

Subterranean biota of the European part of Russia: A review

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ABSTRACT. The endogean flora and fauna of European Russia, including those of the northwestern Caucasus, but excluding those of Crimea, presently comprise at least 389 species or subspecies (some still unidentified) from 229 genera (a few still unidentified), 150 families, 75 orders, 48 classes and 25 phyla, among which 96 species or subspecies represent presumed stygo- or troglobionts. The taxonomically most diverse phylum is Arthropoda which encompasses the bulk of the fauna, in particular due to crustaceans, beetles and collembolans. Whereas the troglofauna of northern Russia is completely devoid of such strongly cave-adapted animals, in the Urals, Cis-Urals and central Russia there are a few, but the greatest diversity of hypogean species in the region is observed in the northwestern Caucasus, in particular its maritime western part, as an "Ice Age" refugium of nemoral biota rich in karst.

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Подземная биота европейской части России: Обзор

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РЕЗЮМЕ. Подземные флора и фауна европейской части России, включая таковые Северо-Западного Кавказа, но исключая таковые Крыма, в настоящее время насчитывают по меньшей мере 389 вида и подвида (некоторые пока не определены) из 229 родов (малая часть пока не определена), 150 семейств, 75 отрядов, 48 классов и 25 типов, среди которых 96 видов и подвидов — предположительно стиго- и троглобионты. Таксономически самый разнообразный тип — это Arthropoda, который включает большинство фауны, особенно за счет ракообразных, жуков и коллемболов. В то время, как троглофауна северной части России совершенно лишена сильно адаптированных в жизни в пещерах и подземных водах животных, на Урале, в Предуралье и центре России таковых немного, а наибольшее разнообразие гипогейных видов в регионе наблюдается на Северо-Западном Кавказе, прежде всего, в его приморской западной части, как богатого карстом «ледникового» рефугиума неморальной биоты. Как цитировать эту статью: Golovatch S.I., Palatov D.M., Turbanov I.S., Kniss V.A., Gazaryan S., Snit'ko V.P., Decu V., Juberthie Ch., Nazareanu G. 2018. Subterranean biota of the European part of Russia: A review // Invert. Zool. Vol.15. No.2. P.153–213. doi: 10.15298/invertzool.15.2.01

КЛЮЧЕВЫЕ СЛОВА: Восточная Европа, Урал, Предуралье, Северный Кавказ, подземные беспозвоночные, летучие мыши, стигофилы, стигобионты, троглофилы, троглобионты.

Introduction

The present paper is the result of a compromise. It was initiated by one of us (CJ) to become a chapter entitled “RUSSIA (Russian Federation: European part)” in a forthcoming volume of “ENCYCLOPAEDIA BIOSPEOLOGICA”. The chapter was duly prepared, but then remained shelved for more than a year waiting for some other contributions to be com-

pleted for the same volume. However, because of uncertainty and an apparent delay in publication, let alone an unexpected abortion of the part pertaining to mammals in our prepared draft, we have finally decided to publish this material elsewhere in a reputed journal and before it is outdated. This decision actually follows that of Juberthie et al. (2016) who published their chapter on the cave faunas of Siberia and the Russian Far East as a journal paper. The same concerns

the chapter on the Mexican hypogean fauna by Palacios-Vargas et al. (2017). As regards the present contribution that covers European Russia, a separate chapter will be devoted to the troglofauna of Crimea.

I. General description of the area

The Russian Federation is the largest country in the world (17,075,000 km²), spanning 10,000 km from the Baltic Sea in the West to the Pacific (the Sea of Japan, the Okhotsk Sea, the Bering Sea) in the East. The Ural Mountain Range represents the traditional border between European Russia and Siberia (Asian Russia), lying between Europe and Asia.

The European part consists of large plains; the southern part of European Russia consists of the northern and western Caucasus, including a part of Transcaucasia stretched along the Black Sea coast until Sochi and the Psou River, both bordering on Abkhazia. Central Siberia is mostly a large plateau; southern Siberia bordering on Mongolia and China, as well as the Far East as far as the Sea of Okhotsk and the Sea of Japan are mountainous regions.

Climate. Temperate and continental to the West, with marine influence of the Baltic Sea and the Sea of Japan; cold and subpolar to the North, nearly subtropical in the Sochi region along the Black Sea. The latitude, the distance to the ocean and the localization of mountains account for climate continentality; the climate of Siberia is characterized by mostly very severe and harsh winters.

Vegetation. From north to south, the pattern of nature zonation is formed by a marked succession of the following biomes: polar deserts, tundras, taiga (= boreal, mostly coniferous forest), broadleaved forest, forested steppes, steppes (= grasslands), semi-deserts and deserts.

II. History

II. 1. Karst

In Russia, the first descriptions of karst forms and caves were made as early as the 18th century by several academic expeditions, fol-

lowing the conquest of the huge territories of the Urals, Siberia and, later, the Far East. The first detailed field manual on caves was published by J. Gmelin as a result of the Great North Expedition carried out between 1733 and 1743.

At the beginning of the 19th century, V. Severgin published a review of the caves in the Russian Empire.

In 1887, Yuri Listov published a field manual on cave studies with notes on their geology, morphology, hydro-geology, speleogenesis, sediments and microclimate.

In 1900, Alexander Kruber published an important book, "*About karst phenomena in Russia*". The role of Kruber in Russia is somewhat comparable to that of E.A. Martel in Western Europe. Martel visited Russia in 1903.

From the beginning of the 20th century, the number of regional karst cave studies continued to grow in all of the main regions of Russia.

The revolution of 1917 interrupted karst and cave research in the country, but it resumed in the USSR.

The first Karst Conference in the USSR was held in 1933 at Kizel, Perm Region. Since 1947, the Perm State University sponsored all-Union conferences on karst and played important roles in the coordination of karst speleological investigations.

Regional thematic conferences on karst and speleology were organized by the Karst Commission, for instance on Applied Karstology, Russian Plain karst, Bashkirian karst, Primorsky Krai karst, Caves, engineering karstology etc.

According to A. Klimchouk (2003c), modern speleology in the USSR was born in 1958, when the Academy of Sciences created the Interdepartmental Commission on Geological and Geographical Karst Investigations.

General studies on Russian karst were published by Klimchouk (2003b), Maksimovitch (1962, 1963), Maksimovitch and Kostarev (1973), Gorbunova et al. (1992) and many others. Special studies were published on gypsum karsts of the Russian Eastern-European Plain and the Pre-Ural region by Andrejchuk (1996), and Andrejchuk and Klimchouk (1996).

Until 1958, only about 500 caves and shafts were reported in the Soviet Union as a whole. From 1958 to 1962, cave-exploring groups were formed, with as many as 3,800 caves discovered in the USSR (Russia, Ukraine, Caucasus) (Dubyanskiy, Ilyukhin, 1982; Kiselyov, Klimchouk, 1991).

II. 2. Cave fauna

The first mention concerning Russia's cave fauna belonged to P. Pallas, a famous academician and traveler, who, in 1811, reported the presence of bat colonies in caves of Crimea and the Urals. Then around the middle of the 19th century, as industrial development required resources, geological research was conducted in the eastern regions such as the Urals, the Altai and Transbaikalia, as well as in the Caucasus and other regions of the Russian Empire.

Victor von Motschoulsky, a famous entomologist, first visited several Caucasian caves in 1850, then some caves in Crimea.

In 1889, G. Jakobson and R. Schmidt sampled fauna in the Murandimovskaya and Kapova caves in the southern Urals and recorded the dipteran *Blepharoptera modesta*, Culicidae larvae and adults, Collembola and Aranei. From among the species collected, Skorikow (1899) described a new species of springtail, *Tomocerus baschkiricus*.

Understanding the importance of cave studies in resolving biogeographical problems and those linked to evolutionary theory, G. Kozhevnikov, professor of the Moscow University, created in the early 20th century, inside the Zoological Museum, a "dark room" for experimenting on the impact of darkness upon Crustacea and fishes (Ognev, 1910; Kapterev, 1910, 1912).

Nevertheless, the true beginning of biospeleological research in Russia is dated 1912, when A. Shugurov generalized the then available data, relatively few, on the cave fauna of the Caucasus and Crimea (Shugurov, 1912).

Biospeleological investigations were resumed only in 1926–1927, already in the USSR, with explorations of some caves in the Urals and the description by E. Borutzky in 1928 of the first stygobiont, the amphipod *Crangonyx chlenikovi* from the central Urals. In 1929, Borutz-

ky joined the first biospeleological survey of two karstic caves in the Kutaisi region of Georgia, Transcaucasia, and published the first data about the cave fauna of Transcaucasia (Borutzky, 1930, 1934).

In 1927 and 1930, A.N. Derzhavin published two papers containing descriptions of new cave amphipods.

At the end of 1930, K. Verhoeff described a diplopod, *Leucogeorgia longipes*, from a cave near Kutaisi, Georgia (Verhoeff, 1930).

Since 1935, Ya. Birstein undertook 6 trips in the Caucasus and explored 39 caves: 31 along the Black Sea coast, 4 in the Imeretian region of Georgia and 3 in Crimea.

In 1940, Birstein and Lopashov published a synthesis of the cave fauna of the USSR as revealed in 1935–1940. That paper also marked the onset of the series "*Biospelogica Sovietica*" (Birstein, Lopashov, 1940). At the same time, I. Lapshov (1940) reviewed the pseudoscorpion cave fauna of Transcaucasia.

In 1950, Birstein generalized and updated all available information on the cave fauna of western Transcaucasia (Birstein, 1950).

In 1950, E. Borutzky described a stygobiont copepod, *Speocyclops lussianus*, from Ciscaucasia (Borutzky, 1950).

From 1950 to 1970, Birstein alone or together with Ljovuschkin, Borutzky, Levanidov or Lopashov, published mostly on aquatic cave fauna. This work culminated in a milestone synthesis of biospeleological research in the USSR (Birstein, Ljovuschkin, 1967a). During the same period, Ljovuschkin alone or with co-authors described a number of cave beetles, crustaceans and arachnids, Borutzky described numerous new species of cave copepods and isopods, Ya. Starobogatov and P. Matiokin worked on molluscs, N. Zalesskaja on lithobiomorphs, I. Malevich on earthworms, etc.

Since the 1970's, V. Kniss has studied the fauna of caves and springs, mostly in the Urals and in Siberia. In 2001, he published a summarizing monograph, "*Cave fauna of Russia and adjacent regions*". From 1984 to 2006, V. Kniss published mostly on springtail cave fauna (Kniss, 1984a, b, 1985, 1989, 1991, 2001, 2004, 2006).

It is Birstein who may be credited as the pioneer of biospeleology in the USSR, with several of his colleagues or direct students having provided the foundations for our present knowledge of the endogean faunas of the ex-USSR countries.

The cave invertebrate fauna of the former Soviet Union, which represents the bulk of endogean biodiversity, has very recently been revised and summarized (Turbanov et al., 2016a, b, c). Members of 17 phyla, 38 classes, 90 orders and 278 families of invertebrates which contain at least 308 species or subspecies of mostly presumed stygo- or troglobionts and no fewer than 735 species or subspecies of stygo- or troglophiles are currently known to populate the caves and subterranean waters of Russia and other countries of the former USSR. The main evolutionary burst in the endogea, including the MSS (*milieu souterrain superficiel*, or *meso-void shallow stratum*), is due to arthropods, primarily crustaceans, collembolans and beetles. The major centres of taxonomic diversity among stygo- and troglobionts thereby remain the Caucasus (181, or almost 59%) and Crimea (44, or over 14%), both montane “glacial” refugia of nemoral biota rich in karst, whereas the contributions of the other major regions, sometimes strongly karstified as well, are considerably smaller, gradually decreasing towards Central Asia (35, or more than 11%), the Far East (33, or nearly 11%), the Ukrainian Carpathians together with Podolia (12, or almost 4%), the Russian Plain (7, or over 2%), the Urals and Cisuralia (7, also more than 2%) and Siberia (5, or 1.6%). The problem of inventorying is still among the most topical in assessing the stygo- and troglofaunas of the territories in question.

Although occasional findings of bats in caves were reported by many Soviet zoologists (see Kuzyakin (1950)) and the importance of these sites was obvious, Petr Petrovich Strelkov was the first Russian bat researcher who focused on underground sites and conducted an extensive survey of those caves and artificial underground roosts that were known at that time in European Russia (Strelkov, 1958), establishing a tradition for winter bat monitoring. Following his pilot

survey, underground sites had become a key element of all regional studies of bat fauna. They gained a momentum after the first all-USSR bat research conference that was held in Leningrad (now Saint Petersburg) in 1974 and where the commission on bats was organized under the auspices of the Soviet Theriological Society. The conference had become a regular event with a number of attendees from the former USSR who reported new findings in a compendium of proceedings (1974, 1980, 1982, 1988, 1990). Altogether, more than 120 papers and short communications on the distribution of bats in the territory of the former USSR had been published by 1990 (Strelkov, 1990); a great deal of them containing data collected in caves and underground sites.

After the dissolution of the Soviet Union, the coordination of bat studies in Russia was taken over by the Russian Bat Research Group that was established at Seventh All-Russian Bat Research Conference (13–16 April 1999). The Group issues its own periodical, *Plecotus et al.*, and maintains a website at <http://zmmu.msu.ru/bats>

Apart from papers and proceedings, several comprehensive regional bat surveys have recently been conducted and subsequently published as dissertations and monographs. With respect to the cave bat fauna, it is worth mentioning a study on bats of the Western Caucasus (Gazaryan, 2002) and those for the central and southern Ural regions (Orlov, 2000; Snit'ko, 2004). The results of the latter two studies largely constitute the monograph “*Bats of the Urals*” (Bol'shakov et al., 2005) that was later amended by several new publications of Vladimir Snit'ko, who explored summer and winter bat assemblages in the caves of Bashkiria and the Orenburg and Chelyabinsk regions. In 1999, S. Gazaryan and A. Ostapenko published the first list of 49 caves which are important for bats in the Russian Caucasus and should be legally and physically protected; the paper included recommendations to cavers concerning bat-friendly conduct and the timing of visits to these caves. In a series of further publications S. Gazaryan appended this list with many new important sites which he had discovered during his field trips in 1999–2012.

Since 1975, several groups have become particularly well studied in the Russian Caucasus, such as cave diplopods (Golovatch, 1975, 1978, 1983, 1984–1985, 1990, 2011; Golovatch, Enghoff, 1990; Golovatch, Chumachenko, 2013; Golovatch et al., 2016; Antić, Makarov, 2016; Antić et al., 2018); cave carabids (Belousov, 1989, 1999, 1998; Belousov, Zamotajlov, 1999, 1997; Belousov, Koval, 2009, 2011) and a few other higher taxa, mostly with descriptions of numerous new species.

A highly detailed survey of the invertebrate cave fauna of the former Soviet Union, including Russia, and a complete bibliography was published recently by Turbanov et al. (2016a, b, c). The present paper is not only restricted to the European part of Russia, including the northern Caucasus, but excluding Crimea (the latter is to be treated separately), but it incorporates all previously unpublished data contained in the PhD Thesis of S.I. Ljovuschkin (1966). It is also slightly updated using relevant information, both new and missed old, but in addition it covers bats as a highly important component of cave fauna. Besides this, a geological background is provided here.

No zoogeographical analysis is undertaken here since such is available and still quite valid as regards the entire subterranean fauna of the former USSR (Kniss, 2004). In addition, European Russia, especially the northern Caucasus with its particularly rich endogean fauna, is an artificial and heterogeneous region from a biogeographical point of view.

III. Karst and caves

The Precambrian craton occupies most of the European part of Russia. Karst is mainly developed in intrastratal settings in limestones, dolomites, chalk, gypsum and salt of different ages. Most of the caves are in gypsum.

The karstic caves were developed in rocks from a wide range of geological age: Archaean, Proterozoic, Palaeozoic, Triassic, Jurassic, in limestones, dolomites, mixed carbonate rocks, carbonate conglomerates, and gypsum. Pseudokarstic caves are known in sandstones.

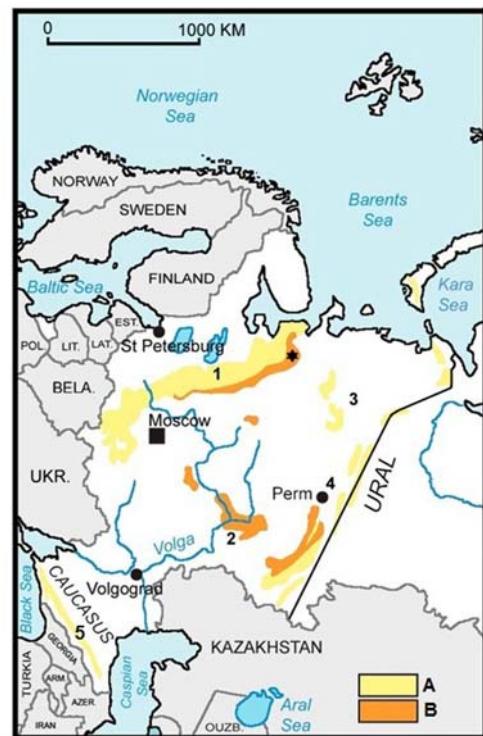


Fig. 1. Karsts of European Russia. A — Carbonated rocks. B — Carbonated and Gypsum rocks. Numbers: 1 — Valdai-Kuloi: limestone and gypsum karsts; 2 — Volga-Kama; 3 — Timan Plateau; 4 — Urals; 5 — Great and Lesser Caucasus. * Pinega gypsum caves. (After Pulina (2005), modified; drawing by B. Juberthie and G. Nazareanu).

Рис. 1. Карсты европейской части России. А — карбонатные породы. В — карбонатные и гипсовые породы. Номера: 1 — Валдай-Кулой: известняковые и гипсовые карсты; 2 — Волго-Камские; 3 — Тиманское плато; 4 — Урал; 5 — Большой и Малый Кавказ. * Пинежские гипсовые пещеры. (По Pulina (2005) с изменениями; рисунок B. Juberthie и G. Nazareanu).

A. Chikishev (1966, 1973, 1978, 1984) distinguished 12 speleological areas in the former USSR. To date, based on morpho-structural criteria, we distinguish 5 karstic-speleologic regions in the European part of Russia: Valdai-Kuloi, Volga-Kama, Timan Plateau, Russian Great Caucasus, Ural (Fig. 1).

1. The Valdai-Kuloisk speleological region. The northern part of the Russian Plain

Located in the northwestern part of European Russia, between Moscow and St. Petersburg, this region is characterized by a very large, but fragmented limestone and gypsum karst strip, 50–100 km broad, 1000 km from south to north near the Baltic Sea.

These northern karsts of European Russia are subjected to hard climate below the arctic anticyclone, with oceanic traits. The rugged karst landscape is mostly overgrown with taiga forest of birch and spruce.

The northwestern Russian area includes some of the largest gypsum karst regions in Europe. The gypsum-anhydrite sequence, often intercalated with limestones and dolomites, is usually 40–60 m thick and lies at shallow depths. Near 40% of the caves are active, partly phreatic, air and water temperature often being near 0 °C.

More than 360 gypsum caves are known, their total length is over 100 km. The longest caves occur in gypsum karst and include the Kulogorskaya-1-2-Troya (14 km), Konstitutionaya (5.8 km) and Olimpiyskaya (5.5 km) caves (Malkov, Gurkalo, 1999; Klimchouk, 2003b).

They include **Pinega gypsum caves** in a Permian gypsum outcrop west of the Urals, around the small town of Pinega, east of Arkhangelsk, just outside the Arctic zone of permafrost, in the main bed of evaporites (gypsum and anhydrite). The ground never freezes to depths of more than a few meters, and the cave streams continue flowing throughout the winter. Over 50 km of passages have been mapped in the group of Pinega caves, among them 22 caves are longer than 1 km each. Three of the most important caves are the Olimpiyskaya, Lomonosovskaya and Muzeynskaya (=Muzeyskaya) caves, in the Iron Gates Sanctuary and the Pinega (=Pinezhskiy) Nature Reserve (Fig. 2) (Waltham, 1994, 2003; Waltham, Cooper, 1998).

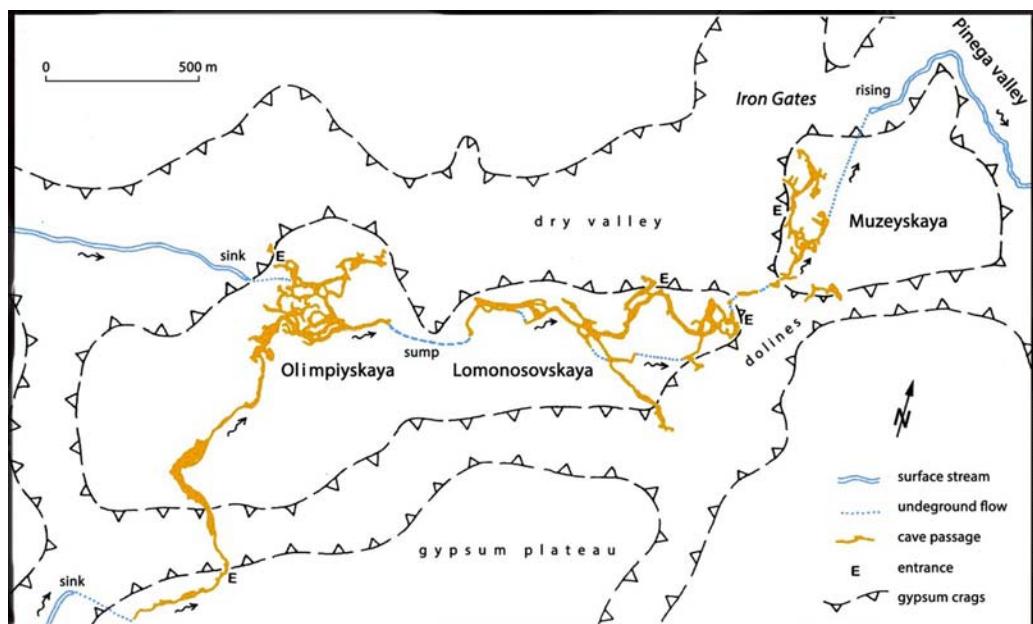


Fig. 2. Pinega Gypsum caves. Maps of three caves located at the Iron Gates (near the Pinezhskiy Nature Reserve). After surveys by "Arkhangel'sk Geologiya" and Waltham (2003); coloured by B. Juberthie.

