykova, 2018, 2019, 2020), *Arctodiaptomus (R.) bacillifer* is common in Mongolian brackish and salt lakes, with TDS up to 58.1 g/dm^3. M. Alonso's studies do not confirm the presence of *A. (R.) bacillifer* in saline waterbodies of Mongolia, including those (Kholboo nuur, Tsagaan nuur, Baga nuur, Uvs nuur, Nogoon nuur, Goluut nuur) cited in the works mentioned above. M. Alonso (2010) emphasises that the indication of *A. (R.) bacillifer* inhabiting these waterbodies is erroneous; two other species of the subgenus are presented here, *A. (R.) rectispinosus* Kikuchi, 1940 and *A. (R.) salinus*. The first inhabits waters with TDS from 4.2 to 61.4 g/dm^3, the second is found at 3.4–29.5 g/dm^3. The TDS gradient for *A. (R.) salinus* given by M. Alonso (2010) generally coincides with its ecological preferences in Kazakhstan, where it inhabits waterbodies with TDS over 1.0 g/dm^3, with the highest abundance at 4.2–18.0 g/dm^3 (Krupa, 2012).

The given examples demonstrate the data on the wide distribution in mineralised waterbodies and, accordingly, the euryhaline nature of *A. (R.) bacillifer* (Afonina, Tashlykova, 2018, 2019, 2020; Forró, 1989; Tashlykova *et al*., 2020; Ermolaeva, Fetter, 2021; Kirova, Oydup, 2022) needs to be confirmed. The results of our research and the analysis of literary data allow us, following V.M. Rylov (1930) and T.M. Meshkova (1975), to classify *A. (R.) bacillifer* as a freshwater species that prefers cold-water and moderately warm-water waterbodies.

In the optimal TDS gradient, the rarity of *A. (R.) bacillifer* encounters in Kazakhstan may be due to interspecific competition, which is most pronounced in oligotrophic (low-food) mountain lakes. The dominance of *A. (R.) bacillifer* is noted in some high-altitude alpine lakes (e.g., the Campo Lakes), where no other diaptomids exist (Ferrari, 1971; Seefried, Czygan, 1978). In mountain lakes of Italy at altitudes below 1800 m above sea level, *A. (R.) bacillifer* is often replaced by *Acanthodiaptomus denticornis* (Bossone, Tonolli 1954). In high-mountain conditions, *A. (R.) bacillifer* is found in colder waters than *A. denticornis* (Tonolli, 1954), which is also true for the Kolsay Lakes. *A. (R.) bacillifer* was found in Upper Kolsay at an altitude of 2642 m above sea level with a water temperature of 10.1°C; below, at altitudes of 2242 and 1829 m, with water temperatures of 12.0–14.5°C, *Acanthodiaptomus denticornis* was present. According to (Bossone, Tonolli, 1954), *A. (R.) bacillifer* can coexist with *A. denticornis* only if suitable conditions are located near the lower boundary of its distribution.

In lower mountain lakes, trophic conditions for planktonic invertebrates are more favourable. According to our data, in the Markakol Lake (altitude 1445 m), two species coexist simultaneously: *A. (R.) bacillifer* and *A. denticornis*, but the first dominates in summer, the second in autumn. The coexistence of *A. (R.) bacillifer, A. spinosus* and *A. denticornis* are also observed in the Sevan Lake (altitude 1900 m) (Meshkova, 1975). In the 1950s, the first species reproduced from December to March–April (May) without a dormant period, the second – in June and July, the third – from the second half of August to December. Against the background of rising water levels and increased eutrophication of the lake due to the influx of nutrients from flooded areas, a change in the life cycles of the aforementioned copepod species occurred. In 2007–2009, *A. (R.) bacillifer* dominated in July, *A. denticornis* in October (Ayrapetyan *et al*., 2014). In autumn 2012, *A. (R.) bacillifer* became a dominant species along with *A. denticornis* (Krylov *et al*., 2013, 2015, 2016). In July 2007, 2012, and 2013, *A. (R.) bacillifer* and *A. denticornis* were part of the zooplankton of the Sevan Lake (Krylov *et al*., 2016), and in May 2016–2018, they played a leading role in the zooplankton communities (Krylov *et al*., 2021). In October 2013, another previously uncharacteristic species, *A. spinosus*, appeared in the dominant complex (Krylov *et al*., 2016). Thus, the enrichment of the Sevan Lake with nutrients and the improvement of the food supply led to a change in the life cycles of competing copepod species: the separation in periods of mass reproduction was replaced by their joint existence. These changes occurred against rising water levels, eutrophication, a decrease in fish populations, and the formation of all zooplankton's maximum biomass due to cladocerans' mass development.