Рис. 2. Пинежские гипсовые пещеры. Карта трех пещер, расположенных у Железных Ворот (рядом с Пинежским заповедником). По обследованиям «Архангельской геологии» и Waltham (2003); раскрасил B. Juberthie).

Many caves are truncated in the valley walls. A large proportion of caves have dendritic passages that carry or carried subterranean streams.

The Simfoniya (3.2 km long) and Golubinskaya (1.6 km long) caves are both maze caves without stream, located at higher levels in the gypsum plateau. They are comparable in appearance to those in the gypsum of Ukraine.

Below some large entrances cave glaciers are created; the oldest ice has been dated to 3000 years ago (Andrejchuk, Klimchouk, 1996; Malkov et al., 1986, 1988).

2. Volga-Kama (the Volgo-Kamsky region)

This region lies between the Volga and the Urals. Karst is developed in Permian limestones, dolomites and sulfates, and is in Carboniferous and Devonian carbonate rocks.

In the middle Volga and Kama basins, four relatively large zones of limestone and gypsum karst are recorded. They consist in gypsum beds, thickness 10–45 m, interstratified to limestone and dolomite of lower Permian age. There are springs, commonly discharging sulfate-rich water from deep-seated or semi-confined aquifers (Stupishin, 1965; Andrejchuk, Klimchouk, 1996).

The caves are not numerous, their length modest (as far as 100 m), and they still remain poorly-studied in a biospeological aspect (Klimchouk, 2003b).

3. The Timanskiy Mountain Ridge

Within the taiga, or the boreal forest belt, from the northern Urals to the Arctic Ocean, lies the **Timanskiy Mountain Ridge** which contains Devonian and lower Permian gypsum karsts intercalated in dolomites and limestones (Torsuev, 1975). Boreholes and mines have intersected numerous cavities yielding sulfate-rich water.

4. The Urals (Fig. 3)

Karst, gypsum karst, and caves were explored, described and studied by Andrejchuk (1996), Andrejchuk and Klimchouk (1996),

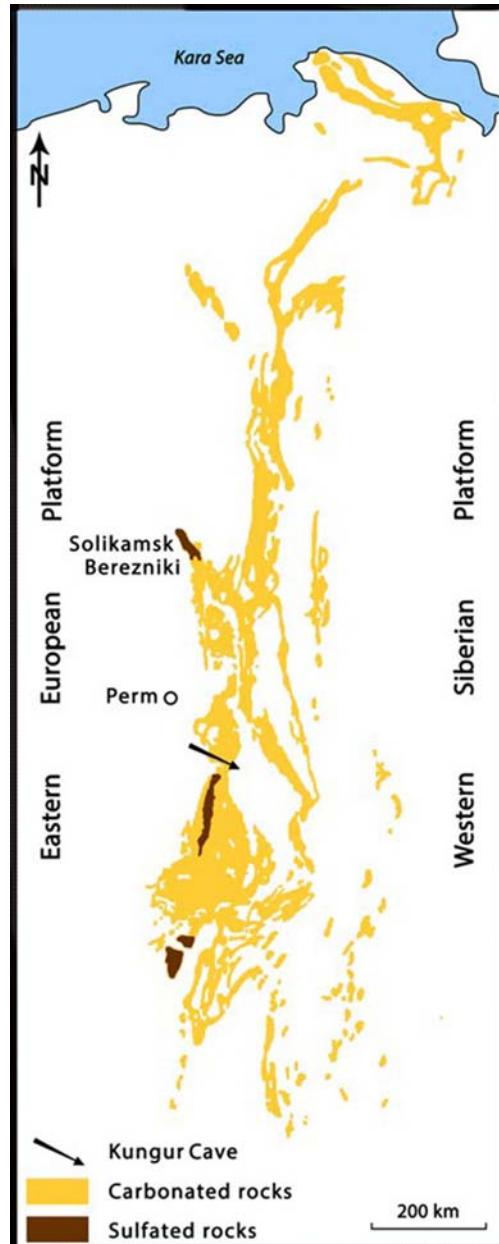


Fig. 3. Karsts of the Urals: carbonated and sulfated rocks.

After Salomon and Pulina (2005), modified by G. Nazareanu.

Рис. 3. Карсты Урала: карбонатные и сульфатные породы.

По Salomon and Pulina (2005), изменения G. Nazareanu.

Chikishev (1973), Dublyanskiy and Ilyukhin (1982), Gorbunova (1965, 1977, 1979), Gorbunova et al. (1992); Kiselyov and Klimchouk (1991), Maksimovitch (1963), Maksimovitch and Gorbunova (1958), Maksimovitch and Kostarev (1973) etc.

The Ural Mountain Ridge covers 2000 km from north to south and represents the traditional boundary between Europe and Asia. It is a Hercynian folded and eroded system largely covered by woodlands. Approximately 1,800 caves are recorded in gypsum and anhydrite rocks of Permian age, as well as in Devonian and Carboniferous limestones and dolomites.

The largest caves are located in the middle and southern Urals: the Sumgan-Kutuk (9.9 km), Divya (9.1 km) and Kinderlinskaya (7.9 km) caves, as well as the Kungurskaya Cave (5.4 km) show in the Perm Region. The Shulgan-Tash Cave, 2.6 km of passages, is famous for its Palaeolithic paintings. The most important karst springs are located in the western Urals: the Goluboe Ozero springs and the Krasnyi Klyuch Spring.

In the northern Urals, near the Polar Circle (Paykhoy and arctic regions), karst was developed under and inside the permafrost (Klimchouk, 2003b).

Gypsum karst in the Urals is widespread, mainly present along the Urals' western periphery (Maksimovitch, Gorbunova, 1958; Gorbunova, 1965, 1977, 1979; Maksimovitch, Kostarev, 1973; Lysenin, 1981; Makukhin, Molodkin, 1988; Gorbunova et al., 1992; Andrejchuk, 1996).

These extend from the Arctic islands of Novaya Zemlya in the North as far as the hot deserts of the northern Caspian region in the South.

In the central Urals, several hundred publications concern gypsum karsts. About 200 caves have been explored in the gypsum: the largest are the Kungurskaya (= Kungur Ice Cave) (5.6 km) and the Zuyatskaya (1,410 m long) caves. Karstic springs are numerous.

Studies on cave fauna were mainly performed in caves of the western macro-slope of the central Urals.

5. The Russian Great Caucasus

The Great Caucasus, or Caucasus Major (Bolshoy Kavkaz), is the highest mountain ridge in European Russia, where many mountain peaks are 3,000–5,000 m in elevation (Mt Elbrus, volcanic peak, 6,642 m a.s.l.), spanning 1,250 km from the Black Sea to the Caspian Sea.

Only the northern macro-slope (Ciscaucasia, or Circassia) and the westernmost part of the Caucasus, from Novorossiysk as far as Sochi and the Psou River, neighbouring to Abkhazia, along the Black Sea coast, is Russian.

On the northern macro-slope, the karsts were developed in monoclonal and folded structures, mostly in Jurassic and lower Cretaceous limestones, dolomites, and gypsum. Alpine karst and deep caves are present in the northern slope and Russian western region. As of 2003, the Gorlo Barloga Cave was the deepest (~900 m), located in the Zagedan Massif in Devonian and Carboniferous metamorphosed limestones and schists. Among other caves, there are the Zagedanskaya (~570 m, 5,300 m long) and Alekseeva (~465 m, 4,410 long).

In the Dzhentu Massif, the Mayskaya Cave is ~500 deep and 4,410 m long.

In the alpine Fisht Massif at the western flank of the core zone and the westernmost summit of the Caucasus Major Range, explored from 1980 to 1996, deep caves in Upper Jurassic limestones are present: the Krestik-Turist (~633 m, 14 km long), Paryashchaya Ptitsa (~595 m, 4,500 m long) and Ol'ga (~520 m, 3,500 m long) caves; most springs are located at the range bottom 1,200 m a.s.l. (Reisner, Shelepin 1997; Klimchouk 2003a).

Numerous zones of gypsum karst are present along the northern macro-slope of the Great Caucasus. Many caves support subterranean streams. The longest are the Popova (1,670 m), Ammonal'naya (1,460 m) and Seteney (980 m) caves (Kazanbiev, 1975; Klimchouk et al., 1996; Makukhin, Molodkin, 1988; Ostapenko, 1993, 1994; Sukhovey, 1992).

On the northern macro-slope of the Caucasus Major, the most important biospeleological areas are located along the Black Sea in the Krasnodar Province (the Alek, Akhtsu, Voron-

tsovky, Dzykhra, Akhshtyr, Akhun and Fisht-Oshten-Lagonaki massifs of Jurassic dolomites). As of 2003, the longest and deepest caves are the Vorontsovskaya (10.6 km) and Rucheinaya-Shkol'naya-Zabladshikh (-601 m) (Gvozdetski, 1965a, 1965b).

Cave fauna is relatively well known.

IV. Subterranean biota

Birstein and Ljovuschkin (1950) divided Russia into two major biospeleological zones:

1. A northern zone covering most of the Russian territory: the Russian Plain and the northern Urals, both characterized by very poor subterranean faunas, with only a few stygobionts belonging to copepods, *Bathynella* syncarids and amphipods that correspond to old widespread groups.

2. A southern zone (Ciscaucasia and western Transcaucasia), characterized by numerous endemic stygo- and troglobionts.

About 100 exclusively subterranean taxa have been recorded from European Russia, more than 50% being aquatic. Most of them inhabit the Russian Great Caucasus.

Based on actual knowledge, there are three biospeleological zones: central Russia, the Urals and the Russian Great Caucasus.

IV. 1. Valdai-Kuloisk. The northern part of the Russian Plain

Mostly microorganisms are surveyed in gypsum caves of the Belomorsko-Kuloiskoe Plateau: the Golubinskaya, Pekhorovskiy Proval and G-1 caves, all by Semikolennykh (1997). These gypsum caves are embedded 3–15 m deep under the surface and are very wet, with high-level flood waters annually. The mean temperature is about 2–8 °C in summer and nearly 0 °C in winter.

The following species have been identified, none of which represents troglo- or stygobionts: Domain **Bacteria** Woese, Kandler et Wheelis, 1990

Division **Actinobacteria** Goodfellow, 2012

Order **Micromonosporales** Genilloud, 2015

Family **Micromonosporaceae** Krassilnikow, 1938 em. Zhi, Li et Stackebrandt, 2009
– *Micromonospora* sp., from mineral clay samples;

Order **Actinomycetales** Buchanan, 1917

Family **Streptomycetaceae** Waksman et Henrici, 1943
– *Streptomyces* sp., from mineral clay samples;

Unidentified sulfate-reducing bacteria were also discovered.

Domain **Eukaryota** (Chatton, 1925) Whittaker et Margulis, 1978

Kingdom **Fungi** Linnaeus, 1753 stat. nov. Neck-er, 1783 em. Cavalier-Smith, 1998

Division **Ascomycota** Berkeley, 1857 stat. nov. Cavalier-Smith, 1987

Class **Eurotiomycetes** O.E. Eriksson et Winka, 1997

Order **Eurotiales** G.W.Martin ex Benny et Kimbrough, (1980)

Family **Trichocomaceae** E. Fischer, (1897)
– *Penicillium italicum* (Wehmer, 1894), on dead insects;
– *Penicillium viridicatum* Westling, 1911, with stable colonies on cave clay;

Class **Dothideomycetes** O.E. Eriksson et Winka, 1997

Order **Pleosporales** Luttrell ex M.E. Barr, (1987)

Family: Incertae sedis

– *Pyrenophaeta* sp.;

Division **Zygomycota** Barr, 1982

Order **Mucorales** Fries, 1832

Family **Mucoraceae** Dumortier, (1822)
– *Rhizopus* sp., on organic matter (flooded or penetrated through infiltration);

Kingdom **Viridiplantae** Cavalier-Smith, 1981

Division **Chlorophyta** Reichenbach, 1828, em. Pascher, 1914, em. Lewis et McCourt, 2004

Order **Chlorococcales** Pascher, 1915

Family **Chlorococcaceae** Blackman et Tansley, 1902

– *Chlorococcus* sp., forming green spots near the entrance, always situated in reflected light.

Kingdom **Protozoa** R. Owen, 1858

Subkingdom **Sarcomastigota** Cavalier-Smith, 1983

Group **Excavata** (Cavalier-Smith), 2002

Phylum **Amoebozoa** Lühe, 1913

Class **Tubulinea** Smirnov, Nassonova, Berney, Fahrni, Bolivar et Pawlowski, 2005

Order **Arcellinida** Kent, 1880

Family Centropyxidae Jung, 1942

– *Centropyxis aerophila* Deflandre, 1929. Found in a cave at the bank of Pechora River within the Pechoro-Ilychskiy Nature Reserve (Trotsk-Pechorsk District, Komi Republic) (Mazei et al., 2012).

Family Phryganellidae Jung, 1942

– *Phryganella hemisphaerica* Penard, 1902. Found in a cave at the bank of Pechora River within the Pechoro-Ilychskiy Nature Reserve (Trotsk-Pechorsk District, Komi Republic) (Mazei et al., 2012).

Kingdom **Animalia** Linnaeus, 1758

Phylum **Nematoda** Diesing, 1861

Nematoda indet. Unidentified nematodes have been recorded in the caves Olimpiyskaya and Muzeynaya, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

Phylum **Annelida** Lamarck, 1809

Class **Oligochaeta** Grube, 1850

Order **Enchytraeida** Vejdovský, 1879

Family Enchytraeidae Vejdovský, 1879

Enchytraeidae indet. Unidentified enchytraeids have been recorded in the Olimpiyskaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

Phylum **Arthropoda** Siebold, 1848

Subphylum **Crustacea** Brünnich, 1772

Class **Copepoda** Milne-Edwards, 1840

Order **Cyclopoida** Burmeister, 1834

Family Cyclopidae Rafinesque, 1815

– *Megacyclops viridis* (Jurine, 1820). Recorded in waterbodies inside the Muzeynaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

Class **Malacostraca** Latreille, 1817

Order **Amphipoda** Latreille, 1816

Family Pallaseidae Tachteew, 2000

– *Pallasea* sp. Recorded in waterbodies inside the Kitezh Cave, Pinezhskiy Nature

Reserve, Arkhangelsk Region (Sidorov et al., 2011; Chertoprud et al., 2011).

Class **Arachnida** Cuvier, 1812

Subclass **Acari** Leach, 1817

The fauna of free-living gamasid mites of the Pinezhskiy Nature Reserve is unusually diverse and rich (117 species) (Makarova, 2009), but its caves support only few presumed trogloxenes. Apparently, the caves are too cold to sustain a characteristic terrestrial fauna.

Superclass **Hexapoda** Blainville, 1816

Class **Collembola** Lubbock, 1870

The springtail fauna of the Pinezhskiy Nature Reserve is unusually diverse and rich (126 species) (Babenko, 2008), but its caves support only few presumed trogloxenes. Apparently, the caves are too cold to sustain a characteristic terrestrial fauna.

Class **Insecta** Linnaeus, 1758

Order **Ephemeroptera** Hyatt et Arms, 1891

Family Baetidae Leach, 1815

– *Baetis rhodani* (Pictet, 1843). Recorded in waterbodies inside the Olimpiyskaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

– *Centroptilum luteolum* Müller, 1776. Recorded in waterbodies inside the Olimpiyskaya and Muzeynaya caves, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

Family Siphlonuridae Ulmer, 1920

– *Siphlonurus lacustris* Eaton, 1870. Recorded in waterbodies inside the Muzeynaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

Order **Plecoptera** Burmeister, 1839

Family Nemouridae Newman, 1853

– *Nemurella pictetii* (Klapálek, 1900). Recorded in waterbodies inside the Olimpiyskaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

– *Nemoura sahlbergi* Morton, 1896. Recorded in waterbodies inside the Olimpiyskaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

- *Nemoura* aff. *avicularis* Morton, 1894.
Recorded in waterbodies inside the Muzeynaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).
- Family Perlodidae Klapálek, 1912
 - *Diura nanseni* (Kempny, 1900). Recorded in waterbodies inside the Olimpiyskaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).
- Family Taeniopterygidae Klapálek, 1905
 - *Taeniopteryx nebulosa* (Linnaeus, 1758). Recorded in waterbodies inside the Olimpiyskaya and Muzeynaya caves, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).

Table 1. List of *stygobionts, stygophile and troglophile species from the northern part of the Russian Plain.
 Таблица 1. Список *стигобионтов, стигофилов и троглофилов из северной части Русской равнины.

A — Stygobionts*: stygophiles

BACTERIA	EPHEMEROPTERA
<i>Micromonosporaceae</i>	<i>Siphlonuridae</i>
<i>Micromonospora</i> sp.	<i>Siphlonurus lacustris</i> Eaton, 1870
<i>Streptomycetaceae</i>	<i>Baetidae</i>
<i>Streptomyces</i> sp.	<i>Centroptilum luteolum</i> Müller, 1776; <i>Baetis rhodani</i> (Pictet, 1843)
FUNGI	PLECOPTERA
<i>Trichocomaceae</i>	<i>Perlodidae</i>
<i>Penicillium italicum</i> (Wehmer, 1894);	<i>Diura nanseni</i> (Kempny, 1900)
<i>Penicillium viridicatum</i> Westling, 1911	<i>Taeniopterygidae</i>
<i>Pleosporales</i>	<i>Taeniopteryx nebulosa</i> (Linnaeus, 1758)
<i>Pyrenophaeta</i> sp.	<i>Nemouridae</i>
<i>Mucoraceae</i>	<i>Nemurella pictetii</i> (Klapálek, 1900); <i>Nemoura sahlbergi</i> Morton, 1896; <i>Nemoura</i> af. <i>avicularis</i> Morton, 1894
<i>Rhizopus</i> sp.	HETEROPTERA
VIRIDIPLANTAE	<i>Corixidae</i>
<i>Chlorococcaceae</i>	<i>Sigara semistriata</i> (Fieber, 1848)
<i>Chlorococcus</i> sp.	DIPTERA
PROTOZOA	<i>Pediciidae</i>
<i>Centropyxidae</i>	<i>Dicranota bimaculata</i> (Schummel, 1829)
<i>Centropyxis aerophila</i> Deflandre, 1929	<i>Limoniidae</i>
Phryganellidae	<i>Eloeophila mundata</i> (Loew, 1871)
<i>Phryganella hemisphaerica</i> Penard, 1902	<i>Simuliidae</i>
NEMATODA	<i>Cnetha</i> sp.
Nematoda indet.	<i>Chironomidae</i>
OLIGOCHAETA	<i>Guttipelopia guttipennis</i> (Wulp, 1874)
Enchytraeidae indet.	CHIROPTERA
COPEPODA	<i>Vespertilionidae</i>
Cyclopidae	<i>Myotis brandtii</i> (Eversmann, 1845)
<i>Megacyclops viridis</i> (Jurine, 1820)	<i>Eptesicus nilssonii</i> (Keyserling et Blasius, 1839)
Pallaseidae	
<i>Pallasea</i> sp.	
INSECTA	

- Family Pediciidae Osten-Sacken, 1860
 – *Dicranota bimaculata* (Schummel, 1829). Recorded in waterbodies inside the Olimpiyskaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).
- Family Simuliidae Newman, 1834
 – *Cnetha* sp. Recorded in waterbodies inside the Olimpiyskaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).
- Family Chironomidae Jacobs, 1900
 – *Guttipelopia guttipennis* (Wulp, 1874). Recorded in waterbodies inside the Muzeynaya Cave, Pinezhskiy Nature Reserve, Arkhangelsk Region (Chertoprud et al., 2011).
- Phylum **Chordata** Haeckel, 1874
- Subphylum **Vertebrata** J.-B. Lamarck, 1801
- Class **Mammalia** Linnaeus, 1758
- Order **Chiroptera** Blumenbach, 1779
 Famaly Vespertilionidae Gray, 1821
 – *Myotis brandtii* (Eversmann, 1845). Solitarily hibernating individuals of this species were reported from the Golubinskiy Proval Cave, Pinezhskiy Nature Reserve, where they were found twice in 1980 (Rykov, 2014).
 – *Eptesicus nilssonii* (Keyserling et Blasius, 1839). Hibernating Northern bats were reported from several karst caves of the Belomorsko-Kuloiskoe Plateau, with the maximum number of 16 bats observed in one visit to the Golubinskiy Proval Cave (Rykov, 2014).
- IV. 2. Central Russia**
- The cave biota of central Russia is little-known and poorly studied. Below is only a preliminary evaluation.
- This karstic region lies too northerly to be subjected to either Mediterranean or Balkan, or Asiatic influence.
- Bacteria, Algae and Fungi were surveyed in the Poneretka Cave, Borovichskiy District, Novgorod Region, located in limestones of the Valdai Plateau, temperature 9 °C, by Semikolennykh (1997). The numbers of microorgan-
- isms are about 10⁷ per sediment gram.
- Domain **Bacteria** Woese, Kandler et Wheelis, 1990
- Division **Actinobacteria** Goodfellow, 2012
- Order **Actinomycetales** Buchanan, 1917
- Family Mycobacteriaceae Chester, 1897
 – *Mycobacterium hyalinum* Söhngen, 1913;
 – *M. licheniforme* Krassilnikow, 1949;
 – *M. luteum* Söhngen, 1913;
 – *M. mucosum* Krassilnikow, 1941
- Family Propionibacteriaceae Delwiche, 1957
 – *Propionibacterium* sp.
- Family Streptomycetaceae Waksman et Henrici, 1943
 – *Streptomyces* sp.;
 – *Streptoverticillium* sp.;
 – *Streptosporangium* sp.
- Family Micrococcaceae Pribram, 1929
 – *Arthrobacter globiformis* Conn et Dimmick, 1947
- Class **Bacilli** Ludwig, Schleifer et Whitman, 2010
- Order **Bacillales** Prévot, 1953
- Family Bacillaceae Fischer, 1895
 – *Bacillus mycoides* Flügge, 1886
- Division **Cyanobacteria** Stanier, 1973
- Order **Nostocales** Cavalier-Smith, 2002
 Family Nostocaceae C.A. Agardh, 1824 ex Kirchner, 1898
 – *Nostoc* sp.
- Division **Proteobacteria** Stachebrandt, Murray et Trüper, 1988, Garrity, Bell et Lilburn, 2005
- Class **Gammaproteobacteria** Garrity, Bell et Lilburn, 2005
- Order **Pseudomonadales** Orla-Jensen, 1921
 Family Pseudomonadaceae Winslow, Broadhurst, Buchanan, Krumwiede, Rogers et Smith, 1917
 – *Pseudomonas desmolyticum* Cray et Thornton, 1928
- Kingdom **Fungi** Linnaeus, 1753 stat. nov. Neck-er, 1783 em. Cavalier-Smith, 1998
- Division **Ascomycota** Berkeley, 1857 stat. nov. Cavalier-Smith, 1987
- Class **Eurotiomycetes** O.E. Eriksson et Winka, 1997
- Order **Onygenales** Ciferri ex Benny et Kimbrough, (1980)

- Family Gymnoascaceae Baranetsky, (1872)
 – *Pseudoarachniotus* sp.
- Kingdom **Viridiplantae** Cavalier-Smith, 1981
- Division **Chlorophyta** Reichenbach, 1828, em. Pascher, 1914, em. Lewis et McCourt, 2004
- Class **Trebouxiophyceae** Friedl, 1995
 Chlorellales sp. is the only species collected.
- Protists are extremely poorly known in caves of the central part of European Russia. Only two papers deal with this group in the region in question. One is by Semikolennykh (1997), dedicated to the study of Protista in the Poneretka Cave, Borovichskiy District, Novgorod Region. The other is by Mazei et al. (2012), which focuses on microfauna in artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region.
- Kingdom **Chromista** Cavalier-Smith, 1981
- Phylum **Ciliophora** Doflein, 1901
- Class **Oligohymenophorea** de Puytorac et al., 1974
- Order **Pleuronematida** Fauré-Fremiet in Corliss, 1956
 Family Pleuronematidae Kent, 1881
 – *Balantiophorus elongatus* Schewiakoff, 1892. Recorded from the Poneretka Cave, Borovichskiy District, Novgorod Region (Semikolennykh, 1997).
- Kingdom **Protozoa** R. Owen, 1858
- Subkingdom **Sarcomastigota** Cavalier-Smith, 1983
- Group **Excavata** (Cavalier-Smith), 2002
- Phylum **Euglenozoa** Cavalier-Smith, 1981
- Class **Euglenophyceae** Schoenichen, 1925
 Order **Peranemida** Bütschli, 1884
 Family Bodonaceae Bütschli, 1884
 – *Bodo globosus* Stein, 1878. Recorded from the Poneretka Cave, Borovichskiy District, Novgorod Region (Semikolennykh, 1997).
 – *B. lens* (O.F. Müller) Klebs (1892). Recorded from the Poneretka Cave, Borovichskiy District, Novgorod Region (Semikolennykh, 1997).
 – *Bodo* sp. Recorded from the Poneretka Cave, Borovichskiy District, Novgorod Region (Semikolennykh, 1997).
- Phylum **Amoebozoa** Lühe, 1913
- Class **Tubulinea** Smirnov, Nassonova, Berney, Fahrni, Bolivar et Pawłowski, 2005
- Order **Arcellinida** Kent, 1880
 Family Arcellidae Ehrenberg, 1843
 – *Arcella arenaria compressa* Chardez, 1974. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).
- Family **Centropyxidae** Jung, 1942
 – *Centropyxis aerophila* Deflandre, 1929. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).
 – *C. aerophila sphagnicola* Deflandre, 1929. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).
 – *C. plagiostoma* Thomas et Bonnet, 1955. Recorded from the Poneretka Cave, Borovichskiy District, Novgorod Region (Semikolennykh, 1997).
- Family **Hyalosphaeniidae** Schultze, 1877
 – *Hyalosphenia papilio* Leidy, 1879. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).
- Family **Nebelidae** Taranek, 1882
 – *Nebela parvula* Cash, 1909. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).
 – *N. tincta* Leidy, 1879. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).
- Family **Phryganellidae** Jung, 1942
 – *Phryganella acropodia* (Hertwig et Lesser, 1874). Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).
 – *P. hemisphaerica* Penard, 1902. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).
- Phylum **Amoebozoa** Lühe, 1913 em. Cavalier-Smith, 1998
- Class **Archamoeba** Cavalier-Smith, 1998
 Family Mastigamoebidae Goldschmidt, 1907
 – *Mastigamoeba* sp. Recorded from the Poneretka Cave, Borovichskiy District, Novgorod Region (Semikolennykh, 1997).

Class **Tubulinea** Smirnov, Nassonova, Berney, Fahrni, Bolivar et Pawlowski, 2005

Order **Tubulinida** Smirnov, Nassonova, Berney, Fahrni, Bolivar et Pawlowski, 2005

Family Hartmannellidae Volkonsky, 1931

– *Hartmannella* sp. Recorded from the Ponteretka Cave, Borovichskiy District, Novgorod Region (Semikolennykh, 1997).

Kingdom **Rhizaria** Cavalier-Smith, 2002

Phylum **Cercozoa** Cavalier-Smith, 1998

Class **Imbricatea** Cavalier-Smith, 2003

Order **Euglyphida** Copeland, 1956

Family Euglyphidae Wallich, 1864

– *Assulina seminulum* (Ehrenberg, 1848).

Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).

– *Euglypha rotunda* Wailes, 1915. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).

Family Trinema Hoogenraad et de Groot, 1940

– *Trinema complanatum* Penard, 1890. Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).

– *T. encelys* (Ehrenberg, 1838). Recorded from artificial adits of the Zhiguli Hills, Stavropolskiy District, Samara Region (Mazei et al., 2012).

Kingdom **Animalia** Linnaeus, 1758

Phylum **Rotifera** Cuvier, 1817

Phylum **Annelida** Lamarck, 1809

Class **Oligochaeta** Grube, 1850

Order **Crassiclitellata** Jamieson, 1988

Family Lumbricidae Claus, 1876

– *Eisenia foetida* (Savigny, 1826), first recorded by Michaelsen in 1926 (Malevich, 1947) from moist clay in the deep part of a cave on the right bank of Volga River, downstream the mouth of Kama River. It was found again by Birstein in several caves of the Russian Caucasus and in Abkhazia. The species is troglobene in Western Europe and abundant in farmyard manure. It is perhaps troglophilic in Russian and Georgian caves with bat guano.

– *Eiseniella tetraedra* (Savigny, 1826). Recorded from wells in the city of Saratov (Behning, 1928).

Order **Enchytraeida** Vejdovský, 1879

Family Enchytraeidae Vejdovský, 1879

– *Henlea ventriculosa* (d'Udekem, 1854). Recorded from wells in the city of Saratov (Behning, 1928).

– *Enchytraeus albidus* Henle, 1837. Recorded from wells in the city of Saratov (Behning, 1928).

– *Fridericia bulbosa* (Rosa, 1887). Recorded from wells in the city of Saratov (Behning, 1928).

Order **Tubificida** Brinkhurst, 1982

Family Naididae Ehrenberg, 1828

– *Nais communis* Piguet, 1906. Repeatedly recorded from numerous wells in European Russia, including those in the city of Saratov (Behning, 1928).

– *N. pseudobtusa* Piguet, 1906. Recorded from wells in the city of Saratov (Behning, 1928).

Family Tubificidae Vejdovský, 1884

– *Potamothrix hammoniensis* (Michaelsen, 1901). Recorded from wells in the city of Saratov (Behning, 1928).

Phylum **Nematoda** Diesing, 1861

Nematodes have almost never been studied in caves of the central part of European Russia. The only relevant paper is that by Behning (1928) which puts on record 11 species of the group found in wells in the city of Saratov. This city is located on the Volga Upland within the Saratov Region:

Class **Enoplea** Inglis, 1983

Order **Monhysterida** Filipjev, 1929

Family Dorylaimidae De Man, 1876

– *Eudorylaimus carteri* (Bastian, 1865);
– *E. carteri rotundatus* (Micoletzky, 1922);
– *E. monohystera* (De Man, 1880);
– *E. obtusicaudatus* (Bastian, 1865);
– *Laimydorus pseudostagnalis* (Micoletzky, 1927).

Family Monhysteridae De Man, 1876

– *Monhystera paludicola* De Man, 1881.

Order **Mononchida** Jairajpuri, 1969

Family Mononchidae Chitwood et Chitwood, 1937

– *Mononchus macrostoma* Bastian, 1865;

– *M. papillatus* Bastian, 1865.

- Order **Triplonchida** Cobb, 1920
 Family Tobrilidae Filipjev, 1918
 – *Tobrilus allophysoides* (Micoletzky, 1925).
- Class **Chromadorea** Inglis, 1932
 Family Rhabditidae Örley, 1880
 – *Rhabditis curvicaudata* (Schneider, 1866).
- Class **Secernentea** Lorenzen, 1981
 Order **Tylenchida** Thorne, 1949
 Family Cephalobidae Filipjev, 1934
 – *Cephalobus rigidus* Schneider, 1866.
- Phylum **Arthropoda** Siebold, 1848
 Subphylum **Crustacea** Brünnich, 1772
- Class **Copepoda** Milne-Edwards, 1840
 Order **Cyclopoida** Burmeister, 1834
 – *Diacyclops bicuspitatus* (Claus, 1857). Stygoxene, recorded from the Bornukovskaya Cave in the Nizhniy Novgorod Region (Birstein, Ljovuschkin, 1966).
 – *Acanthocyclops vernalis* (Fischer, 1853). Stygophile, recorded from the Bornukovskaya Cave in the Nizhniy Novgorod Region (Birstein, Ljovuschkin, 1966).
- Order **Harpacticoida** G.O. Sars, 1903
 Family Canthocamptidae Brady, 1880
 – *Canthocamptus staphylinus* (Jurine, 1820). Stygoxene, recorded from wells near the city of Saratov (Behning, 1928).
- Family Parastenocarididae Chappuis, 1940
 – *Parastenocaris fonticola* Borutzky, 1926, described from a well at Kosino near Moscow City (Borutzky, 1926), currently known to be a widespread species (Borutzky, 1926).
- Class **Ostracoda** Latreille, 1802
 Order **Podocopida** G.O. Sars, 1866
 Family Cyprididae Baird, 1845
 – *Potamocypris wolfi* Brech, 1920. Crenobiont, found in underground streams near the city of Voronezh below Tertiary sandstone plates (Bronstein, 1947).
- Class **Malacostraca** Latreille, 1817
 Superorder **Syncarida** Packard, 1885
 Order **Bathynellacea** Chappuis, 1915
 Family Bathynellidae Grobbon, 1904
 – *Bathynella* sp. Formerly referred to as *Bathynella chappuisi* Delachaux, 1919, from a well 65 km W of Kalach-on-Don, Volgograd (Schäfer, 1951). The species identity requires confirmation (Birstein, Ljovuschkin, 1967b).
- Order **Amphipoda** Latreille, 1816
 Family Crangonyctidae Bousfield, 1973
 – *Synurella ambulans* (F. Müller, 1847) (= *S. meschtscherica* Borutzky, 1929). Stygophile, widespread across European Russia. Recorded from springs in the Ryazan (Borutzky, 1927), Moscow (Chertoprud, 2006), Vladimir, Kaluga, Pskov and Bryansk regions (Sidorov, Palatov, 2012).
 – *Synurella derzhavini* Behning, 1928. Stygobiont, eyes and integument unpigmented. Described from wells near the city of Saratov (Behning, 1928).
 – *Synurella donensis* (Martynov, 1919). Stygobiont, described from springs in the Kiziterinka River valley, now within the city of Rostov-on-Don (Martynov, 1919).
- Class **Arachnida** Cuvier, 1812
 Order **Aranei** Clerck, 1758
 Family Nesticidae Simon, 1894
 – *Nesticus cellulanus* (Clerck, 1758). Troglophil, found in caves at Kamennoe, Nizhniy Novgorod Region (Kapralov, Chernorudskiy, 2009).
- Family Tetragnathidae Menge, 1866
 – *Metellina merianae* (Scopoli, 1763). Troglophil, widespread in Europe at cave entrances, found in caves at Kamennoe, Nizhniy Novgorod Region (Kapralov, Chernorudskiy, 2009).
- Superclass **Hexapoda** Blainville, 1816
 Class **Insecta** Linnaeus, 1758
 Order **Coleoptera** Linnaeus, 1758
 Family Cryptophagidae Kirby, 1937
 – *Cryptophagus setulosus* Sturm, 1845. Troglophil, recorded from caves in the Novgorod Region (Kapralov, 2015).
 – *C. schmidti* Sturm, 1845. Troglophil, recorded from caves of the Novgorod Region (Kapralov, 2015).
 – *Henoticus serratus* (Gyllenhal, 1808). Troglophil, recorded from the Baskunchakskaya Cave, Akhtubinskiy District, Astrakhan Region (Kapralov, 2015).
- Family Leiodidae Fleming, 1821
 – *Catops morio* (Fabricius, 1792). Troglophil, recorded from caves in the Novgorod Region (Kapralov, 2015).

- *Choleva glauca* (Britten, 1918). Subtroglophilic, recorded from caves in the Novgorod Region (Kapralov, 2015).
- *Ch. lederiana* Reitter, 1902. Subtroglophilic, a mass species both in natural and artificial caverns in the Novgorod Region, also reported from quarries in the Tver and Ryazan regions (Kapralov, 2015).
- *Cholevinus pallidus* (Ménétrier, 1832). Subtroglophilic, recorded in a cave near Lake Baskunchak, Akhtubinskiy District, Astrakhan Region (Perkovsky, 1991).

Order Lepidoptera Linnaeus, 1758

Family Noctuidae Latreille, 1809

- *Scoliopteryx libatrix* (Linnaeus, 1758). Troglophilic, recorded in European Russia from numerous caves in the Novgorod and Astrakhan regions (Kapralov, Chernorudskiy, 2009; Mukhanov, Kapralov, 2010; Kapralov, 2015).

Order Diptera Linnaeus, 1758

Suborder **Nematocera** Schiner, 1862

Family Trichoceridae Rondani, 1841

- *Trichocera maculipennis* Meigen, 1818. Troglophilic, common in caves of European Russia in the Novgorod and Astrakhan regions, as well as the Perm Province (Kapralov, Chernorudskiy, 2009; Pan'kov et al., 2009b; Kapralov, 2015).
- *Trichocera regelationis* (Linnaeus, 1758). Troglophilic, common in caves of European Russia in the Novgorod and Astrakhan regions (Kapralov, Chernorudskiy, 2009; Kapralov, 2015).

Suborder **Brachycera** Zetterstedt, 1842

Family Phoridae Gray, 1840

Phoridae gen. spp. Likely troglophiles, larvae found in numerous caves of European Russia, but identified closer to neither genera nor species (Kapralov, 2015).

Phylum **Chordata** Haeckel, 1874

Subphylum **Vertebrata** J.-B. Lamarck, 1801

Class **Mammalia** Linnaeus, 1758

Order **Chiroptera** Blumenbach, 1779

Family Vespertilionidae Gray, 1821

Strictly speaking, only a few records of bats have been made in natural undergrounds due to scarcely available karst caves. Hence, the ma-

jority of findings refer to mines, cellars, rock-cut cells and cave monasteries. In many cases naturally presented cavities and crevices were deepened and transformed into artificial underground chambers; therefore, it is virtually impossible to estimate the past importance of these roosts to bats. Whereas no bats reproduce in central Russia, underground chambers, regardless of their origin, represent the only kind of winter shelter suitable for the hibernation of seven resident species. Aside from many dozens of other records from various underground roosts, all seven of these species were recorded from the natural caves of the Ichalkovskiy Nature Reserve, Novgorod Region, where they have been either netted at entrances during swarming or observed hibernating (Bakka, Bakka, 1999):

- *Myotis dasycneme* (Boie, 1825);
- *Myotis daubentonii* (Kuhl, 1817);
- *Myotis nattereri* (Kuhl, 1817);
- *Myotis brandtii* (Eversmann, 1845);
- *Myotis mystacinus* (Kuhl, 1817);
- *Plecotus auritus* (Linnaeus, 1758);
- *Eptesicus nilssonii* (Keyserling et Blasius, 1839).

Conclusion. The terrestrial and aquatic cave biota in central Russia is scarce because the Quaternary glaciations must have destroyed all old cave species. Apparently, the only way for survival was in subterranean phreatic and hyporheic habitats (Table 2) (Kniss, Smirnov, 1990; Kniss, 2001, 2004).

IV. 3. Ural

In the Urals, caves are relatively well studied compared to northern Russia's caverns. Microarthropod cave fauna is diversified. The subterranean fauna consists of numerous trogophilic species, as well as several troglobionts and stygobionts. Troglobionts are known only amongst Collembola.

Studies on microorganisms in the sediment of the Ledyanaya and Kungurskaya ice caves in the central Urals show them to range from 44,000 to 500,000 ex. per gram from winter to spring (Volodin, Pshenichnikov, 1949).

Table 2. List of *stygobionts, stygophile and troglophilic species from central Russia.
 Таблица 2. Список *стигобионтов, стигофильных и троглофильных видов
 из Центральной России.

A — Stygobionts *: stygophiles	
BACTERIA	Arcellidae
Mycobacteriaceae	<i>Arcella arenaria compressa</i> Chardez, 1974
<i>Mycobacterium hyalinum</i> Söhngen, 1913	Centropyxidae
<i>Mycobacterium licheniforme</i> Krassilnikow, 1949	<i>Centropyxis aerophila</i> Deflandre, 1929
<i>Mycobacterium luteum</i> Söhngen, 1913	<i>Centropyxis aerophila sphagnicola</i> Deflandre, 1929
<i>Mycobacterium mucosum</i> Krassilnikow, 1941	<i>Centropyxis plagiostoma</i> Thomas et Bonnet, 1955
Propionibacteriaceae	Hyalospheniidae
<i>Propionibacterium</i> sp.	<i>Hyalosphenia papilio</i> Leidy, 1879
Streptomycetaceae	Nebelidae
<i>Streptomyces</i> sp.	<i>Nebela parvula</i> Cash, 1909
<i>Streptoverticillium</i> sp.	<i>Nebela tinctoria</i> Leidy, 1879
Streptosporangiaceae	Phryganellidae
<i>Streptosporangium</i> sp.	<i>Phryganella acropodia</i> (Hertwig et Lesser, 1874)
Micrococcaceae	<i>Phryganella hemisphaerica</i> Penard, 1902
<i>Arthrobacter globiformis</i> Conn et Dimmick, 1947	Mastigamoebidae
Bacillaceae	<i>Mastigamoeba</i> sp.
<i>Bacillus mycoides</i> Flügge, 1886	Hartmannellidae
Nostocaceae	<i>Hartmannella</i> sp.
<i>Nostoc</i> sp.	Oligochaeta
Pseudomonadaceae	Enchytraeidae
<i>Pseudomonas desmolyticum</i> Cray et Thornton, 1928	<i>Henlea ventriculosa</i> (d'Udekem, 1854)
FUNGI	<i>Enchytraeus albidus</i> Henle, 1837
Gymnoascaceae	<i>Fridericia bulbosa</i> (Rosa, 1887)
<i>Pseudoarachniotus</i> sp.	Haplotauxida: Naididae
VIRIDIPLANTAE	<i>Nais communis</i> Piguet, 1906
Chlorophytia: Trebouxiophyceae	<i>Nais pseudobtusa</i> Piguet, 1906
<i>Chlorella</i> sp.	Haplotauxida: Tubificidae
CILIOPHORA	<i>Potamothrix hammoniensis</i> (Michaelsen, 1901)
Pleuronematidae	COPEPODA
<i>Balantiophorus elongatus</i> Schewiakoff, 1892	Cyclopoida: Cyclopidae
EUGLENOZOA	<i>Acanthocyclops vernalis</i> Fischer, 1853
Bodonaceae	Harpacticoida: Parastenocarididae
<i>Bodo globosus</i> Stein, 1878	* <i>Parastenocaris fonticola</i> Borutzky, 1926
<i>Bodo lens</i> (O.F. Müller) Klebs, (1892)	OSTRACODA
<i>Bodo</i> sp.	Podocopida: Cyprididae
RHIZARIA	<i>Potamocyparis wolfi</i> Brech, 1920
Euglyphidae	Syncarida
<i>Assulina seminulum</i> (Ehrenberg, 1848)	Bathynellacea: Bathynellidae
<i>Euglypha rotunda</i> Wailes, 1915	* <i>Bathynella</i> sp.
Trinematidae	Amphipoda
<i>Trinema complanatum</i> Penard, 1890	Crangonyctidae
<i>Trinema enchelys</i> (Ehrenberg, 1838)	* <i>Synurella derzhavini</i> Behning, 1925
AMOEBOZOA	* <i>Synurella donensis</i> (Martynov, 1919)
	<i>Synurella ambulans</i> (F. Müller, 1846)
B — Troglobionts*: troglophones	
Oligochaeta	Nesticidae
Lumbricidae	<i>Nesticus cellularis</i> (Clerck, 1758)
<i>Eisenia foetida</i> Savigny, 1826	COLEOPTERA
<i>Eiseniella tetraedra</i> (Savigny, 1826)	Cryptophagidae
Aranei	<i>Cryptophagus setulosus</i> Sturm, 1845
Tetragnathidae	<i>Cryptophagus schmidti</i> Sturm, 1845
<i>Metellina merianae</i> (Scopoli, 1763)	<i>Henoticus serratus</i> (Gyllenhal, 1808)

Leiodidae	Phoridae
<i>Catops morio</i> (Fabricius, 1792)	<i>Phoridae</i> gen. spp.
<i>Choleva glauca</i> (Britten, 1918)	CHIROPTERA
<i>Choleva lederiana</i> Reitter, 1902	Vespertilionidae
<i>Cholevinus pallidus</i> (Ménétriés, 1832)	<i>Myotis dasycneme</i> (Boie, 1825)
LEPIDOPTERA	<i>Myotis daubentonii</i> (Kuhl, 1817)
Noctuidae	<i>Myotis nattereri</i> (Kuhl, 1817)
<i>Scoliopteryx libatrix</i> (Linnaeus, 1758)	<i>Myotis brandtii</i> (Eversmann, 1845)
DIPTERA	<i>Myotis mystacinus</i> (Kuhl, 1817)
Trichoceridae	<i>Plecotus auritus</i> (Linnaeus, 1758)
<i>Trichocera maculipennis</i> Meigen, 1818	<i>Eptesicus nilssonii</i> (Keyserling et Blasius, 1839)
<i>Trichocera regelationis</i> (Linnaeus, 1758)	

Phylum Annelida Lamarck, 1809

Class Oligochaeta Grube, 1850

Order Crassiclitellata Jamieson, 1988

Family Lumbricidae Claus, 1876

- *Dendrobaena octaedra* (Savigny, 1826). Troglophilic, recorded from the Shulgan-Tash Cave, Burzianskiy District, Bashkortostan (= Republic of Bashkiria) (Kniss, 1984b, 2001).
- *Dendrodrilus rubidus* (Savigny, 1826). Troglophilic, recorded from caves of Bashkortostan (Kniss, 2001).
- *Eiseniella tetraedra* (Savigny, 1826). Likely troglophilic, recorded from the Shulgan-Tash Cave, Burzianskiy District, Bashkortostan (Kniss, 1984b, 2001).