In European lowland lakes, *A. (R.) bacillifer* often occurs together with *Arctodiaptomus spinosus* (Forró, 1989), with both species dominating during the cold season.

Thus, comparison of our research results with literature data allows us to conclude that *A. (R.) bacillifer* cannot be classified as a stenothermic cold-water species, since it is capable of reproducing in a relatively wide temperature gradient. Under conditions of food resource deficiency, which is observed, for example, in mountain oligotrophic lakes, the life strategy of *A. (R.) bacillifer* consists either of spatial isolation (Kolsay Lakes, mountain lakes of Italy) or of separation of reproduction times (Lake Sevan in the 1950s). With an improved food supply, *A. (R.) bacillifer* can coexist with other calanoid species, as happened in Lake Sevan. With regard to water TDS, it is difficult to draw final conclusions in the absence of reliable information on the findings of this species in a number of regions. According to the results of our research, we classify *A. (R.) bacillifer* as a typical freshwater inhabitant. This is also evidenced by the numerous confirmed finds of this species in mountain lakes, usually ultra-fresh or fresh, in Europe.

Conclusion

Comparison of our research results with literature data allows us to conclude that *A. (R.) bacillifer* cannot be classified as a stenothermic cold-water species, since it can reproduce in a relatively wide temperature gradient. Under conditions of food resource deficiency, which is observed, for example, in mountain oligotrophic lakes, the life strategy of *A. (R.) bacillifer* consists of spatial isolation (Kolsay Lakes, mountain lakes of Italy) or separation of reproduction times (Lake Sevan in the 1950s). With an improved food supply, *A. (R.) bacillifer* can coexist with other calanoid species, as happened in the Sevan Lake. With regard to water TDS, it is difficult to draw final conclusions in the absence of reliable information on the findings of this species in several regions. According to the results of our research, we classify *A. (R.) bacillifer* as a typical freshwater inhabitant. This is also evidenced by the numerous confirmed finds of this species in Europe's mountain lakes, usually ultra-fresh or fresh.

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References

Afonina, E.Y., Tashlykova, N.A. (2018) Plankton community and the relationship with the environment in saline lakes of Onon-Torey plain, Northeastern Mongolia. *Saudi journal of biological sciences*, 25 (2), 399–408. https://doi.org/10.1016/j.sjbs.2017.01.003

Afonina, E.Y., Tashlykova, N.A. (2020) Long-term data on plankton communities in Torey lakes, a shallow saline lake, Transbaikalia, Russia. *Limnology and Freshwater Biology*, 4, 707–709. https://doi.org/10.31951/2658-3518-2020-A-4-707

Afonina, E.Y., Tashlykova, N.A. (2019) Plankton of saline lakes in Southeastern Transbaikalia: transformation and environmental factors. *Contemporary Problems of Ecology*, 12 (2), 155–170. https://doi.org/10.1134/S1995425519020021

Akbulut, N. (1998) Biomass Analysis of Dominant Zooplanktonic Organisms Living in Lake Mogan (Turkey). *Turkish Journal of Zoology*, 22 (4), 333–340.

Alonso, M. (2010) Branchiopoda and Copepoda (Crustacea) in Mongolian Saline Lakes. *Mongolian Journal of Biological Sciences*, 8 (1), 9–16. https://doi.org/10.22353/MJBS.2010.08.02

Ayrapetyan, A.O., Krylov, A.V., Gabrielyan, B.K. (2014) Zooplankton of two types of shallow waters of Lake Sevan formed during the rise in water level. *Biol. J. of Armenia*, 1 (66), 12–17.

Ayuushsuren, Ch. (2012) Species composition, structure and dynamics of quantitative indicators of zoobenthos of Lake Ulaagchny Khar (Western Mongolia). *Bulletin of Irkutsk State University, Series: Biology, Ecology*, 10, 82–91.

Bossone, A., Tonolli, V. (1954) The problem of the co-existence of *Arctodiaptomus bacillifer* (Koelb.), *Acanthodiaptomus denticornis* (Wierz.) and *Heterocope saliens* Lill. *Memorie dell'Istituto Italiano di Idrobiologia Dott*, 8, 81–94.