Phylum Arthropoda Siebold, 1848

Subphylum Crustacea Brünnich, 1772

Class Malacostraca Latreille, 1817

Order Amphipoda Latreille, 1816

Family Crangonyctidae Bousfield, 1973

- *Crangonyx chlebnikovi chlebnikovi* Borutzky, 1928 (= *Crangonyx chlebnikovi maximovitshi* Pankov et Pankova, 2004). Stygobiont, found in several caves in the Perm Province of the Urals (Pan'kov, 2008b; Pan'kov, Pan'kova, 2004; Pan'kov, Starova, 2009a, 2009c; Pan'kov et al., 2005, 2010, 2011; Sidorov et al., 2010, 2012).

Class Arachnida Cuvier, 1812

Order Aranei Clerck, 1758

Family Linyphiidae Blackwall, 1859

- *Improphanes improbulus* (Simon, 1929). Troglophilic, recorded from the Kurmanayevskaya and Grot Tashastinskiy caves, both in Bashkortostan (Esyunin, Efimik, 1999).

– *Megalephyphantes pseudocollinus* Saaristo, 1997. Troglophilic, recorded from the Kungurskaya Cave in the Perm Province (Pan'kov, 2008a; Pan'kov et al., 2009b).

– *Neriene montana* (Clerck, 1758). Troglophilic, recorded from the Kungurskaya Cave in the Perm Province (Pan'kov, 2008a; Pan'kov et al., 2009b).

– *Neriene radiata* (Walckenaer, 1841). Troglophilic, recorded from the Chudesnitsa Cave in the Perm Province (Pan'kov, 2008a; Pan'kov et al., 2009b).

Family Nesticidae Simon, 1894

– *Nesticus cellulanus* (Clerck, 1758). Troglophilic, recorded from the Shulgan-Tash (= Kapovaya) Cave in Bashkortostan (Abdullin et al., 2012), as well as in the Obvalnaya and Letuchikh Myshey caves in the Perm Province (Pan'kov et al., 2009).

Subclass Acari Leach, 1817

Superorder Acariformes Zakhvatkin, 1952

Order Prostigmata Kramer, 1877

Suborder Anystina Van der Hammen, 1972

Family Rhagidiidae Oudemans, 1922

– *Rhagidia breviseta* Zacharda, 1995. Apparently troglobiont, recorded from the Shulgan-Tash (= Kapovaya) Cave in Bashkortostan (Kapralov, 2015).

– *Rhagidia* sp. Apparently troglobiont, recorded from several caves in Bashkortostan, southern Urals, Russia (Kniss, 1984b, 2001).

– *Foveacheles* sp. Troglobiont, recorded from the Shulgan-Tash (= Kapovaya) Cave in Bashkortostan (Abdullin et al., 2012; Kapralov, 2015).

- Suborder **Eleutherengona** Oudemans, 1909
- Family Pygmephoridae Cross, 1965
- *Pygmephorus* sp. Troglophilic, recorded from several caves in Bashkortostan, southern Urals (Kniss, 1984b, 2001).
- Order **Sarcoptiformes** Reuter, 1909
- Suborder **Oribatida** Van der Hammen, 1968
- Family Aleurodamaeidae Paschoal et Johnston, 1984
- *Epidamaeus* sp. Troglophilic, recorded from several caves in Bashkortostan, southern Urals (Kniss, 1984b, 2001).
- Family Mochlozetidae Grandjean, 1960
- *Sphaerobates* sp. Troglophilic, recorded from several caves in Bashkortostan, southern Urals (Kniss, 1984b, 2001).
- Superclass **Hexapoda** Blainville, 1816
- Class **Collembola** Lubbock, 1870
- As many as 34 troglophilic and 4 troglobiont species of springtails are known from Ural caves (Table 3).
- Order **Poduromorpha** Börner, 1913, sensu D'Haese, 2002
- Superfamily **Neanuroidea** Massoud, 1967, sensu D'Haese, 2002
- Family Neanuridae Börner, 1906
- *Philotella olgae* Kniss et Thibaud, 1995. Likely troglobiont, described and only known from caves in Bashkortostan (Kniss, Thibaud, 1995; Kniss, 2001, 2006).
- Superfamily **Hypogastruroidea** Salmon, 1964, sensu Deharveng, 2004
- Family Hypogastruridae Börner, 1906
- *Schaefferia baschkirica* Kniss, 1985. Troglobiont, described from the Klyka and Kiekbayevskaya caves, both on the right bank of Belaya River, as well as from the Kanskaya-2 Cave on the left bank of Kana River, all in Bashkortostan (Kniss, 1985, 2001; Babenko et al., 1994).
 - *Ceratophysella kapoviensis* (Babenko, 1994). Troglobiont with faint traces of troglomorphism. Described from the Shulgan-Tash (= Kapovaya) Cave in Bashkortostan (Babenko et al., 1994; Kniss, 2001).
- Order **Entomobryomorpha** Börner, 1916, sensu Soto-Adames et al., 2008
- Superfamily **Isotomoidea** Szeptycki, 1979, sensu Soto-Adames et al., 2008
- Family Isotomidae Schäffer, 1896
- *Heteroisotoma stebajevae* (Rusek, 1991). Troglophilic, recorded from the Planovaya-3 Cave in the Burzianskiy District of Bashkortostan, as well as from the entrance to the Druzhba Cave near Serga River, Sverdlovsk Region (Jie et al., 2011).
 - *Sericeotoma knissi* Potapov, 1991. Troglobiont, described from the Yakshingulovskaya-1 Cave on the right bank of Belaya River in Bashkortostan (Potapov, 1991).
- Superfamily **Tomoceroidea** Szeptycki, 1979
- Family Tomoceridae Schäffer, 1896
- *Plutomurus baschkiricus* (Skorikow, 1899), troglobiont, endemic to many caves in Bashkortostan (Turbanov et al., 2016b), populations studied by Kniss (1984a).
 - *Tomocerus asiaticus* Martynova, 1969 and four other troglophilic *Tomocerus* spp. are recorded from the Urals.
- All these species are recent cave-dwellers which must have survived in caves during the glacial Pleistocene period (Kniss, Thibaud, 1999; Kniss, 1984a, 1984b, 1985, 2004).
- Class **Insecta** Linnaeus, 1758
- Order **Psocoptera** Shipley, 1904
- Family Psyllipsocidae Lienhard et Smithers, 2002
- *Psyllipsocus* sp. Troglophilic, recorded from caves of Bashkortostan, southern Urals (Kniss, 2001).
- Order **Coleoptera** Linnaeus, 1758
- Family Carabidae Latreille, 1802
- *Bembidion obscurellum turanicum* Csiki, 1928. Troglophilic, recorded from caves of Bashkortostan, southern Urals (Kniss, 2001).
 - *Bembidion quadrimaculatum* (Linnaeus, 1761). Mistakenly referred to as a troglophilic, recorded from the Zapovednaya Cave, Beloretskiy District, Bashkortostan (Kniss, 2001), but actually, just like the previous subspecies, a trogloxene.
- Family Cryptophagidae Kirby, 1937
- *Micrambe nigricollis* Reitter, 1876. Troglophilic, recorded from the Shulgan-Tash Cave, Burzianskiy District, Bashkortostan (Kaprakov, 2015).

Table 3. List of *stygobionts, stygophiles and *troglobionts, troglobiophiles from the Urals.
 Таблица 3. Список *стигобионтов, стигофилов и *тrogлобионтов, троглофилов с Урала.

A — Stygobionts *: stygophiles

AMPHIPODA

Crangonyctidae

**Crangonyx chlebnikovi chlebnikovi* Borutzky, 1928

B — Troglobionts *: troglobiophiles

Oligochaeta

Lumbricidae

Eiseniella tetraedra (Savigny, 1826)*Dendrobaena octaedra* (Savigny, 1826)*Dendrodrilus rubidus* (Savigny, 1826)

ARANEI

Linyphiidae

Improphanes improbulus (Simon, 1929)*Megalepthyphantes pseudocollinus* Saaristo, 1997*Neriene montana* (Clerck, 1758)

Nesticidae

Nesticus cellulanus (Clerck, 1758)

ACARI

Prostigmata: Eupodina: Rhagidiidae

Rhagidia breviseta* Zacharda, 1995*Rhagidia* sp.Foveacheles* sp.

Sarcoptiformes: Oribatida: Damaeidae

Epidamaeus sp.

Sarcoptiformes: Oribatida: Mochlozetidae

Sphaerobates sp.

ACARI PARASITI

Parasitidae

Parasitus oudemansi Berlese, 1903*Parasitus remberti* (Oudemans, 1912)

Rhodacaridae

Cyrtolaelaps mucronatus Canestrini, 1881

CHILOPODA

Monotarsobius curtipes C.L. Koch, 1847

COLLEMBOLA

Dicyrtomidae

Dicyrtoma fusca (Lubbock, 1873)

Hypogastruridae

Ceratophysella armata* (Nicolet, 1842)*Ceratophysella bengtssoni* (Agren, 1904)*Ceratophysella denticulata* (Bagnall, 1941)*Ceratophysella kapoviensis* (Babenko, 1994)*Ceratophysella sigillata* (Uzel, 1890)*Ceratophysella succinea* (Gisin, 1949)*Hypogastrura sahlbergi* (Reuter, 1895)*Hypogastrura sensilis* (Folsom, 1919)*Hypogastrura subboldorii* Delamare et Jacquemin, 1962*Hypogastrura vernalis* (Carl, 1901)Schaefferia baschkirica* Kniss, 1985*Typhlogastrura cf. alabamensis* Thibaud, 1975

Entomobryidae

Entomobrya puncteola Uzel, 1891*Lepidocyrtus curvicollis* (Bourlet, 1839)*Lepidocyrtus lanuginosus* Gmelin, 1788*Lepidocyrtus violaceus* (Fourcroy, 1785)

Isotomidae

Desoria olivacea (Tullberg, 1871)*Folsomia diplophthalma* (Axelson, 1902)*Folsomia multiseta* Stach, 1947*Folsomia quadrioculata* Tullberg, 1871*Folsomia spinosa* Kseneman, 1936*Heteroisotoma stebajevae* Rusek, 1999*Isotoma albella* Packard, 1873*Isotoma knissi* Potapov, 1991*Isotoma viridis* Bourlet, 1839*Proisotoma notabilis* (Schaeffer, 1896)

Neanuridae

**Philotella olgae* Kniss et Thibaud, 1996

Onychiuridae

Hymenaphorura sibirica (Tullberg, 1876)*Onychiurodes granulosus* (Stach, 1930)*Onychiurus furcifer* (Börner, 1901)*Onychiurus schoetti* Lie-Pettersen, 1896*Protaphorura armata* (Tullberg, 1869)

Tomoceridae

**Plutomurus baschkiricus* (Skorikow, 1899)*Tomocerina minuta* (Tullberg, 1876)*Tomocerus asiaticus* Martynova, 1969*Tomocerus minor* (Lubbock, 1862)*Tomocerus cf. punctatus* Yosii, 1967*Tomocerus vulgaris* (Tullberg, 1871)

Arrhopalitidae

Arrhopalites principalis Stach, 1945

PSOCOPTERA

Psyllipsocidae

Psyllipsocus sp.

COLEOPTERA

Carabidae

Bembidion obscurellum turanicum Csiki, 1928*Bembidion quadrimaculatum* (Linnaeus, 1761)

Cryptophagidae

Micrambe nigricollis Reitter, 1876

Leiodidae

Choleva glauca (Britten, 1918)*Choleva lederiana* Reitter, 1902

Staphylinidae

Atheta sp.*Falagria thoracica* Curtis, 1833*Geostiba circellaris* Gravenhorst, 1802

LEPIDOPTERA	Scathophagidae
Noctuidae	Scathophagidae gen. spp.
<i>Scoliopteryx libatrix</i> (Linnaeus, 1758)	
DIPTERA	CHIROPTERA
Mycetophilidae	Vesptilionidae
<i>Speolepta leptogaster</i> (Winnertz, 1863)	<i>Myotis dasycneme</i> (Boie, 1825)
Sciaridae	<i>Myotis daubentonii</i> (Kuhl, 1817)
Sciaridae gen. spp.	<i>Myotis nattereri</i> (Kuhl, 1817)
Trichoceridae	<i>Myotis brandtii</i> (Eversmann, 1845)
<i>Trichocera maculipennis</i> Meigen, 1818	<i>Myotis mystacinus</i> (Kuhl, 1817)
Phoridae	<i>Myotis davidii</i> Peters, 1869
Phoridae gen. spp.	<i>Plecotus auritus</i> (Linnaeus, 1758)
	<i>Eptesicus nilssonii</i> (Keyserling et Blasius, 1839)

Family Leiodidae Fleming, 1821

- *Choleva glauca* (Britten, 1918). Subtroglophile, recorded from the Shulgan-Tash Cave, Burzianskiy District, Bashkortostan (Kapralov, 2015).
- *Choleva lederiana* Reitter, 1902. Subtroglophile, recorded from the Kungurskaya Ice Cave (Koz'minykh, 2012).

Family Staphylinidae Lameere, 1900

- *Atheta* sp. Troglophile, recorded from caves of the southern Urals: Ishcheevskaya-2, Ishimbayskiy District, and Shulgan-Tash, Burzianskiy District, both Bashkortostan (Kniss, 2001).
- *Falagria thoracica* Curtis, 1833. Troglophile, recorded from the Bortovoy Otpor Cave and the Zilimskiy grotto, Gafuriyskiy District, Bashkortostan (Kniss, 2001).
- *Geostiba circellaris* Gravenhorst, 1802. Troglophile, recorded from caves of Bashkortostan, southern Urals (Kniss, 2001).

Order Lepidoptera Linnaeus, 1758

Family Noctuidae Latreille, 1809

- *Scoliopteryx libatrix* (Linnaeus, 1758). Troglophile, recorded from numerous caves in the Perm Province and Bashkortostan (Pan'kov et al., 2009b; Kapralov, 2015).

Order Diptera Linnaeus, 1758

Suborder Nematocera Schiner, 1862

Family Mycetophilidae Newman, 1835

- *Speolepta leptogaster* (Winnertz, 1863). Troglophile, recorded from the Shulgan-Tash Cave, Burzianskiy District, Bashkortostan; the characteristic hunting nets also reported from the Dudkinskaya adit, Ufa City, and the Butylka Cave, both Bashkortostan as well (Kapralov, 2015).

Family Sciaridae Billberg, 1820

- Sciaridae gen. spp. Likely troglophiles, larvae encountered in several caves of European Russia, including the southern Urals. A reliable record concerns the Starosaitovskaya-1 Cave, Ishimbayskiy District, Bashkortostan (Kniss, 2001; Kapralov, 2015).

Family Trichoceridae Rondani, 1841

- *Trichocera maculipennis* Meigen, 1818. Troglophile, common in caves of the Perm Province (Pan'kov et al., 2009b; Kapralov, 2015).

Suborder Brachycera Zetterstedt, 1842

Family Phoridae Gray, 1840

- Phoridae gen. spp. Likely troglophiles, larvae encountered in several caves in the southern Urals, but remain unidentified as to genus and species (Kapralov, 2015).

Family Scathophagidae Robineau-Desvoidy, 1830

- Specimens unidentified to genus and species have been encountered in the Babinogorskaya Cave, Kungurskiy District, Perm Province (Pan'kov et al., 2009b).

Phylum Chordata Haeckel, 1874

Subphylum Vertebrata J.-B. Lamarck, 1801

Class Mammalia Linnaeus, 1758

Order Chiroptera Blumenbach, 1779

Family Vesptilionidae Gray, 1821

According to recent data, eight bat species of the 14 occurring in the Urals are resident in the region, while others perform seasonal long-distance migrations and depart in winters. No maternity roosts have been found underground so far, as all records in caves were related to swarming or hibernating bats belonging to the

following eight species (see Bol'shakov et al. (2005), Snit'ko (2007, 2009, 2011), and Snit'ko and Snit'ko (2016, 2017a, 2017b) for details):

– *Myotis dasycneme* (Boie, 1825) (Fig. 4A). This species, common in the region, was found in more than 50 cave hibernacula located from north to south along the Urals, with the largest known aggregations in the Smolinskaya and Arakaevskaya caves in the Sverdlovsk Region (up to 2,000 and over 200, respectively). In the southern Urals, no substantial winter colonies have been discovered, although this bat is relatively abundant at cave entrances during swarming time.

– *Myotis daubentonii* (Kuhl, 1817) (Fig. 4D). Daubenton's bat is as fairly common in the Urals as elsewhere within its distribution range in Russia; it was recorded in over 50 caves throughout the region. Unlike the Pond Bat, it forms no large winter aggregations. Therefore, it is usually undercounted during surveys at hibernation sites. The Smolinskaya and Arakaevskaya caves in the Sverdlovsk Region alongside the Nadezhda and Sukhokamenskaya caves in the Chelyabinsk Region, and the Kueshta Cave in Bashkiria comprise the largest winter colonies which range from 50 to 110 individuals.

– *Myotis nattereri* (Kuhl, 1817). The species was considered rare in the region because only few records from the middle and southern Urals were reported in the 20th century. However, Natterer's bats turned out to be very common in caves of the southern Urals in late summer and autumn, where these bats were caught in large numbers at cave entrances as they swarmed, with the largest number of 1,000 animals counted in the Kyzyl-Yar Cave in Bashkiria.

– *Myotis brandtii* (Eversmann, 1845) (Fig. 4E). Brandt's bat was found in >20 and 29 underground roosts in the middle and southern Urals, respectively. The Divya Cave in the Perm Province represents the northernmost hibernation roost in the Urals with the

largest winter colony (up to 1,000 individuals); only a few Brandt's bats were found hibernating in other caves. Despite its relative rarity in winter, a number of Brandt's bats were netted at swarming sites in the southern Urals, where *M. brandtii* was the second most abundant species following *E. nilssonii* in Bashkiria and following *P. auritus* in the Chelyabinsk Region.

– *Myotis mystacinus* (Kuhl, 1817) (Fig. 4F). A few reliable records from the northern Urals were made in the Divya Cave. In the southern Urals, the species is abundant in swarming and hibernation undergrounds in Bashkiria, where about 50 bats were netted at the entrances to the caves Kueshta, Laklinskaya, Oktyabrskaya, Nadezhda and Sukhokamenskaya.

– *Myotis davidii* Peters, 1869. It is unclear yet, which of the previous records of bats from the *M. mystacinus* morpho-group should be assigned to this species (see Ben-David et al. (2016) for a taxonomic review). Two individuals identified as undoubtedly *M. davidii* were found in the Podarok Cave, Orenburg Region in September 2016.

– *Plecotus auritus* (Linnaeus, 1758) (Fig. 4B). The Brown long-eared bat is widely distributed, albeit not abundant in hibernation sites in the Urals. It was found in more than 60 caves throughout the region, northwards up to the Divya Cave. It was also very common in samples netted during swarming in the southern part of the region (Chelyabinsk Region and Bashkiria), where it constituted 15 and 24% of all captured bats, respectively.

– *Eptesicus nilssonii* (Keyserling et Blasius, 1839) (Fig. 4C). The Northern Bat is the most widely distributed and abundant species in the Urals. It has been found in more than 70 underground sites across the region, with the largest winter aggregation in the Arakaevskaya Cave, Perm Province. *E. nilssonii* comprised a large proportion of swarming bats at the entrances to caves in the southern Urals, being the most abundant species in the Chelyabinsk Region.

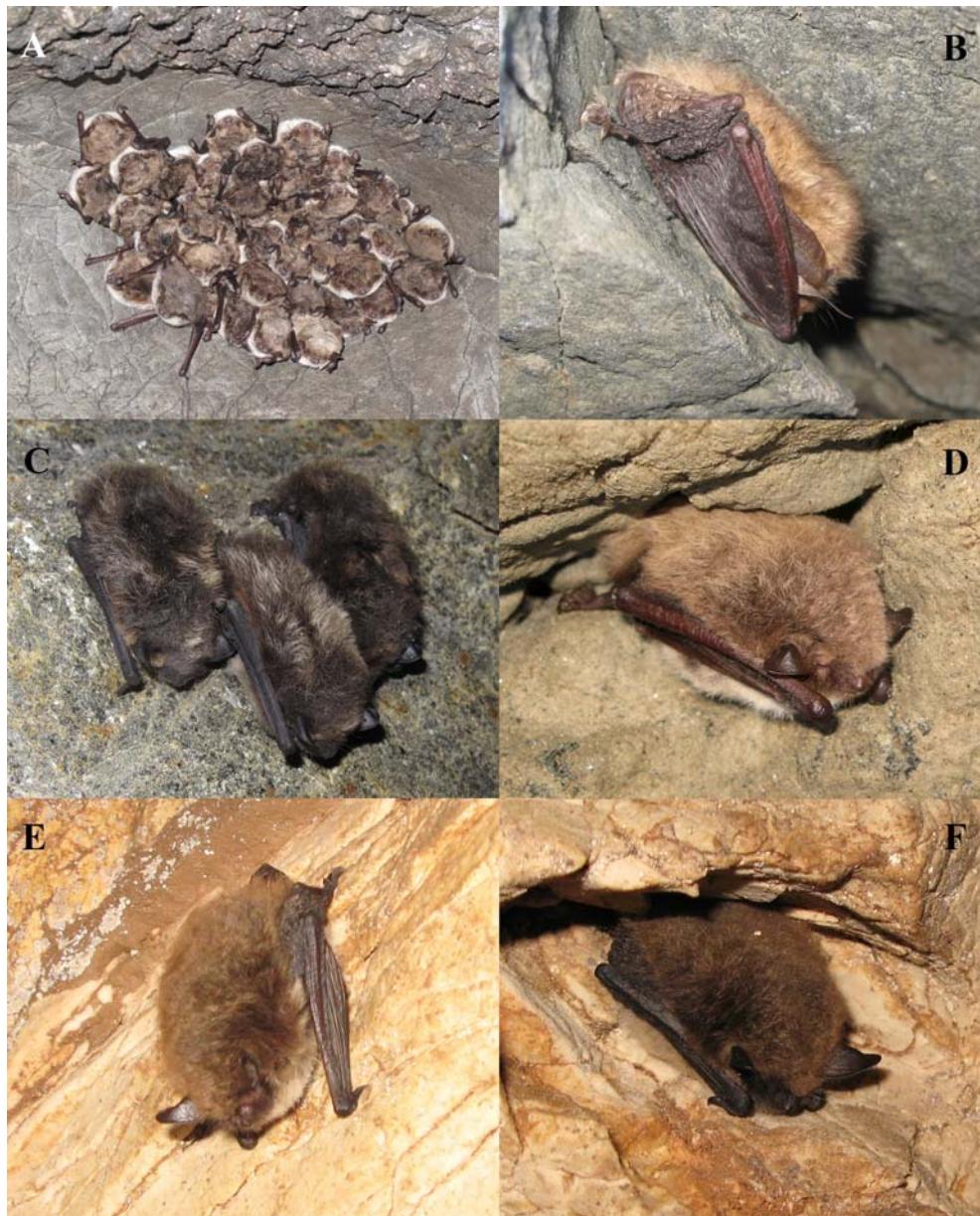


Fig. 4. Some species of bats during hibernation in caves of the Urals. A — hibernating colonies of the Pond bat, *Myotis dasycneme* (Boie, 1825) in the Smolinskaya Cave, Sverdlovsk Region. B — a hibernating Brown long-eared bat, *Plecotus auritus* (Linnaeus, 1758) in the Nadezhda Cave, Chelyabinsk Region. C — a hibernating Northern bat, *Eptesicus nilssonii* (Keyserling et Blasius, 1839) in the Nukatovskaya Cave, Bashkiria. D — a hibernating Daubenton's bat, *Myotis daubentonii* (Kuhl, 1819) in the Sukhaya Atya Cave, Chelyabinsk Region. E — a hibernating Brandts bat, *Myotis brandtii* (Eversmann, 1845) in the Kyzyl-Yar Cave, Bashkiria. F — a hibernating Whiskered bat, *Myotis mystacinus* (Kuhl, 1817) in the Sukhokamenskaya Cave, Chelyabinsk Region. All pictures by Ksenia Snit'ko.

Conclusion. The subterranean fauna of the Urals, both terrestrial and aquatic, is mainly troglophilic and stygophile, with a reduced number of endemic and relict cave species (Table 3). The impact of glacial Pleistocene phases may account for the scarcity of troglobionts and the relatively high number of recent troglophiles.

IV. 4. The Russian Great Caucasus

Charitonov (=Kharitonov) (1947), Malevich (1947), Borutzky (1934, 1948a, b, 1950a, b, 1961, 1965, 1967a, b), Birstein (1948, 1950, 1952, 1954, 1967), Starobogatov (1962), Ljovuschkin and Starobogatov (1963), Rudjakov (1963), Zalesskaja (1963, 1973a, b, 1978), Ljovuschkin and Matiokin (1965), Ljovuschkin (1962, 1963, 1965, 1966, 1970, 1972a, b, 1973), Birstein and Ljovuschkin (1967a), Danielopol (1969), Golovatch (1975, 1978, 1983, 1984–1985, 1990, 2011), Read (1992), Belousov (1999), Kniss and Thibaud (1999), Kantor and Sysoev (2005), Belousov and Koval (2009, 2011), Chemeris (2009), Karaman (2012), Antić and Makarov (2016) and several other authors have provided much of the information on invertebrates of the region in question. A full updated checklist and an as complete bibliography as possible concerning the entire territory of the former Soviet Union are available in Turbanov et al. (2016a, b, c).

The Russian Caucasus consists of Ciscaucasia (= Circassia) and the western part of Transcaucasia as far south as Psou River, bordering on Abkhazia. The subterranean biota can be estimated as being relatively well known in Russia, also being the richest in endemic and relict species with more than 80 troglo- and stygobionts revealed (Table 4).

Kingdom **Chromista** Cavalier-Smith, 1981

Phylum **Ochrophyta** Cavalier-Smith, 1995

Class **Chrysophyceae** Pascher, 1914

Order **Ochromonadales** Pascher, 1910

Family Paraphysomonadaceae Preisig et Hibberd, 1983

— *Paraphysomonas bandaiensis* (Hibberd, 1979). Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).

Family Chromulinaceae Engler, 1897

— *Spumella* sp. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).

Class **Raphidophyceae** Chadeauf et Silva, 1980

Order **Thaumatomonadida** Shirkina, 1987

Family Thaumatomastigidae Patterson et Zolffel, 1991

— *Thaumatomonas seravini* Mylnikov and Karpov, 1993. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).

Superphylum **Alveolata** Cavalier-Smith, 1991

Phylum **Ciliophora** Doflein, 1901

Class **Phyllopharyngea** de Puytorac et al., 1974

Subclass **Suctorria** Claparède et Lachmann, 1858

— *Suctoria* gen. sp. Epibiont forms found on hypogean amphipods in the Beloskal'skaya and Pionerskaya (= Ushchel'naya) caves, Khostinsky City District, Greater Sochi, Krasnodar Province (Birstein, 1950).

Kingdom **Rhizaria** Cavalier-Smith, 2002

Phylum **Cercozoa** Cavalier-Smith, 1998

Class **Sarcomonadea** Cavalier-Smith, 1993

Order **Glissomonadida** Howe, Bass, Vickerman, Chao et Cavalier-Smith, 2009

Family Allapsidae Howe, Bass, Vickerman, Chao et Cavalier-Smith, 2009

Рис. 4. Некоторые виды летучих мышей во время зимовки в пещерах Урала. А — зимующие колонии ночницы прудовой (*Myotis dasycneme* (Boie, 1825)) в Смолинской пещере (Свердловская обл.). В — зимующий ушан (*Plecotus auritus* (Linnaeus, 1758)) в пещере Надежда (Челябинская обл.). С — зимующий северный кожанок (*Eptesicus nilssonii* (Keyserling et Blasius, 1839)) в пещере Нукатовская (Башкирия). Д — зимующая водяная ночница (*Myotis daubentonii* (Kuhl, 1819)) в пещере Сухая Атя (Челябинская обл.). Е — зимующая ночница Брандта (*Myotis brandtii* (Eversmann, 1845)) в пещере Кызыл-Яр (Башкирия). F — зимующая усатая ночница (*Myotis mystacinus* (Kuhl, 1817)) в пещере Сухокаменская (Челябинская обл.). Все фотографии Ксении Снитько.

Table 4. List of *stygobionts, possible stygobionts, stygophiles, possible troglobionts and troglobiophiles from the Caucasus.
 Таблица 4. Список *стигобионтов, вероятных стигобионтов, стигофилов, возможных троглобиотов и троглофилов с Кавказа.

A — Stygobionts *: stygophiles

CHROMISTA	Physaridae
Paraphysomonadaceae	<i>Physarum flagellatum</i> (Alexeieff, 1923)
<i>Paraphysomonas bandaiensis</i> (Hibberd, 1979)	PLATYHELMINTHES
Chromulinaceae	Tricladida gen. sp.
<i>Spumella</i> sp.	Dugesiidae
RHIZARIA	<i>Dugesia taurocaucasica</i> (Livanov, 1951)
Thaumatomastigidae	Dendrocoelidae
<i>Thaumatomonas seravini</i> Mylnikov et Karpov, 1993	Dendrocoelidae gen. sp.
<i>Thaumatomonas seravini</i> Mylnikov et Karpov, 1993	* <i>Dendrocoelum</i> sp. 1
Allapsidae	* <i>Dendrocoelum</i> sp. 2
<i>Allantion tachyploon</i> Sandon, 1924	MOLLUSCA: GASTROPODA
Heteromitidae	Hydrobiidae
<i>Heteromita globosa</i> (Stein, 1878)	<i>Belgrandiella caucasica</i> Starobogatov, 1962
<i>Heteromita</i> sp.	**“ <i>Geyeria</i> ” <i>valvataeformis</i> Starobogatov, 1962
ALVEOLATA	**“ <i>Lartetia</i> ” sp.
<i>Suctoria</i> gen. sp.	* <i>Paladilhiopsis orientalis</i> Starobogatov, 1962
MYZOOZA	* <i>Paladilhiopsis pulcherrima</i> Starobogatov, 1962
Protaspidaeae	* <i>Paladilhiopsis subovata</i> Starobogatov, 1962
<i>Protaspis simplex</i> Vors, 1992	MOLLUSCA: BIVALVIA
Colponemidae	Euglesidae
<i>Colponema edaphicum</i> Mylnikov et Tikhonenkov, 2007	<i>Euglesa personata</i> (Malm, 1855)
SARCOMASTIGOTA	* <i>Euglesa cavatica</i> (Shadin, 1952)
Bodonaceae	HIRUDINEA
<i>Bodo designis</i> Skuja, 1948	Erpobdellidae
<i>Bodo saliens</i> Larsen et Paterson, 1990	<i>Erpobdella octoculata</i> (Linnaeus, 1758)
<i>Bodo saltans</i> Ehrenberg, 1838	COPEPODA
<i>Cercomonas granulifera</i> (Hollande, 1942)	Cyclopoida
<i>Cercomonas laciniaegerens</i> (Krassiltschick, 1886)	Cyclopidae
<i>Cercomonas</i> sp.	* <i>Acanthocyclops venustus stammeri</i> (Kiefer, 1930)
<i>Dimastigella mimosae</i> Frolov, Mylnikov et Malysheva, 1997	<i>Diacyclops bisetosus</i> (Rehberg, 1880)
<i>Rhynchosomona nasuta</i> (Stokes) Klebs, 1892	<i>Paracyclops fimbriatus imminutus</i> Kiefer, 1929
AMOEBOZOA	* <i>Speocyclops cinctus</i> Monchenko, 1982
Centropyxidae	* <i>Speocyclops lussitanus</i> Borutzky, 1950
<i>Centropyxis constricta</i> (Ehrenberg, 1841)	* <i>Speocyclops psezuapsensis</i> Borutzky, 1965
<i>Centropyxis ecornis</i> (Ehrenberg, 1841)	Harpacticoida
<i>Centropyxis orbicularis</i> Deflandre, 1929	Ameiridae
<i>Centropyxis plagiostoma</i> Bonnet et Thomas, 1955	* <i>Nitocrella hirta caucasica</i> Borutzky, 1967
<i>Centropyxis platystoma</i> (Penard, 1890)	* <i>Megastygonitocrella l'jovuschkini</i> (Borutzky, 1967)
<i>Centropyxis spinosa</i> Cash, 1905	Canthocamptidae
Difflugiidae	<i>Attheyella crassa</i> (G.O. Sars, 1863)
<i>Difflugia avellana</i> Penard, 1890	* <i>Bryocamptus aqueductus</i> Borutzky, 1940
<i>Difflugia avellana gigas</i> Gauthier-Lievre et Thomas, 1958	<i>Bryocamptus hostensis</i> Borutzky, 1972
<i>Difflugia penardi</i> Hopkinson, 1909	* <i>Bryocamptus innominatus</i> Borutzky, 1940
<i>Difflugia oblonga</i> Ehrenberg, 1838	<i>Bryocamptus pygmaeus</i> (G.O. Sars, 1863)
<i>Pontigulasia incisa</i> Rhumbler, 1896	<i>Bryocamptus tarnogradskyi</i> Borutzky, 1934
Heleoperidae	<i>Bryocamptus zschorkei caucasicus</i> Borutzky, 1930
<i>Heleopera sphagni</i> Leidy, 1874	<i>Canthocamptus staphylinus</i> (Jurine 1820)
MYCETOZOA	<i>Elaphoidella bidens coronata</i> (G.O. Sars, 1904)
	* <i>Pilocamptus georgevitchi</i> (Chappuis, 1923)
	* <i>Elaphoidella czerkessica</i> Borutzky, 1972
	* <i>Moraria hostensis</i> Borutzky, 1972

- **Moraria operculata* Borutzky, 1948
 **Moraria poppei* (Mrazek, 1893)
 **Moraria varica* (Graeter, 1910)
 Parastenodarididae
 **Parastenocaris tenuis* Borutzky, 1948
 **Parastenocaris* sp.
 Ostracoda
 Candonidae
 **Trapezicandona ljoschkinii* (Rudjakov, 1963)
 Cyprididae
Cypria reptans Bronstein, 1947
 Limnocytheridae
 **Kovalevskilla rudjakovi* (Danielopol, 1969)
 Syncorida
 Bathynellidae
 **Antrobathynella stammeri ciscaucasica* (Birstein et Ljovuschkin, 1964)
 **Bathynella natans natans* Vojdovsky, 1882
 Isopoda
 Asellota: Asellidae
 **Proasellus linearis* (Birstein, 1967)
 **Proasellus ljoschkinii* (Birstein, 1967)
 **Proasellus similis* (Birstein, 1967)
- Asellota: Microparasellidae
 **Microcharontantalus* Birstein et Ljovuschkin, 1964
 AMPHIPODA
 Crangonyctidae
 **Lyurella shepsiensis* Sidorov, 2015
 Niphargidae
 **Niphargus abchasicus* Martynov, 1932
 **Niphargus caelestis* G. Karaman, 1982
 **Niphargus cubanicus* Birstein, 1954
 **Niphargus krasnodarus* G. Karaman, 2012
 **Niphargus latimanus* Birstein, 1952
 **Niphargus cf. magnus* Birstein, 1940
 **Niphargus potamophilus* Birstein, 1954
 **Niphargus pseudolatimanus* Birstein, 1952
 **Niphargus smirnovi* Birstein, 1952
 **Niphargus submersus* (Derzhavin, 1945)
 Typhlogammaridae
 **Zenkevitchia* sp.
 DECAPODA
 Caridea: Atyidae
 **Troglocaris (Xyphocaridella) jusbashjani* Birstein, 1948
 Brachyura: Potamidae
Potamon ibericum tauricum (Czerniavsky 1884)

B — Troglobionts *: troglophiles

- OLIGOCHETA
 Lumbricidae
Allolobophora cavatica Michaelsen, 1910
Dendrobaena veneta crassa (Malevics, 1947)
Eisenia fetida (Savigny, 1826)
 Naididae
Homochaeta sp.
Peloscolex sp.
 NEMATODA
 Monhysteridae
Monchystera paludicola De Man, 1880
 Dorylaimidae
Dorylaimus stagnalis Dujardin, 1845
Dorylaimus callosus Skwarra, 1921
Eudorylaimus laticollis (De Man, 1907)
Eudorylaimus condamni (Vanhé, 1893)
Eudorylaimus iners (Bastian, 1865)
 Actinolaimidae
Trachactinolaimus radulatus Andrassy, 1963
 Mononchidae
Mononchus truncatus Bastian, 1865
Prionchulus muscorum (Dujardin, 1845)
 Tripylidiae
Tripyla papillata Bütschli, 1873
Tripyla filicaudata De Man, 1880
 Prismatolaimidae
Prismatolaimus dolichurus De Man, 1880
 Criconematidae
Criconema fimbriatum Cobb in Taylor, 1936
Criconema sp.
Criconemoides sp.
- Mollusca
 Orculidae
Lauria sp.
 Trigonochlamydidae
 **Trogloleutes sokolovi* Ljovuschkin et Matiokin, 1965
 Orculidae
 **Euxinolauria vitrea* (Schileyko, 1988)
 Clausiliidae
Scrobifera taurica (L. Pfeiffer, 1848)
Serrulina sp.
 Zonitidae
 **Conulopolita cavatica* (Riedel, 1966)
Oxychilus (Longiphallus) sp.
 ISOPODA TERRESTRIA
 Oniscidea
 Ligidae
Ligidium zaitzevi Borutzky, 1950
 **Ligidium cavaticum* Borutzky, 1950
 Buddelundiellidae
 **Pseudobuddelundiella hostensis* Borutzky, 1967
 **Pseudobuddelundiella ljoschkinii* Borutzky, 1967
 **Trichoniscus pygmaeus tuapsensis* Borutzky, 1972
 Cylisticidae
Cylisticus birsteini Borutzky, 1961
 Trichoniscidae
 **Caucasoclyphonethes cavaticus* Borutzky, 1948
 **Psachonethes czerkessicus* Borutzky, 1969
 ARANEI
 Agelenidae
Tegenaria abchasica Charitonov, 1941

- Tegenaria pontica* Charitonov, 1947
Tegenaria sp.
 Hahniidae
Iberina ljosuschkini Pichka, 1965
 Tetragnathidae
Meta bourneti Simon, 1922.
Metellina merianae (Scopoli, 1763)
 Linyphiidae
Troglolophantes birsteini Charitonov, 1943
 Nesticidae
Carpathonesticus birsteini (Charitonov, 1947)
Carpathonesticus ljosuschkini (Pichka, 1965)
Carpathonesticus zaitzevi (Charitonov, 1939)
Carpathonesticus sp.
Aituaria pontica (Spassky, 1932)
 Pholcidae
Hoploholcus longipes (Spassky, 1934)
PSEUDOSCORPIONES
 Neobisiidae
**Neobisium(Neobisium) speleophilum* Krumpal, 1986
**Neobisium* sp.
OPILIONES
 Nemastomatidae
Histicostoma caucasicum (Redikorzev 1936)
**Nemaspela abchasica* (Ljovuschkin et Starobogatov, 1963)
**Nemaspela sokolovi* (Ljovuschkin et Starobogatov, 1963)
**Nemaspela kovalii* Chemeris, 2009
 Phalangiidae
Nelima pontica Charitonov, 1941
ACARI
 Phthiracaridae
Phthiracarus globosus (C.L. Koch, 1841)
 Ixodidae
Ixodes vespertilionis C.L. Koch, 1844
CHILOPODA
 Lithobiidae
Harpolithobius perplexus Zalesskaja, 1973
Lithobius liber Lignau, 1903
Lithobius reconditus Zalesskaja, 1973
Lithobius stuxbergii Seliwanoff, 1880
DIPLOPODA
 Glomeridellidae
Typhloglomeris caucasica Golovatch, 1975
 Doderidae
Trachysphaera costata (Waga, 1857)
Trachysphaera minuta Golovatch, 1976
 Anthroleucosomatidae
**Caucaseuma elephantum* Antić et Makarov, 2016
**Caucaseuma fanagoriyskaya* Antić et Makarov, 2016
**Caucaseuma lohmanderi* Strasser, 1970
**Caucaseuma minellii* Antić et Makarov, 2016
**Heterocaucaseuma feminaepectorum* Antić et Makarov, 2016
Metamastigophorophyllum giljarovi (Lang, 1959)
- Blaniulidae
**Nopoilulus ammonites* Enghoff, 1984
Nopoilulus kochii (Gervais, 1847)
 Julidae
Archileucogeorgia sp.
Cylindroiulus placidus (Lignau, 1903)
Cylindroiulus pterophylacum Read, 1992
Cylindroiulus schestoperovi Lohmander, 1932
 Paradoxosomatidae
Strongylosoma kordylamythrum Attems, 1898
 Polydesmidae
Brachydesmus furcatus Lohmander, 1936
 Trichopolydesmidae
**Caucasodesmus inexpectatus* Golovatch, 1985
 Collembola
 Hypogastruridae
**Typhlogastrura preobrazhenskyi* Babenko, 1987
 Isotomidae
Desoria fennica (Reuter, 1895)
 Tomoceridae
**Plutomurus jelesnovodskii* Kniss et Thibaud, 1999
**Plutomurus kelasuricus* (Martynova, 1969)
**Plutomurus sorosii* Kniss et Thibaud, 1999
ORTHOPTERA
 Rhaphidophoridae
**Dolichopoda euxina* Semenov, 1901
TRICHOPTERA
 Polycentropodidae
Plectrocenia sp. sensu Lepneva, 1940
COLEOPTERA
 Carabidae
**Caucasaphaenops molchanovi* Belousov, 1999
**Caucasorites kovali amplicolis* Belousov, 1999
**Caucasorites kovali* Belousov, 1999
**Caucasorites shchurovi* Belousov et Zamotajlov, 1997
**Caucasorites victori* Belousov, 1999
Cimmerites circassicus Reitter, 1888
**Cimmerites kryzhanovskii* Belousov 1999
**Cimmerites maximovitchi* Belousov et Koval, 2011
Cimmerites zamotajlovi Belousov, 1998
**Duvalius miroshnikovi* Belousov et Zamotajlov, 1995
Duvalius gusevi Belousov, 1989
**Jeannelius birsteini* Ljovuschkin, 1965
Jeannelius zhicharevi Lutshnik, 1915
Laemostenus koenigi (Reitter, 1887)
Laemostenus tschitscherini Semenov, 1909
Meganophthalmus irinae Belousov et Zamotajlov, 1999
**Meganophthalmus kravetzi* Komarov, 1993
**Nannotrechus ciscaucasiens* (Ljovuschkin, 1972)
Nannotrechus fishtensis Belousov, 1989
Nannotrechus kovali Belousov, 1989
Porocimmerites imitator Belousov, 1998
Pterostichus lacunosus (Chaudoir 1844)
Trechus heniochicus Ljovuschkin, 1970