Borutskiy, E.V., Stepanova, L.A., Kos, M.S. (1991) *Calanoida Identifier of Fresh Waters of the USSR*. Nauka, St. Petersburg. [unknown pagination]

Dobrokhotova, O.V. (1979) Fauna of Diaptomidae (Copepoda, Calanoida) of Kazakhstan and their participation in the circulation of Hymenolipedid aquatic birds; Fauna, ecology and zoogeography of helminths of animals of Kazakhstan; *Deposited in the All-Russian Institute of Scientific and Technical Information*, 581–79, 55–78.

Ermolaeva, N.I., Fetter, G.V. (2021) Influence of the ionic composition of water on the structure of zooplankton in lakes of the Tazheran steppe (Western Baikal region). *Arid Ecosystems*, 27, 4 (89), 107–117. https://doi.org/10.1134/S2079096121040041

Ermolaeva, N.I., Burmistrova, O.S. (2017) Zooplankton of Lake Bolshoe Shchuchye. *Scientific Bulletin of the Yamalo-Nenets Autonomous Okrug*, 1, 15–20.

Ferrari, I. (1971) Notes on the dynamics of the reproductive activity of *Arctodiaptomus bacillifer* in high altitude alpine lakes. *Italian Journal of Zoology*, 38 (3), 221–235. https://doi.org/10.1080/11250007109429153

Flößner, D., Horn, W., Paul, M. (2005) Notes on the Cladoceran and Copepod fauna of the Uvs Nuur basin (Northwest Mongolia). *International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology*, 90 (5–6), 580–595. https://doi.org/10.1002/iroh.200410782

Forró, L. (1989) Composition and seasonal changes of the microcrustacean fauna of sodic waters near Fülöpháza (Kiskunság National Park, Hungary). *Miscellanea Zoologica Hungarica*, 5, 33–41.

Gaviria, S. (1998) Checklist and distribution of the free-living copepods (Arthropoda: Crustacea) from Austria. *Annalen des Naturhistorischen Museums in Wien. Serie für Botanik und Zoologie*, 1998, 539–594.

Inaotombi, S., Sarma, D. (2024) A new species of *Arctodiaptomus* Kiefer, 1932 (Copepoda: Diaptomidae) from the Kumaun Himalaya of India. *J. of Threatened Taxa*, 16 (12), 26251–26263.
https://doi.org/10.11609/jott.8032.16.12.26251-26263

Kirova, N.A., Oydup, C.K. (2022) Taxonomic composition of zooplankton of brackish lakes of the Turano-Uyuk depression (Tuva Republic). *Journal of the Siberian Federal University: Biology*, 15 (1), 31–47.
https://doi.org/10.17516/1997-1389-0373

Kiefer, F., Fryer, G. (1978) *Das Zooplankton der Binnengewässer, 2. Teil. Freilebende Copepoda*. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 26.

Krupa, E.G. (2012) *Zooplankton of Limnic and Lotic Ecosystems of Kazakhstan. Structure and Formation Patterns*. Palmarium Academic Publishing, Saarbrucken. [unknown pagination]

Krylov, A.V., Gerasimov, Y.V., Gabrielyan, B.K., Borisenko, E.S., Akopyan, S.A., Nikoghosyan, A.A., Malin, M.I., Hovsepyan, A.A. (2013) Zooplankton of Lake Sevan during the period of continuing rise in water level and decrease in fish density. *Biology of Inland Waters*, 3, 37–45.
https://doi.org/10.7868/S032096521303008X

Krylov, A.V., Romanenko, A.V., Gerasimov, Y.V., Borisenko, E.S., Ayrapetyan, A.O., Hovsepyan, A.A., Gabrielyan, B.K. (2015) Distribution of plankton and fish in Lake Sevan (Armenia) during mass development of cladocerans. *Biology of Inland Waters*, 1, 60–70.
https://doi.org/10.7868/S032096521501012X

Krylov, A.V., Ayrapetyan, A.O., Bolotov, S.E., Gerasimov, Y.V., Malin, M.I., Kosolapov, D.B., Hovsepyan, A.A. (2016) Changes in autumn zooplankton in the pelagic zone of Lake Sevan (Armenia) with an increase in fish abundance. *Biology of Inland Waters*, 2, 37–44.
https://doi.org/10.7868/S0320965216020091

Krylov, A.V., Ayrapetyan, A.O., Hovsepyan, A.A., Sabitova, R.Z., Gabrielyan, B.K. (2021) Interannual changes in spring zooplankton of Lake Sevan (Armenia) pelagic zone during the increase in ichthyomass. *Biology of Inland Waters*, 1, 95–98.
https://doi.org/10.31857/S032096522101006X

Malin, M.I., Zhdanova, S.M., Kosolapov, D.B., Malina, I.P., Kosolapova, N.G., Sabitova, R.Z., Krylov, A.V. (2021) Unusual vertical distribution of zooplankton and fish in the pelagic zone of Lake Sevan during summer stratification. *Ecosystem Transformation*, 4 (3), 27–41.
https://doi.org/10.23859/estr-210312

Meshkova, T.M. (1975) *Patterns of zooplankton development in Lake Sevan*. Academy of Sciences of the Armenian SSR, Yerevan. [unknown pagination]

Meshkova, T.M. (1953) *Zooplankton of Lake Sevan. Transactions of the Sevan Hydrobiological Station*, 13, 170.