Cryptophagidae	CHIROPTERA
<i>Cryptophagus pilosus</i> Gyllenhal, 1827	<i>Rhinolophidae</i>
Curculionidae	<i>Rhinolophus euryale</i> Blasius, 1853
* <i>Otiorynchus vargovitchi</i> Davidian, 2007	<i>Rhinolophus ferrumequinum</i> (Schreber, 1774)
Elmidae	<i>Rhinolophus hipposideros</i> (Borkhausen, 1797)
<i>Limnius colchicus</i> Delève, 1963	<i>Rhinolophus mehelyi</i> Matschie, 1901
Leiodidae	Vespertilionidae
<i>Catops subfuscus</i> Kellner, 1846	<i>Barbastella barbastellus</i> (Schreber, 1774)
<i>Choleva</i> sp.	<i>Barbastella caspica</i> Satunin, 1908
Pselaphidae	<i>Eptesicus serotinus</i> (Schreber, 1774)
<i>Bryaxis balneator</i> Besuchet et Kurbatov, 2007	<i>Hypsugo savii</i> (Bonaparte, 1837)
<i>Bryaxis kovali</i> Besuchet et Kurbatov, 2007	<i>Myotis alcathoe</i> von Helversen et Heller, 2001
* <i>Seracamarops komarovi</i> Hlaváč, Kodada et Kovář, 1999	<i>Myotis davidii</i> Peters, 1869
Ptiliidae	<i>Myotis bechsteinii</i> (Kuhl, 1817)
<i>Ptenidium intermedium</i> Wankowicz, 1896	<i>Myotis blythii</i> (Tomes, 1857)
Scirtidae	<i>Myotis brandtii</i> (Eversmann, 1845)
<i>Odeles</i> sp.	<i>Myotis dasycneme</i> (Boie, 1825)
Staphylinidae	<i>Myotis daubentonii</i> (Kuhl, 1817)
<i>Bisnius parcus</i> (Sharp, 1874)	<i>Myotis emarginatus</i> (Geoffroy, 1806)
<i>Heinzia caucasica</i> Gusarov et Koval, 2002	<i>Myotis mystacinus</i> (Kuhl, 1817)
DIPTERA	<i>Myotis nattereri</i> (Kuhl, 1817)
Limoniidae	<i>Nyctalus noctula</i> (Schreber, 1774)
<i>Limonia nubeculosa</i> Meigen, 1804	<i>Pipistrellus pipistrellus</i> (Schreber, 1774)
Sciaridae	<i>Plecotus auritus</i> (Linnaeus, 1758)
<i>Neosciara</i> sp.	<i>Plecotus macrobullaris</i> Kuzyakin, 1965
Heleomyzidae	Miniopteridae
<i>Heteromyza atricornis</i> Meigen, 1830	<i>Miniopterus schreibersii</i> (Kuhl, 1817)
	Molossidae
	<i>Tadarida teniotis</i> (Rafinesque, 1814)

- *Allantion tachyploon* Sandon, 1924. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Mylnikov et al., 2006).
- Order **Cercomonadida** Poche, 1913
- Family Heteromitidae Kent, 1880
- *Heteromita globosa* (Stein, 1878). Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Mylnikov et al., 2006).
- *Heteromita* sp. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Mylnikov et al., 2006).
- Phylum **Myzozoa** Cavalier-Smith et Chao, 2004
- Class **Dinophyceae** Fritsch, 1927
- Order **Desmomastigales** Bourrelly, 1970
- Family Protaspidae Skuja, 1939
- *Protaspis simplex* Vors, 1992. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District,
- Greater Sochi, Krasnodar Province (Mylnikov et al., 2006).
- Class **Colponemea** Cavalier-Smith, 1993
- Order **Colponemida** Cavalier-Smith, 1993
- Family Colponemidae Cavalier-Smith et Chao, 2004
- *Colponema edaphicum* Mylnikov et Tikhonenkov, 2007. Likely stygophile, described from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Mylnikov et al., 2006; Mylnikov, Tikhonenkov, 2007).
- Kingdom **Protozoa** R. Owen, 1858
- Subkingdom **Sarcomastigota** Cavalier-Smith, 1983
- Group **Excavata** (Cavalier-Smith), 2002
- Phylum **Euglenozoa** Cavalier-Smith, 1981
- Class **Kinetoplastea** Honigberg, 1963
- Order **Eubodonida** Vickerman, in Moreira et al., 2004
- Family Bodonaceae Bütschli, 1884
- *Bodo designis* Skuja, 1948. Likely stygophile, recorded from the Vorontsovskaya

Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).

- *Bodo saliens* Larsen et Paterson, 1990. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).
- *Bodo saltans* Ehrenberg, 1838. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).
- *Cercomonas granulifera* (Hollande, 1942). Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).
- *Cercomonas laciniaegegens* (Kras-siltschick, 1886). Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).
- *Cercomonas* sp. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).
- *Dimastigella mimosa* Frolov, Myl'nikov et Malysheva, 1997. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).
- *Rhynchomonas nasuta* (Stokes) Klebs, 1892. Likely stygophile, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Myl'nikov et al., 2006).

Phylum **Amoebozoa** Lühe, 1913

Class **Tubulinea** Smirnov, Nassonova, Berney, Fahrni, Bolivar et Pawłowski, 2005

Order **Arcellinida** Kent, 1880

Family **Centropyxidae** Jung, 1942

- *Centropyxis constricta* (Ehrenberg, 1841). Stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

- *Centropyxis ecornis* (Ehrenberg, 1841). Likely stygophile, recorded from sulfuric springs in the karst canyon of Agura River, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

- *Centropyxis orbicularis* Deflandre, 1929. Stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

- *Centropyxis plagiostoma* Bonnet et Thomas, 1955. Stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967; Ljovuschkin 1972b).

- *Centropyxis platystoma* (Penard, 1890). Stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

- *Centropyxis spinosa* Cash, 1905. Stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

Family **Difflugiidae** Wallich, 1864

- *Difflugia avellana* Penard, 1890. Stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

- *Difflugia avellana gigas* Gauthier-Lievre et Thomas, 1958. Stygophile, recorded from the Pionerskaya (= Ushchel'naya) Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

- *Difflugia penardi* Hopkinson, 1909. Stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

- *Difflugia oblonga* Ehrenberg, 1838. Stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).

- *Pontigulasia incisa* Rhumbler, 1896. Stygophile, recorded from the Labirintovaya

- Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).
- Family Heleoperidae Jung, 1942
 – *Heleopera sphagni* Leidy, 1874 (= *Heleopera picta* Leidy, 1879). Likely stygophile, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Chibisova, 1967).
- Subphylum **Conosa** Cavalier-Smith, 1998
- Infraphylum **Mycetozoa** de Bary, 1859
- Class **Myxogastria** Macbride, 1899
- Order **Physarida** Macbride, 1922
 Family Physaridae Rostafinski, 1873
 – *Physarum flagellatum* (Alexeieff, 1923) (= *Hyperamoeba flagellata* Alexeieff, 1923). Likely stygophile, recorded from the Labirintovaya Cave, Khosta District, Greater Sochi, Krasnodar Province (Mylnikov et al., 2006).
- Kingdom **Animalia** Linnaeus, 1758
- Phylum **Platyhelminthes** Claus, 1887
- Class **Turbellaria** Ehrenberg, 1831
- Order **Tricladida** Lang, 1884
 Unidentified unpigmented planarians have long been recorded from the Bolshaya Vorontsovskaya (=Vorontsovskaya) Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Birstein, 1950). Recorded from a tectonic cave on the Psebe River, Tuapse District, as well as the Kirovskaya (Lazarevsky City District, Greater Sochi) and Labirintovaya caves (Khostinsky City District, Greater Sochi), all in Krasnodar Province (Ljovuschkin, 1966).
- Family Dugesiidae Ball, 1974
 – *Dugesia taurocaucasica* (Livanov, 1951). Stygophile, recorded from a cave on Mt Armovka, Tryu-Yatyrgvarta Massif, Mostovskoy District, as well as from the Fanagoriyskaya Cave near Goryachi Klyuch, both Krasnodar Province (Shumeev, 2008).
- Family Dendrocoelidae Hallez, 1892
 – Dendrocoelidae gen. sp. Likely stygobiont, closer unidentified, recorded from a spring inside the Anglo-Russkaya Cave on Mt Pshekha-Su, Maikopsky District, Adygea Republic (Shumeev, 2008).
- *Dendrocoelum* sp. 1. Stygophile, an undescribed species from the running waters of the Tryu-Yatyrgvarta Massif, including a spring inside a cave on Mt Armovka, Mostovskoy District, Krasnodar Province (Shumeev, 2008).
- *Dendrocoelum* sp. 2. Stygobiont, an undescribed species from the running waters inside the Fanagoriyskaya Cave near Goryachi Klyuch, Krasnodar Province (Shumeev, 2008).
- Phylum **Nematoda** Diesing, 1861
 Uncertain species of nematodes have been recorded from the Pionerskaya (=Ushchel'-naya) Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).
- Class **Enoplea** Inglis, 1983
- Order **Monhysterida** Filipjev, 1929
- Family Monhysteridae De Man, 1876
 – *Monchystera paludicola* De Man, 1880. Troglobile, recorded from the Labirintovaya (= Novaya) Cave, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).
- Family Actinolaimidae Thorne, 1939
 – *Trachactinolaimus radulatus* Andrássy, 1963. Troglobile, recorded from the Tonnel Kuzmenko Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).
- Family Dorylaimidae De Man, 1876
 – *Dorylaimus stagnalis* Dujardin, 1845. Troglobile, recorded from the Bolshaya Kazachebrodskaya Cave, Adlersky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).
- *Dorylaimus callosus* Skwarra, 1921. Troglobile, recorded from the karst waters on the Agura River, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).
- *Eudorylaimus laticollis* (De Man, 1907). Troglobile, recorded from the Labirintovaya (= Novaya) Cave, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).
- *Eudorylaimus condamni* (Vanha, 1893). Troglobile, recorded from the Dolgaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

— *Eudorylaimus iners* (Bastian, 1865). Troglophilic, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Order Mononchida Jairajpuri, 1969

Family Mononchidae Chitwood et Chitwood, 1937

— *Mononchus truncatus* Bastian, 1865. Troglophilic, recorded from the Zapovednaya (= Podparapetnaya) Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

— *Prionchulus muscorum* (Dujardin, 1845). Troglophilic, recorded from the Dolgaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Order Triplonchida Cobb, 1920

Family Tripylidae (De Man, 1876)

— *Tripyla papillata* Bütschli, 1873. Troglophilic, recorded from the karst waters on the Agura River, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

— *Tripyla filicaudata* De Man, 1880. Troglophilic, recorded from the Krasnoaleksandrovskaya, Labirintovaya (= Novaya) and Bolshaya Kazachebrodskaya caves, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Family Prismatolaimidae Micoletzky, 1922
— *Prismatolaimus dolichurus* De Man, 1880. Troglophilic, recorded from the Labirintovaya (= Novaya) Cave, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Class Secernentea Lorenzen, 1981

Order Tylenchida Thorne, 1949

Family Criconematidae Taylor, 1936

— *Criconema fimbriatum* Cobb in Taylor, 1936. Troglophilic, recorded from the Krasnoaleksandrovskaya and Pionerskaya (= Ushchel'naya) caves, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

— *Criconema* sp. Troglophilic, recorded from the Fanagoriyskaya Cave near Goryachi Klyuch, Krasnodar Province (Ljovuschkin, 1966).

— *Criconemoides* sp. Troglophilic, recorded from the Labirintovaya (= Novaya) Cave,

Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Phylum Annelida Lamarck, 1809

Class Hirudinea Lamarck, 1818

Order Arhynchobdellida Blanchard, 1894

Family Erpobdellidae Blanchard, 1894

— *Erpobdella octoculata* (Linnaeus, 1758), troglobene, recorded by Birstein and Ljovuschkin (1967a) from the Fanagoriyskaya Cave near Goryachi Klyuch, Krasnodar Province; also reported from several Balkan caves (Montenegro, Republic of Macedonia, Greek Macedonia).

Class Oligochaeta Grube, 1850

Order Crassiclitellata Jamieson, 1988

Family Lumbricidae Claus, 1876

— *Allolobophora cavatica* Michaelsen, 1910. Troglophilic, described from a cave at the Khodz' River, Adygea Republic or Krasnodar Province. Also recorded from epigean habitats in Transcaucasia (Lenkoran, Azerbaijan) (Michaelsen, 1910).

— *Dendrobaena veneta crassa* (Malevics, 1947). Troglophilic, described as a separate form from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Malevich, 1947).

— *Eisenia foetida* (Savigny, 1826). Troglophilic, recorded from the Podzemnaya Khos-ta (in the publication of Malevich, it was referred to as Khostinskaya Mokraya) and Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya, Mzymtinskaya) caves, both in Greater Sochi, Krasnodar Province (Malevich, 1947).

Order Enchytraeida Vejdovský, 1879

Family Enchytraeidae Vejdovský, 1879

Uncertain enchytraeid species have been recorded from the Fanagoriyskaya, Zapovednaya (= Podparapetnaya), Labirintovaya (= Novaya) and Vorontsovskaya caves, all Krasnodar Province (Ljovuschkin, 1966).

Order Tubificida Brinkhurst, 1982

Family Naididae Ehrenberg, 1828

— *Homochaeta* sp. Troglophilic, recorded from the Zapovednaya (= Podparapetnaya) Cave, Khostinsky City District, Greater

Sochi, Krasnodar Province (Ljovuschkin, 1966).

Peloscolex sp. Troglophilic, recorded from the Labirintovaya (= Novaya) Cave, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Phylum **Mollusca** Linnaeus, 1758

Class **Gastropoda** Cuvier, 1797

Order **Littorinimorpha** Golikov et Starobogatov, 1975

Family Hydrobiidae Stimpson, 1865

– *Belgrandiella caucasica* Starobogatov, 1962 (= *B. nemethi* Schütt in Schütt et Şeşen, 1993). Stygo- and crenobiont, described from a spring inside the Krasnoaleksandrovskaya (= Peshchera Ved'm) Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Starobogatov, 1962). Inhabiting cave (e.g. the Dolgaya Cave) and creek waters along the Black Sea coast between Tuapse and Psou (Starobogatov, 1962; Schütt, Şeşen, 1993; Palatov, Vinarski, 2015; Vinarski, Kantor, 2016).

– “*Geyeria*” *valvataeformis* Starobogatov, 1962. Stygobiont, known only from the type locality, a spring inside the Krasnoaleksandrovskaya (= Peshchera Ved'm) Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Starobogatov, 1962; Vinarski, Kantor, 2016).

– “*Lartetia*” sp. Recorded from the Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya) Cave, Adlersky City District, Greater Sochi, Krasnodar Province (Birstein, 1950), but actually it seems to concern one of the Transcaucasian species of *Paladilhiopsis* (Turbanov et al., 2016a).

– *Paladilhiopsis orientalis* Starobogatov, 1962. Stygobiont, known only from the type locality, a spring inside the Krasnoaleksandrovskaya (= Peshchera Ved'm) Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Starobogatov, 1962; Vinarski, Kantor, 2016).

– *Paladilhiopsis pulcherrima* Starobogatov, 1962. Stygo- and crenobiont, described from a spring inside the Krasnoaleksandrovskaya (= Peshchera Ved'm) Cave, Laz-

arevsky City District, Greater Sochi, Krasnodar Province (Starobogatov, 1962). Inhabiting also helo- and rheocrens along the Black Sea coast between Tuapse and Psou (Starobogatov, 1962; Palatov, Vinarski, 2015; Vinarski, Kantor, 2016).

– *Paladilhiopsis subovata* Starobogatov, 1962. Stygobiont, known only from the type locality, a spring inside the Krasnoaleksandrovskaya (= Peshchera Ved'm) Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Starobogatov, 1962; Vinarski, Kantor, 2016).

Order **Geophila** Ferrusac, 1821

Family Oculidae Steenberg, 1925

– *Lauria* sp. Likely troglobiont, recorded from the Shirokopokosskaya and Malaya Kazachebrodskaya caves, Greater Sochi, Krasnodar Province (Birstein, 1950; Ljovuschkin, 1966).

Family Trigonochlamydidae Hesse, 1882

– *Troglolestes sokolovi* Ljovuschkin and Matiokin, 1965. Troglobiont, known only from the type locality, the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, Matiokin, 1965).

Family Oculidae Steenberg, 1925

– *Euxinolauria vitrea* (Schileyko, 1988). Likely troglobiont, described from the Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya) Cave near Mzymta River (Schileyko 1988), also recorded from the nearby Malaya Kazachebrodskaya (= Nizhne-Mzymtinskaya, Akhshtyrskaya) Cave, Adlersky City District, Greater Sochi, Krasnodar Province (Egorov, Greke, 2005).

Family Clausiliidae Gray, 1855

– *Scrobifera taurica* (L. Pfeiffer, 1848). Troglophilic, recorded from the Shirokopokosskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province, previously referred to as *Clausilia foveicollis* Parr. (Birstein, 1950).

– *Serrulina* sp. Troglophilic, recorded from the Beloskalskaya Cave, as well as a cave on the Agura River, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Family Zonitidae Morch, 1864

- *Conulopolita cavatica* (Riedel, 1966). Troglobiont, described from the Shirokopokosskaya Cave (Khostinsky City District), also known from the nearby Bolshaya Kazachebrodskaya and Malaya Kazachebrodskaya caves (Adlersky City District), as well as the Chortova Nora Cave (Khostinsky City District), all in Greater Sochi, Krasnodar Province (Birstein, 1950; Ljovuschkin, 1966; Riedel, 1966; Koval, 2004a).
- *Oxychilus (Longiphallus)* sp. Likely troglobophile, recorded from the Shakal'ya, Chortova Nora, Bolshaya Kazachebrodskaya, Malaya Kazachebrodskaya, Beloskalskaya, Shirokopokosskaya (=Bozhyey Materi) and Vorontsovskaya caves, all in Greater Sochi, Krasnodar Province (Birstein, 1950; Ljovuschkin, 1966; Koval, 2004a).

Class Bivalvia Linnaeus, 1758

Order Veneroida Adams et Adams, 1856

Family Euglesidae Pirogov et Starobogatov, 1974

- *Euglesa* (s. str.) *personata* (Malm, 1855). Likely stygophile, widespread in Europe, the Caucasus and Asia Minor (Kantor et al., 2010; Vinarski, Kantor, 2016), recorded from wells and springs near Adler, Greater Sochi, Krasnodar Province (Starobogatov, 1962).
- *Euglesa* (s. str.) *cavatica* (Shadin, 1952). Stygobiont, described from a spring inside the Pionerskaya (= Ushchel'naya) Cave in the upper reaches of Vostochnaya (= Bolshaya) Khosta River, Khostinsky City District, Greater Sochi, Krasnodar Province. Reported also from caves in Abkhazia (Starobogatov, 1962; Chertoprud et al., 2016; Vinarski, Kantor, 2016, Turbanov et al., 2016a), but with some minor differences from the typical form.

Phylum Arthropoda Siebold, 1848

Subphylum Crustacea Brünnich, 1772

Class Copepoda Milne-Edwards, 1840

Order Cyclopoida Burmeister, 1834

Family Cyclopidae Rafinesque, 1815

- *Acanthocyclops venustus stammeri* (Kiefer, 1930). Stygobiont, interstitial-dweller.

Recorded from the imterstitial of Psezuapse River, Lazarevsky City District, Greater Sochi, and in the interstitial of Djubga River near Djubga, Tuapse District, both in the Krasnodar Province (Monchenko, 1984).

– *Diacyclops bisetosus* (Rehberg, 1880). Stygophile, recorded from the Bolshaya Kazachebrodskaya Cave, Adlersky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

– *Paracyclops fimbriatus imminentus* Kiefer, 1929. Stygophile, recorded from a karst spring on the Vostochnaya (= Bolshaya) Khosta River and from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1950a; Ljovuschkin, 1966).

– *Speocyclops cinctus* Monchenko, 1983. Interstitial of Alibek River, Karachaevo-Cherkessia (Monchenko, 1983).

– *Speocyclops demetiensis* (Scourfield, 1932). Stygobiont, interstitial-dweller. Recorded from the imterstitial of Psezuapse, Khosta, Mzymta and Psou rivers in the Krasnodar Province (Monchenko, 1986).

– *Speocyclops lussianus* Borutzky, 1950. Stygobiont, described from the Vorontsovskaya and Pionerskaya (=Ushchel'naya) caves, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1950a; Ljovuschkin, 1966).

– *Speocyclops psezuapsensis* Borutzky, 1965. Sygobiont, described from the Kirovskaya Cave, Psezuapse River, Lazarevsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1965).

Order Harpacticoida G.O. Sars, 1903

Family Ameiridae Boeck, 1865

– *Nitocrella hirta caucasica* Borutzky, 1967. Stygobiont, described from the Zapovednaya (=Podparapetnaya) Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1967a, 1972b).

– *Megastygonitocrella liovuschkini* (Borutzky, 1967). Stygobiont, described or reported from the Dolgaya and Pionerskaya (= Ushchel'naya) caves near Sochi, and

from the Krasnoaleksandrovskaya Cave near Lazarevskoe, all in the Krasnodar Province (Borutzky, 1967a, 1972b).

Family *Canthocamptidae* Brady, 1880

- *Attheyella crassa* (G.O. Sars, 1863). Stygophile, recorded from the Fanagoriyskaya Cave near Goryachi Klyuch, from the Krasnoaleksandrovskaya Cave (Lazarevsky City District) and from the Pionerskaya (= Ushchel'naya), Labirintovaya and Dolgaya caves, Khostinsky City District, Greater Sochi, all in the Krasnodar Province (Borutzky, 1948a, 1972b).
- *Bryocamptus aquaeductus* Borutzky, 1934. Stygobiont, described from a water pipeline in the town of Teberda, Karachaevo-Chekessia (Borutzky, 1934).
- *Bryocamptus innominatus* Borutzky, 1940. Stygobiont, described from the Pionerskaya (= Ushchel'naya) Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, Mikhailova-Neikova, 1970; Borutzky, 1972b).
- *Bryocamptus pygmaeus* (G.O. Sars, 1863). Stygophile, recorded from the Dolgaya and Labirintovaya caves, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1972b).
- *Bryocamptus tarnogradskyi* Borutzky, 1934. Stygophile, recorded from the Fanagoriyskaya Cave near Goryachi Klyuch, from the Krasnoaleksandrovskaya Cave near Lazarevskoe, and from the Labirintovaya, Podparapetnaya (= Zapovednaya) and Tonnel Kuzmenko caves near Khosta, Greater Sochi, all in the Krasnodar Province (Borutzky, 1948a, 1972b; Ljovuschkin, 1966).
- *Bryocamptus zschorkei caucasicus* Borutzky, 1930. Stygophile, recorded from the Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya), Pionerskaya (= Ushchel'naya), Labirintovaya and Dolgaya caves near Sochi, from the Krasnoaleksandrovskaya Cave near Lazarevskoe, and from the Fanagoriyskaya Cave near Goryachi Klyuch, all in the Krasnodar Province (Borutzky, 1948a, 1972b).

– *Bryocamptus hostensis* Borutzky, 1972. Likely stygobiont, described from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1972b).

– *Bryocamptus* sp. The first copepodid instar recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1952).

– *Canthocamptus staphylinus* (Jurine, 1820). Stygophile, recorded from the karst waters on the Agura River, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

– *Pilocamptus georgevitchi* (Chappuis, 1924). Stygobiont, recorded from the Krasnoaleksandrovskaya Cave (Lazarevsky City District), from the Dolgaya, Labirintovaya and Nikity caves, Greater Sochi, Krasnodar Province (Borutzky, Mikhailova-Neikova, 1970; Borutzky 1972b).

– *Elaphoidella bidens coronata* (G.O. Sars, 1904). Stygophile, discovered in the interstitial (Chappuis pit) of Mzymta River at Adler, Greater Sochi, Krasnodar Province (Borutzky, 1972b).

– *Elaphoidella czerkessica* Borutzky, 1972. Stygobiont, described from the Pionerskaya (= Ushchel'naya) Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1972b).

– *Moraria operculata* Borutzky, 1948. Stygobiont, described from the Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya) and Dolgaya caves, as well as from the interstitial (Chappuis pit) at a bank of the Mzymta River, all in Greater Sochi, Krasnodar Province (Borutzky, 1948a, 1972b).

– *Moraria hostensis* Borutzky, 1972. Stygobiont, described from the Zapovednaya (= Podparapetnaya) Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1972b).

– *Moraria poppei* (Mrazek, 1893). Stygobiont, recorded from the Dolgaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1972b).

– *Moraria varica* (Graeter, 1910). Stygobiont, recorded from the Fanagoriyskaya

Cave near Goryachi Klyuch and from the Labitintovaya Cave, Khostinsky City District, Greater Sochi, both in the Krasnodar Province (Borutzky, 1972b).

— *Moraria* sp. Nauplia recorded from the Dolgaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1972b).

Family Parastenocarididae Chappuis, 1940

— *Parastenocaris tenuis* Borutzky, 1948. Stygobiont, described from the Fanagoriyskaya Cave near Goryachi Klyuch, Krasnodar Province (Borutzky, 1948a, 1972b). — *Parastenocaris* sp. Stygobiont, recorded from the interstitial waters on the banks of Mzymta River (Ljovuschkin, 1966).

Class Ostracoda Latreille, 1802

Order Podocopida G.O. Sars, 1866

Family Candonidae Kaufmann, 1900

— *Trapezicandona liovuschkini* (Rudjakov, 1963). Stygobiont, described and still known only from the Krasnoaleksandrovskaia (= Peshchera Ved'm) Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Rudjakov, 1963).

— *Candona* sp. Recorded without an exact species identification from the Krasnoaleksandrovskaia (= Peshchera Ved'm) Cave (Lazarevsky City District) and the Labirintovaya Cave (Khostinsky City District), both in Greater Sochi, Krasnodar Province (Rudjakov, 1963).

Family Cyprididae Baird, 1845

— *Cypria reptans* Bronstein, 1928. Crenobiont, found in the Dolgaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Rudjakov, 1963).

Family Limnocytheridae Klie, 1938

— *Kovalevskilla (Cordocythere) rudjakovi* (Danielopol, 1969). Stygobiont, described and still known only from the Krasnoaleksandrovskaia (= Peshchera Ved'm) Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Danielopol, 1969). Earlier referred to as *Metacypris* sp. (Rudjakov, 1963).

Class Malacostraca Latreille, 1817

Superorder Syncarida Packard, 1885

Order Bathynellacea Chappuis, 1915

Family Bathynellidae Grobbon, 1904

— *Antrobathynella stammeri ciscaucasica* (Birstein et Ljovuschkin, 1964). Stygobiont, interstitial-dweller, described from a spring in the Fanagoriyskaya Cave near Goryachi Klyuch, Krasnodar Province (Birstein, Ljovuschkin, 1964, 1967b; Serban, 1993).

— *Bathynella natans natans* Vejdovsky, 1882. Stygobiont, interstitial-dweller, discovered in a waterbody inside the Pionerskaya (= Ushchel'naya) Cave, upper reaches of Vostochnaya (= Bolshaya) Khosta River, Greater Sochi, Krasnodar Province (Birstein, Ljovuschkin, 1967b).

Order Isopoda Latreille, 1817

Suborder Asellota Latreille, 1803

Family Asellidae Latreille 1803, sensu Rafinesque-Schmaltz, 1815

— *Proasellus linearis* (Birstein, 1967). Stygobiont, described from a spring at Evstafieva Shchel' near Gelendjik, Krasnodar Province (Birstein, 1967). There are also records of *P. cf. linearis* from near Tuapse, in springs and oozing waters in the valleys of Agoy and Nebug rivers, as well as in streams of Kadosh Park where the animals are washed out from subterranean waters during strong rain flashes (Sokolova, Palatov, 2015).

— *Proasellus liovuschkini* (Birstein, 1967). Stygobiont, described from a karst vaucluse in the lower reaches of Khosta River, Greater Sochi, Krasnodar Province (Birstein, 1967).

— *Proasellus similis* (Birstein, 1967). Stygobiont, described from a waterbody inside the Nikity Cave in the Psakho River basin, a tributary of Kudepsta River, Greater Sochi, Krasnodar Province (Birstein, 1967).

— *Proasellus* sp. (Fig. 5A). Stygobiont, possibly a new species, recorded from the Avgust Cave, Adlersky City District, Greater Sochi, Krasnodar Province (Turbanov et al., 2016a).

Family Microparasellidae Karaman, 1933

— *Microcharon tantalus* Birstein et Ljovuschkin, 1965. Stygobiont, described from



Fig. 5. Some stygo- or troglobiont crustaceans in nature (all caves from Greater Sochi, Krasnodar Province). A — *Proasellus* sp., a stygobiont water louse from the Avgust Cave; B — *Ligidium cavaticum* Borutzky, 1950, a troglobiont wood louse from the Giganov Cave; C — *Niphargus* sp., a stygobiont amphipod from the Gigantov Cave; D — *Troglocaris (Xyphocarinella) jusbaschjani* Birstein, 1948, a stygobiont shrimp from sulphurous springs on the Agura River. All pictures by Ilya Turbanov.

Рис. 5. Некоторые стиго- и троглобионтные ракообразные в природе (все пещеры из Большого Сочи, Краснодарский край). А — *Proasellus* sp., стигобионтный водяной ослик из пещеры Август; В — *Ligidium cavaticum* Borutzky, 1950, троглобионтная мокрица из пещеры Гигантов; С — *Niphargus* sp., стигобионтный бокоплав из пещеры Гигантов; Д — *Troglocaris (Xyphocarinella) jusbaschjani* Birstein, 1948, стигобионтная креветка из серных ручьев у реки Агура. Все фотографии Ильи Турбанова.

the interstitial of Mzymta River, Greater Sochi, Krasnodar Province (Birstein, Ljovuschkin, 1965).

Suborder **Oniscidea** Latreille, 1802

Family Ligiidae Brandt, 1883

— *Ligidium zaitzevi* Borutzky, 1950. Troglophile, described from a series of syntypes stemming from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province, as well as the Mikhailovskaya Cave and the cave near Venetian Bridge, both latter near Sukhum, Abkhazia (Borutzky, 1950b, 1972a).

— *Ligidium hypnorum* (Cuvier, 1792). Troglophile, recorded for the Shirokopokoskaya Cave, Greater Sochi, Krasnodar Province (Borutzky, 1950b, 1972a).

— *Ligidium cavaticum* Borutzky, 1950 (Fig. 5B). Troglobiont, described from a series of syntypes coming from the Pervomayskaya, Podzemnaya Khosta, Shirokopokoskaya (=Bozhey Materi), Vorontsovskaya, Beloskalskaya, Navalishinskaya, Partizanskaya, Pionerskaya (=Ushchel'naya), Zapovednaya (=Podparapetnaya), Malaya Kazachebrodskaya, Bolshaya Kazachebrod-

skaya, Kamenskaya and Giganov (new data) caves, all in Greater Sochi, Krasnodar Province (Borutzky, 1950b, 1972a; Ljovuschkin, 1966).

Family Buddelundiellidae Verhoeff, 1930

- *Pseudobuddelundiella hostensis* Borutzky, 1967. Troglobiont, described from the Labirintovaya and Pionerskaya (=Ushchel'naya) caves, Greater Sochi, Krasnodar Province (Borutzky, 1967b, 1972a).
- *Pseudobuddelundiella liovuschkini* Borutzky, 1967. Troglobiont, described from the Kirovskaya Cave, Lazarevsky City District, Psezuapse River, Krasnodar Province (Borutzky, 1967b, 1972a).

Family Trichoniscidae Sars, 1899

- *Caucasocyphonethes cavaticus* Borutzky, 1948. Troglobiont, represented by 4 subspecies from caves on the Mzymta, Khos-ta and Kudepsta rivers, Greater Sochi, Krasnodar Province: *C. c. cavaticus* Borutzky, 1948 from the Malaya Kazachebrodskaya Cave; *C. c. chostensis* Borutzky, 1948 from the Podzemnaya Khos-ta and Beloskalskaya caves; *C. c. msymticus* Borutzky, 1948 from the Bolshaya Kazachebrodskaya Cave; and *C. c. adlerensis* Borutzky, 1948 from the Shirokopokosskaya and Nikity caves (Borutzky, 1948b, 1972a).
- *Psachonethes czerkessicus* Borutzky, 1969. A troglomorphic species described from a cave on the Psakho River, a tributary of Kudepsta River, Greater Sochi, Krasnodar Province (Borutzky, 1969c, 1972a).
- *Trichoniscus pygmaeus tuapsensis* Borutzky, 1972. Troglobiont, described from a cave on the Psebe River, Tuapse District, Krasnodar Province (Borutzky, 1972a).
- *Trichoniscus* sp. A record is available of a troglomorphic woodlouse from the Shirokopokosskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Borutzky, 1972a).

Family Cylisticidae Verhoeff, 1949

- *Cylisticus birsteini* Borutzky, 1961. Stygophile, described from a cave on the Psakho River, a tributary of Kudepsta River, recorded from the Navalishinskaya (= Mu-

zeynaya) and Podzemnaya Khos-ta (=Khostinskaya Mokraya) caves, Greater Sochi, Krasnodar Province (Borutzky, 1961, 1972a; Ljovuschkin, 1966).

Order Amphipoda Latreille, 1816

Family Crangonyctidae Bousfield, 1973

- *Lyurella shepsiensis* Sidorov, 2015. Stygo- and crenobiont, described from springs in the Shepsi River basin (Sidorov 2015), also recorded in springs of the Ashe River basin near Kalezh and in the Krasnoaleksandrovskaya Cave (Lazarevsky City District), all in the Krasnodar Province (Sokolova, Palatov, 2015).

Family Niphargidae Bousfield, 1977

- *Niphargus abchasicus* Martynov, 1932. Stygophile, described from springs in the interfluve of Khos-ta and Kudepsta rivers, Greater Sochi, Krasnodar Province (Iartynov, 1932), also recorded there later (Ljovuschkin 1963), as well as from springs within and near Sochi (Derzhavin, 1945).
- *Niphargus caelestis* G.S. Karaman, 1982 (= *N. stygius longidactylus* Birstein, 1952). Stygobiont, described from the Pionerskaya (=Ushchel'naya) Cave, Greater Sochi, Krasnodar Province (Birstein, 1952). According to the Code of Zoological Nomenclature the original name was changed since “*longidactylus*” had been preoccupied by *N. kochianus longidactylus* Ruffo, 1937, from springs at Verona, Italy (Karaman, 1982).
- *Niphargus cubanicus* Birstein, 1954. Likely stygophile, described from a well-warmed fish pond at Goryachi Klyuch, Krasnodar Province (Birstein, 1954).
- *Niphargus krasnodarus* Karaman, 2012. Stygobiont, described from the Fanagoriyskaya Cave near Goryachi Klyuch, Krasnodar Province (Karaman, 2012).
- *Niphargus latimanus* Birstein, 1952 (= *N. stygius latimanus* Birstein, 1952). Stygobiont, described from a stream in the Vorontsovskaya Cave, Greater Sochi, Krasnodar Province (Birstein, 1952). Morphologically similar forms recorded also from springs near Tuapse (Sokolova, Palatov, 2015).

- *Niphargus* cf. *magnus* Birstein, 1940. Stygobiont, a possibly new species morphologically similar to *N. magnus*, found in springs near Tuapse, Krasnodar Province (Sokolova, Palatov, 2015).
- *Niphargus potamophilus* Birstein, 1954. Likely stygophile, described from experimental fish ponds in the mouth of Don River near the city of Rostov-on-Don, Rostov Region, as well as in Aktyrskie fish ponds in the mouth of Kuban River, Abinsk District, Krasnodar Province (Birstein, 1954).
- *Niphargus pseudolatimanus* Birstein, 1952 (= *N. stygius pseudolatimanus* Birstein, 1952). Stygobiont, described from a stream inside the Labirintovaya (= Novaya) Cave, Greater Sochi, Krasnodar Province (Birstein, 1952).
- *Niphargus smirnovi* Birstein, 1952. Stygophile, described from the Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya) Cave in the valley of Mzymta River, Greater Sochi, Krasnodar Province (Birstein, 1952). Subsequently recorded in springs of Khosta, Kudepsta and Psou rivers, as well as in the Vorontsovskaya, Labirintovaya, Dolgaya, Pionerskaya (= Ushchel'naya) and Podzemnaya Khosta caves in the same region. The species is thereby fairly variable, each river basin and cave system supporting its own unique morphotype. Perhaps we face a group of closely related species (Ljovuschkin, 1963).
- *Niphargus submersus* (Derzhavin, 1945) (= *Martynovia submersa* Derzhavin, 1945). Stygophile, described from Sochinka River under a bridge in the town of Greater Sochi, Krasnodar Province (Derzhavin, 1945). Subsequently recorded in springs in the Vostochnaya (= Bolshaya) Khosta River basin (Ljovuschkin, 1963).
- *Niphargus* sp. (Fig. 5C). Stygobiont, possibly a new species, recorded from the Gigantov Cave in the Alek Massif, Greater Sochi, Krasnodar Province (new data).
- Family Typhlogammaridae Bousfield, 1977
- *Zenkevitchia* sp. Stygobiont, a new, yet undescribed species recorded in the Avgust Cave, Adlersky City District, Greater Sochi, Krasnodar Province (Turbanov, Marin, 2015, 2017).
- Order Decapoda** Latreille, 1802
- Infraorder Caridea** Dana, 1852
- Family Atyidae De Haan, 1849
- *Troglocaris* (*Xyphocarinella*) *jusbabschjani* Birstein, 1948 (Fig. 5D). Described and still known only from the type locality, i.e. hydrogen sulfide springs on the Agura River, Greater Sochi, Krasnodar Province (Birstein, 1948; Marin, Sokolova, 2014).
- Infraorder Brachyura** Linnaeus, 1758
- Family Potamidae Ortmann, 1896
- *Potamon ibericum tauricum* (Czerniavsky, 1884). Possibly troglobile, recorded from the Chortova Nora Cave, Agura River, Greater Sochi, Krasnodar Province (Koval, 2004a).
- Class Arachnida** Cuvier, 1812
- Order Aranei** Clerck, 1758
- There seem to be no troglobitic spiders not only in the Russian Caucasus, but across the entire former Soviet Union (Turbanov et al., 2016b).
- Family Agelenidae C.L. Koch, 1837
- *Tegenaria abchasica* Charitonov, 1941. Troglophilic, recorded from the Beloskal'skaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Turbanov, Nadolny, 2017).
- *Tegenaria pontica* Charitonov, 1947. Troglophilic, described from the Fanagoriyskaya Cave near Goryachiy Klyuch, Krasnodar Province (Charitonov, 1947).
- *Tegenaria* sp. Troglophilic, a record is available of a closer unidentified species from the Chortova Nora Cave, Khostinsky City District, Greater Sochi (Koval, 2004a).
- Family Hahniidae Bertkau, 1878
- *Iberina ljovuschkini* Pichka, 1965. Troglophilic, described from the Shakal'ya Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Pichka, 1965).
- Family Linyphiidae Blackwall, 1859
- *Troglohyphantes birsteini* Charitonov, 1947. Troglophilic, described from the Bolshaya Kazachebrodskaya and Malaya Kazachebrodskaya caves, Greater Sochi,

Krasnodar Province (Charitonov, 1947). Further records concern the Chortova Nora, Labirintovaya, Vorontsovskaya and Ametist caves, as well as a cave on Kamenka River, all in the same region (Pichka, 1965; Koval, 2004a; Turbanov, Nadolny, 2017).

Family Nesticidae Simon, 1894

— *Aituaria pontica* (Spassky, 1932) (= *Nesticus ponticus* Spassky, 1932). Troglophilic, described from a wine cellar at Khosta, Greater Sochi, Krasnodar Province (Spassky 1932). Later recorded from the Bolshaya Kazachebrodskaya, Chortova Nora and Ametist caves in the same region, as well as in a cave in the middle flow of Psakho River and a karst pit on Agura River, both also in the Krasnodar Province (Charitonov, 1947; Pichka, 1965; Koval, 2004a; Turbanov, Nadolny, 2017).

— *Carpathonesticus birsteini* (Charitonov, 1947). Troglophilic, described from the Podzemnaya Khosta (in the publication of Charitonov it is indicated as Khostinskaya Mokraya) Cave, Greater Sochi, Krasnodar Province (Charitonov, 1947). Subsequently found in the Akhunskaya, Beloskal'skaya, Vorontsovskaya, Labirintovaya (= Novaya), Kamenskaya and Dolgaya caves, as well as in a cave on the Agura River in the same region (Pichka, 1965; Ljovuschkin, 1966; Koval, 2004a, b; Turbanov, Nadolny, 2017).

— *Carpathonesticus ljosuschkini* (Pichka, 1965). Troglophilic, described from the Shakal'ya Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Pichka, 1965).

— *Carpathonesticus zaitzevi* (Charitonov, 1939). Troglophilic, recorded from the Barbana Cave in the Alek Massif, Greater Sochi, Krasnodar Province (Turbanov, Nadolny, 2017).

— *Carpathonesticus* sp. Troglophilic, recorded from the Beloskal'skaya Cave, Greater Sochi, Krasnodar Province (Turbanov, Nadolny, 2017).

Family Pholcidae C.L. Koch, 1851

— *Hoploholcus longipes* (Spassky, 1934). Troglophilic, described from a wine cellar at Khosta, Greater Sochi, Krasnodar Province (Spassky, 1934). Subsequently recorded in the Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya), Shirokopokosskaya, Beloskal'skaya and BS-2 caves, all in the same region (Charitonov 1941; Turbanov, Nadolny, 2017).

Family Tetragnathidae Menge, 1866

— *Meta bourneti* Simon, 1922. Troglophilic, recorded from the Chortova Nora Cave, Khostinsky City District, Greater Sochi (Koval, 2004a), widespread in Europe.

— *Metellina merianae* (Scopoli, 1763). Troglophilic, recorded from the Fanagoriyskaya and Shirokopokosskaya caves in the Krasnodar Province (Charitonov, 1947), widespread in Europe.

Order **Pseudoscorpiones** De Geer, 1778

Family Neobisiidae Chamberlin, 1930

— *Neobisium (Neobisium) speleophilum* Krumpal, 1986. Troglobiont, first recorded without an exact species identification from the Dolgaya and Pionerskaya caves in the Vorontsovka Massif near Adler, Greater Sochi, Krasnodar Province (Birstein, Ljovuschkin, 1960), later described (Krumpal, 1986).

— *Neobisium* sp. (Fig. 6A). Several records are available from caves in the Krasnodar Province: Shkol'naya and Gigantov (new data) in the Alek Massif, Pechal'naya in the Dzykhra Massif, and Dolgaya, Pionerskaya (= Ushchel'naya), Labirintovaya (Khostinsky City District), Greater Sochi (Ljovuschkin, 1986).

пещеры Гигантов; В — *Nemaspela sokolovi* (Ljovuschkin et Starobogatov, 1963), троглобионтный сенокосец из пещеры Гигантов; С — *Heterocaucaseuma feminaepectorum* Antić et Makarov, 2016, троглобионтная двупарногая многоноожка из пещеры Гигантов; Д — *Dolichopoda euxina* Semenov, 1901, троглофильный кузнецик из пещеры Ахунская; Е — *Caucasaphaenops molchanovi* Belousov, 1999, троглобионтный жук-жукалица из пещеры Гигантов; F — *Seracamaurops komarovi* Hlaváč, Kodada et Koval, 1999, троглобионтный жук-ощупник из пещеры Гигантов. Все фотографии Ильи Турбанова.