Reddy, Y.R. (1994) *Copepoda: Calanoida: Diaptomidae. Key to the genera Heliodiaptomus, Allodiaptomus, Neodiaptomus, Phyllodiaptomus, Eodiaptomus, Arctodiaptomus and Sinodiaptomus*. SPB Academic Publishing, Hague. [unknown pagination]

Rylov, V.M. (1930) *Freshwater Calanoida of the USSR: Guides to freshwater organisms of the USSR, Freshwater fauna*. Nauka, Leningrad. [unknown pagination]

Salnikov, V.G., Turulina, G.K., Talanov, E.A., Polyakova, S.E. (2018) Analysis of Climate Change in Kazakhstan over the Past 75 Years. *New Methods and Results of Landscape Research in Europe, Central Asia and Siberia*, 2018, 247–252.

Sergeeva, I.V., Evdokimov, N.A., Sergeeva, E.S., Evdokimova, A.I. (2017) Dependence of the formation of morphometric indicators of *Arctodiaptomus bacillifer* Koelbel, 1885 (Crustacea, Calanoida) on the ecological state of several reservoirs in the Lower Volga region. *Agrarian Scientific Journal*, 7, 47–52.

Seefried, H., Czygan, F.C. (1978) Carotenoid Composition and Metabolism of *Arctodiaptomus bacillifer* KOEBEL (Crustacea, Copepoda). *Zeitschrift für Naturforschung*, 33 (9–10), 671–674.
https://doi.org/10.1515/znc-1978-9-1012

Shaburova, N.I. (2014) Taxonomic composition and quantitative indicators of zooplankton in water bodies of the Tofalar State Nature Reserve. *Baikal Zoological Journal, Hydrobiology*, 2 (15), 49–54.

Sobakina, I.G., Sokolova, V.A., Solomonov, N.M. (2009) Modern composition of zooplankton in the Lena River delta in autumn. *Bulletin of the Samara Scientific Centre of the Russian Academy of Sciences*, 1 (3), 347–349.

Stuge, T.S., Matmuratov, S.A., Akberdina, G.Z. (2007) Structure and development of zooplankton in the Shalkar-Birtaban and Uyaly-Shalkar lakes of the Nura River basin (autumn 2004). *Tethys Aqua Zoological Research*, 3, 103–112.

Stuge, T.S. (2009) Zooplankton of Lake Markakol. *In Proceedings of the Markakol State Nature Reserve*, 1 (1), 82–100.

Stuge, T.S. (2010) On the planktonic fauna of small lakes of the Korgalzhyn system (Akmola region). *Selevinia*, 173–174.

Tashlykova, N.A., Afonina, E.Y., Tsybekmitova, G., Matveeva, M. (2020) Current state of planktonic hydrobiocenoses in the littoral zone of Lake Tsagan-Nor (Onon-Borzinskaya system of lakes in Transbaikalia). *Ecosystems*, 22, 5–14.
https://doi.org/10.18411/2414-4738-2020-22-5-14

Tonolli, V. (1954) Predation and selection in copepod populations of Alpine waters. *Bollettino di Zoologia*, 21, 541–545.
https://doi.org/10.1080/11250005409438209

Ustaoðlu, M.A. (2004) Check-list for Zooplankton of Turkish Inland Waters. *E.U. Journal of Fisheries & Aquatic Sciences*, 21, 191–199.

Vundtsetel, M.F. (1977) *Fauna of the Son-Kul Lake, Ichthyological and hydrobiological studies in Kyrgyzstan*. Ilim, Frunze. [unknown pagination]

WoRMS Editorial Board (2023) World register of marine species. Available from: https://www.marinespecies.org (accessed 25 March 2025)

Zsuga, K., Inelova, Z., Boros, E. (2021) Zooplankton community structure in Shallow Saline steppe inland waters. *Water*, 13 (9), 1164.
https://doi.org/10.3390/w13091164