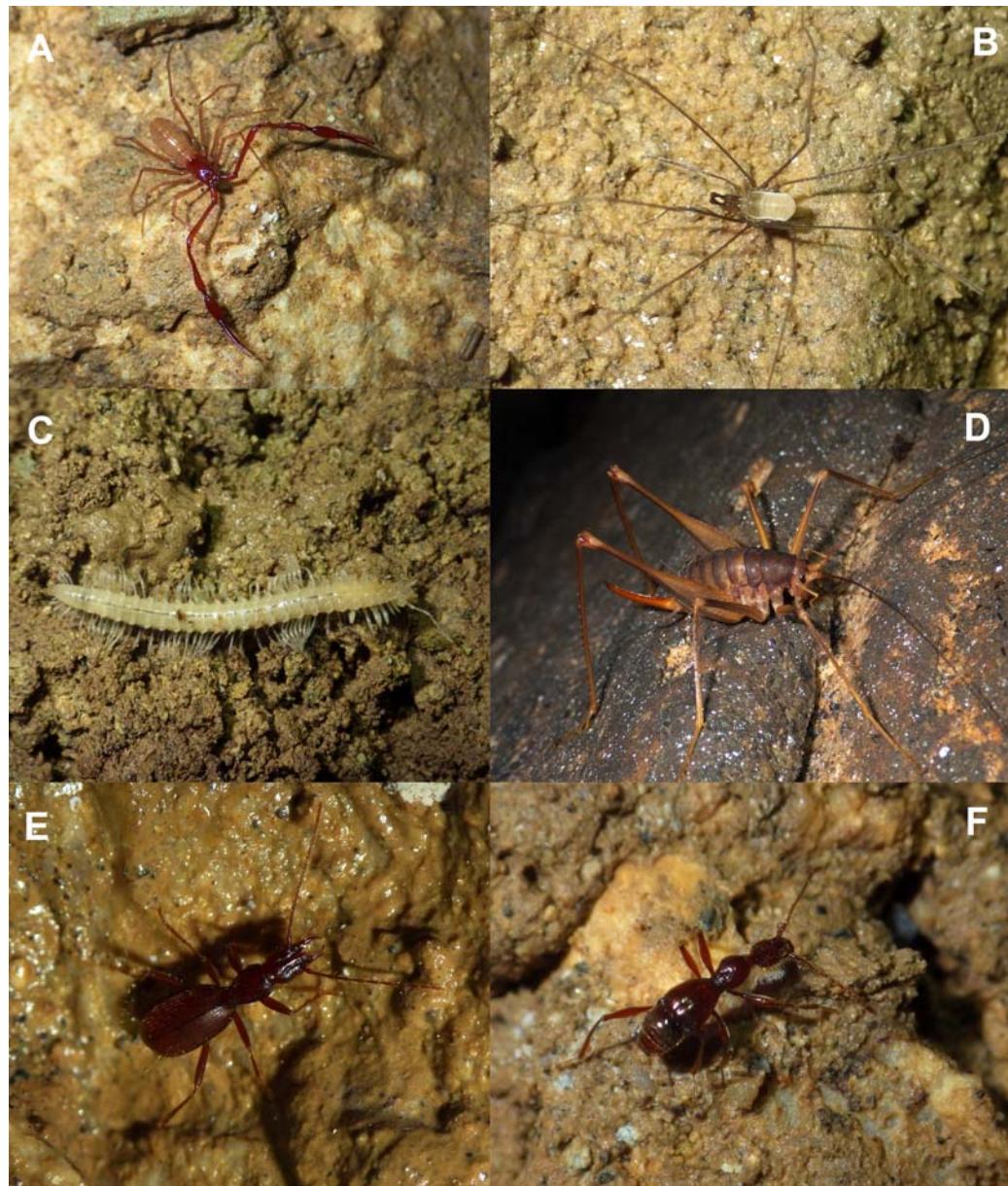


Fig. 6. Some troglobiont or troglophilic arthropods in nature (all caves from Greater Sochi, Krasnodar Province). A — *Neobisium* sp., a troglobiont false scorpion from the Gigantov Cave; B — *Nemaspela sokolovi* (Ljovuschkin et Starobogatov, 1963), a troglobiont harvestman from the Gigantov Cave; C — *Heterocaucaseuma feminaepectorum* Antić et Makarov, 2016, a troglobiont millipede from the Gigantov Cave; D — *Dolichopoda euxina* Semenov, 1901, a troglophilic grasshopper from the Akhunskaya Cave; E — *Caucasaphaenops molchanovi* Belousov, 1999, a troglobiont carabid beetle from the Gigantov Cave; F — *Seracamaurops komarovi* Hlaváč, Kodada et Koval, 1999, a troglobiont pselaphid beetle from the Gigantov Cave. All pictures by Ilya Turbanov.

Рис. 6. Некоторые троглобионтные и троглофильные членистоногие в природе (все пещеры из Большого Сочи, Краснодарский край). А — *Neobisium* sp., троглобионтный ложноскорпион из

chkin, 1966; Dashdamirov, Schawaller, 1992; Turbanov et al., 2016b).

Order Opiliones Sundevall, 1833

Family Nemastomatidae Simon, 1872

– *Histicostoma caucasicum* (Redikorzev, 1936). Likely troglobile, Caucasian endemic, recorded from the Fanagoriyskaya Cave near Goryachiy Klyuch, Krasnodar Province (Martens, 2006).

– *Nemaspela abchasica* (Ljovuschkin et Starobogatov, 1963). Troglobiont, recorded from the Beloskal'skaya, Kolokol'naya and Akhunskaya caves, Greater Sochi, Krasnodar Province (Martens, 2006; Chemeris, 2009).

– *Nemaspela kovali* Chemeris, 2009. Troglobiont, described from the Fontanka, Omega-12, Omega-15 and Otte-Shik caves in Kabardino-Balkaria (Chemeris, 2009).

– *Nemaspela sokolovi* (Ljovuschkin et Starobogatov, 1963) (Fig. 6B). Troglobiont, known from a few caves in the Greater Sochi region (Dolgaya, Labirintovaya, Vorontsovskaya and Gigantov (new data)), anophthalmic with elongated appendages (Ljovuschkin, Starobogatov, 1963; Martens, 2006; Chemeris, 2009).

– *Nemaspela* sp. Troglobiont, without an exact species identification recorded from the Akhunskaya Cave, Greater Sochi, Krasnodar Province (Koval, 2004b).

Family Phalangiidae Latreille, 1802

– *Nelima pontica* Charitonov, 1941. Likely troglobile, recorded from the Shirokopokosskaya, Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya) and Malaya Kazachebrodskaya (= Nizhnyaya Kazachebrodskaya, Nizhne-Mzymtinskaya) caves, Greater Sochi, Krasnodar Province (Charitonov, 1947; Ljovuschkin, Starobogatov, 1963; Ljovuschkin, 1966).

Subclass Acari Leach, 1817

Superorder Acariformes Zakhvatkin, 1952

Order Sarcoptiformes Reuter, 1909

Suborder Oribatida Van der Hammen, 1968

Family Phthiracaridae Perty, 1841

– *Phthiracarus globosus* (C.L. Koch, 1841). Troglobile, recorded from the Voronts-

ovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Superorder Parasitiformes Reuter, 1909

Order Mesostigmata Canestrini, 1891

Suborder Ixodoidea Leach, 1815

Family Ixodidae C.L. Koch, 1844

– *Ixodes vespertilionis* C.L. Koch, 1844. A parasite of bats, recorded from the Pionerskaya (= Ushchel'naya) and Dolgaya caves, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Subphylum Tracheata Haeckel, 1866

Class Chilopoda Latreille, 1817

Order Lithobiomorpha Pocock, 1895

Family Lithobiidae Newport, 1844

– *Harpolithobius perplexus* Zalesskaja, 1973. Troglophilic, recorded from the Chortova Nora Cave, Greater Sochi, Krasnodar Province (Koval, 2004a).

– *Lithobius liber* Lignau, 1903. Troglophilic, recorded from the Chortova Nora Cave, Greater Sochi, Krasnodar Province, but perhaps belongs to a different species (Volkova, 2015).

– *Lithobius reconditus* Zalesskaja, 1973. Troglophilic, recorded from the Pionerskaya (= Ushchel'naya) Cave, Greater Sochi, Krasnodar Province (Zalesskaja, 1973a, b, 1978).

– *Lithobius stuxbergii* Sselianoff, 1881. Troglophilic, recorded from the Vorontsovskaya, Shirokopokosskaya and Chortova Nora caves, all in Greater Sochi, Krasnodar Province (Zalesskaja, 1963, 1973a, b, 1978; Koval, 2004a).

Class Diplopoda de Blainville in Gervais, 1844

Order Glomerida Leach, 1814

Family Glomeridellidae Cook, 1896

– *Typhloglomeris caucasica* Golovatch, 1975. Troglophilic, recorded from several caves near Sochi, Krasnodar Province (Partizanskaya, Dolgaya, Vorontsovskaya etc.) (Golovatch, 1975), but then found epigaeically at Khosta (Golovatch, Chumachenko, 2013).

Family Glomeridae Leach, 1815

– *Trachysphaera costata* (Waga, 1857). Troglophilic, widespread across Central,

Eastern and Southern Europe, as well as Anatolia to northwestern Iran, recorded from a cave in Crimea, from the Fanagoriyskaya Cave near Goryachi Klyuch, and from a karst funnel at Shedok, both Krasnodar Province (Golovatch, 1990).

— *Trachysphaera minuta* Golovatch, 1976. Troglophilic, known from two caves near Sochi — Partizanskaya, Malaya Kazachebrodskaya (= Nizhne-Kazachebrodskaya), as well as epigaeically across much of the Caucasus (Russia, Georgia and Azerbaijan) (Golovatch, 1990).

— *Hyleoglomeris* sp. Troglophilic or troglobiont, from a tectonic cave in the upper basin of Psebe River, Tuapse District, Krasnodar Province (Golovatch, 1984–1985).

Order Chordeumatida Pocock, 1894

Family Anthroleucosomatidae Verhoeff, 1899

— *Caucaseuma elephantum* Antić et Makarov, 2016. Troglobiont, known only from the Yuzhnyi Slon Cave, Mt Dzentu, ca 1800 m a.s.l., Karachaevo-Cherkesskaya Republic, northern Caucasus; body yellowish white, 11–12 ocelli in 3–4 rows (Antić, Makarov, 2016).

— *Caucaseuma fanagoriyskaya* Antić et Makarov, 2016. Troglobiont, known only from the Fanagoriyskaya Cave near Goryachi Klyuch, Krasnodar Province; body greyish yellow with a brown head, 21–24 ocelli in 6 rows (Antić, Makarov, 2016).

— *Caucaseuma lohmanderi* Strasser, 1970. Likely troglobiont, frequent in caves in the western Caucasus (near Sochi, Krasnodar Province): Baribana, Labirintovaya, Navalishinskaya (= Muzeynaya), Vorontsovskaya, and since the description, Ametist Cave (Western Akhtsu Mts), Akhunskaya, Partizanskaya, Dolgaya, Shirokopokoskaya (= Bozhyey Materi), Tisovaya (perhaps this is the Zapovednaya Cave) caves (Strasser, 1970; Antić, Makarov, 2016).

— *Caucaseuma minellii* Antić et Makarov, 2016. Likely troglobiont, known only from the Sukhaya and Bolshaya Azishskaya caves, both near Sochi, Krasnodar Prov-

ince; body yellowish white, 22–24 ocelli in 6 rows (Antić, Makarov, 2016).

— *Heterocaucaseuma feminaepectorum* Antić et Makarov, 2016 (Fig. 6C). Likely troglobiont, from the Krasnoyarskaya and Pechalnaya caves, both in the Dzykhra karst massif, and the Osennyaya, Medvezhya and Gigantov caves in the Alek Massif, Greater Sochi, Krasnodar Province; body yellowish white, 10–18 ocelli in 3–4 rows (Antić, Makarov, 2016; Antić et al., 2018).

— *Metamastigophorophyllum giljarovi* (Lang, 1959). Troglophilic, widespread along the Black Sea coast from Tuapse to Abkhazia, recorded also from the Shirokopokoskaya (= Bozhyey Materi, =Our Lady) Cave, Greater Sochi, Krasnodar Province (Antić, Makarov, 2016).

Order Julida Brandt, 1833

Family Blanulidae C.L. Koch, 1847

— *Nopoiulus* (s. str.) *ammonites* Enghoff, 1984. Likely troglobiont, described from the Ammonitovaya Cave near Shedok, Psebai District, Krasnodar Province (Enghoff 1984), later recorded from the nearby Dedova Cave (Golovatch, Enghoff, 1990).

— *Nopoiulus* (s. str.) *kochii* (Gervais, 1847). Troglophilic, abundant populations observed in the Bolshaya Kazachebrodskaya and Shirokopokoskaya caves near Sochi, Krasnodar Province (Golovatch, 1981, 1984/85; Golovatch, Enghoff, 1990).

Family Julidae Leach, 1814

— *Archileucogeorgia* sp. Troglophilic?, recorded from the Fanagoriyskaya Cave near Goryachi Klyuch, Krasnodar Province (Ljovuschkin, 1966).

— *Cylindroiulus placidus* (Lignau, 1903). Troglophilic, widespread across the western Caucasus, including a record from the Meshok Cave, Maikopsky District, Adygea Republic (Lohmander, 1936).

— *Cylindroiulus pterophylacum* Read, 1992. Troglophilic, widespread across the western Caucasus, including a record from the Beloskal'skaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Read, 1992).

- *Cylindroiulus schestoperovi* Lohmander, 1932. Troglophilic, widespread across the western Caucasus, including records from the Beloskal'skaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province, and a cave in western Georgia (Read, 1992).
- Order Polydesmida** Peach, 1815
- Family Polydesmidae Peach, 1815
- *Brachydesmus furcatus* Lohmander, 1936. Troglophilic, widespread across the north-western Caucasus, including records from the Fanagoriyskaya Cave near Goryachi Klyuch, the Baribana and Akhunskaya caves (Golovatch *et al.*, 2016), as well as the Medvezhya Cave (new data) near Sochi.
- Family Paradoxosomatidae Daday, 1889
- *Strongylosoma kordylamythrum* Attems, 1898. Troglophilic, widespread across the Caucasus, also recorded from the Psebe Cave near Tuapse, as well as the Shirokopokosskaya (= Bozhyey Materi) and Labirintovaya caves, Khostinsky City District, Greater Sochi, Krasnodar Province, and a cave in Abkhazia (Evsyukov *et al.*, 2016).
- Family Trichopolydesmidae Verhoeff, 1910
- *Caucasodesmus inexpectatus* Golovatch, 1985. Troglobiont, unpigmented, antennae and legs elongated, from the Nyvdjinlagat (= Tagardonskaya) Cave in North Ossetia (Golovatch, 1984–1985).
- Superclass Hexapoda Blainville, 1816
- Class Collembola** Lubbock, 1870
- Order Poduromorpha** Börner, 1913, sensu D'Haese, 2002
- Superfamily Hypogastruroidea Salmon, 1964, sensu Deharveng, 2004
- Family Hypogastruridae Börner, 1906
- *Typhlogastrura preobrazhenskyi* Babenko, 1987. Troglobiont, described from the Shuby-Nykasskaya Cave in North Ossetia (Babenko, 1987).
- Order Entomobryomorpha** Börner, 1916, sensu Soto-Adames *et al.*, 2008
- Superfamily Tomoceroidea Szeptycki, 1979
- Family Tomoceridae Schäffer, 1896
- *Plutomurus jeleznovodskii* Kniss et Thibaud, 1999. Troglobiont with traits of troglomorphism, described from a cave near Zheleznovodsk, Stavropol' Province (Kniss, Thibaud, 1999; Kniss, 2006).
- *Plutomurus kelasuricus* Martynova, 1969. Troglophilic devoid of distinct troglomorphic features, recorded from the Baribana Cave, Alek Massif, Greater Sochi, Krasnodar Province (Kniss, Thibaud, 1999; Kniss, 2006).
- *Plutomurus sorosii* Kniss et Thibaud, 1999. Troglobiont with traits of troglomorphism, described from a cave in the Teberda Nature Reserve, Karachaevo-Cherkessia (Kniss, Thibaud, 1999; Kniss, 2006).
- Class Insecta** Linnaeus, 1758
- Order Plecoptera** Burmeister, 1839
- Family Leuctridae Klapálek, 1905
- *Leuctra furcatella* Martynov, 1928. Trogloxene. Larvae and adults recorded from the grotto part of the Krasnoaleksandrovskaya Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Palatov, Sokolova, 2015).
- Family Nemouridae Newman, 1853
- *Nemoura elegantula* Martynov, 1928. Trogloxene. Larvae and adults recorded from the grotto part of the Krasnoaleksandrovskaya Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Palatov, Sokolova, 2015).
- Order Orthoptera** Latreille, 1793
- Family Rhaphidophoridae Walker, 1869
- *Dolichopoda euxina* Semenov, 1901 (Fig. 6D). Troglophilic. Described from caves in the Caucasus (Semenov, 1901), being very common there. Known from caves in the Adygea Republic (Shapovalov *et al.*, 2015), the Krasnodar Province, Abkhazia, western Georgia (Satunin, 1912; Birstein, Lopashov, 1940; Zaitsev, 1948; Birstein, 1950; Barjadze *et al.*, 2015) and South Ossetia (Bey-Bienko, 1965, 1969), altogether over 40 records.
- Order Trichoptera** Kirby, 1813
- Suborder Annulipalpia** Martynov, 1924
- Family Polycentropodidae Ulmer, 1903
- *Plectrocnemia* sp. sensu Lepneva, 1940. Possible troglophilic. In the Krasnodar Prov-

ince, recorded from the Dolgaya Cave, Greater Sochi. Larvae live under stones and in weak currents (Lepneva, 1940; Palatov, Sokolova, 2015).

Order **Coleoptera** Linnaeus, 1758

Family Carabidae Latreille, 1802

- *Caucasaphaenops molchanovi* Belousov, 1999 (Fig. 6E) Troglobiont from the Sokolova and Gigantov (new data) caves, Greater Sochi, Krasnodar Province (Belousov, 1999).
- *Caucasorites kovali* Belousov, 1999. Troglobiont from the Akhunskaya Cave, Greater Sochi, Krasnodar Province (Belousov, 1999).
- *Caucasorites kovali amplicolis* Belousov, 1999. Troglobiont from the Psakho Cave, Greater Sochi, Krasnodar Province (Belousov, 1999).
- *Caucasorites shchurovi* Belousov et Zamotajlov, 1997. Troglobiont from the Entomologicheskaya Cave, Lazarevsky City District, Greater Sochi, Krasnodar Province (Belousov, Zamotajlov, 1997).
- *Caucasorites victori* Belousov, 1999. Troglobiont from the Akhunskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Belousov, 1999).
- *Cimmerites circassicus* Reitter, 1888. A troglomorphic species not yet encountered in caves. Described from mountain regions of the Krasnodar Province, between Tuapse and Sochi. Characterized by reduced eyes and an unpigmented tegument (Reitter, 1888–1889; Winkler, 1926), likely adapted to the MSS.
- *Cimmerites kryzhanovskii* Belousov, 1999. Possible troglobiont, described from the Malaya Kazachebroskaya Cave, Adlerovsky City District, Greater Sochi, Krasnodar Province (Belousov, 1999).
- *Cimmerites maximovitchi* Belousov and Koval, 2011. Possible troglobiont, described from the Akhunskaya and Labirintovaya caves, Khostinsky City District, Greater Sochi, Krasnodar Province; occurring together with *Caucasorites victori* on the

western slope of Mt Akhun, Sochi region (Belousov, Koval, 2011).

- *Cimmerites zamotajlovi* Belousov, 1998. Troglophilic, described from forest litter on Mt Verblyudka near the village of Kalinovoe Ozero, Greater Sochi, Krasnodar Province. Recorded also from other epigean habitats near Khosta, as well as from the Vorontsovskaya Cave, all within Greater Sochi, Krasnodar Province (Belousov, 1998).
- *Duvalius gusevi* Belousov, 1989. A troglomorphic species not yet recorded from caves. Described from the bank of a mountain spring near the sources of Kezadon River, Irafskiy District, North Ossetia, where it occurs under large boulders (Belousov, 1989). Characterized by a light coloration and strongly reduced eyes, likely adapted to the MSS.
- *Duvalius miroshnikovi* Belousov et Zamotajlov, 1995. Troglobiont from the Baribana Cave, Greater Sochi, Krasnodar Province (Belousov, Zamotajlov, 1995).
- *Jeannelius birsteini* Ljovuschkin, 1965. Troglobiont from caves in Greater Sochi, Krasnodar Province (Vorontsovskaya, Akhunskaya, Beloskal'skaya) (Ljovuschkin, 1965).
- *Jeannelius zhicharevi* Lutshnik, 1915. A troglomorphic species not yet recorded from caves. Described from the Mt Achishkho karst massif near Sochi (Luchnik, 1915; Kryzhanovskij et al., 1995); a species related to *J. gloriosus* and *J. magnificus*, both from Abkhazia.
- *Meganophthalmus irinae* Belousov et Zamotajlov, 1999. Troglophilic, described from the Chernogorye karst massif near Maikop, Adygea Republic, occurring both in epigean habitats under stones and in caves (Belousov, Zamotajlov, 1999).
- *Meganophthalmus kravetzi* Komarov, 1993. Troglobiont, described from the Fontanka Cave in the upper reaches of Belya Rechka River, 15 km SW of Nalchik, Cherkesskiy District, Kabardino-Balkaria. Found 25 m off the cave entrance, eyes absent (Komarov, 1993; Belousov, Koval, 2009).

- *Nannotrechus ciscaucasiens* (Ljovuschkin, 1972) (= *Birsteinotrechus ciscaucasiens* Ljovuschkin, 1972). Likely troglobiont, found in the Ammonitovaya Cave near Psebai, Kuban River basin, Mostovskoy District, Krasnodar Province (Ljovuschkin, 1972a). This genus belongs to the *Neotrechus* lineage and is closely related to *Troglocimmerites*.
- *Nannotrechus fishtensis* Belousov, 1989. A troglomorphic species not yet recorded from caves. Described from near Mt Fisht, at the sources of Armyanka River, Mostovskoy District, Krasnodar Province. Characterized by reduced eyes and an unpigmented tegument (Belousov, 1989), likely adapted to the MSS.
- *Nannotrechus kovali* Belousov, 1989. A troglomorphic species not yet encountered in caves. Described from the montane areas near Solokh-Aul, Greater Sochi, Krasnodar Province (Belousov, 1989). Characterized by reduced eyes, likely adapted to the MSS.
- *Porocimmerites imitator* Belousov, 1998. A troglomorphic species not yet encountered in caves. Characterized by reduced eyes and a reddish coloration, occurring in the low flow region of Mzymta River near Sochi (Belousov, 1998), likely adapted to the MSS.
- *Trechus heniochicus* Ljovuschkin, 1970. Troglophilic, described from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province. Found on rotting wood (Ljovuschkin, 1970).
- *Laemostenus koenigi* (Reitter, 1887). Troglophilic, recorded from the Fanagoriyskaya and Stalaktitovaya caves, both near Goryachi Klyuch, Krasnodar Province (Vereshchagina, 1985; Vereshchagina, Makarov, 1986).
- *Laemostenus tschitscherini* Semenov, 1909. Troglophilic, described from the Dakhovskaya Cave, Maikopsky District, Adygea Republic (Semenov-Tian-Shanskiy, 1909), also known from many caves near Maikop (Belya, Sukhaya, Budkova etc.) (Vereshchagina, 1985; Vereshchagina, Makarov, 1986).
- *Pterostichus lacunosus* (Chaudoir, 1844). Likely troglophilic, recorded from the Vorontsovskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1962).
- Family Cryptophagidae Kirby, 1937
- *Cryptophagus pilosus* Gyllenhal, 1827. Troglophilic, recorded from the Chortova Nora Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Koval, 2004a).
- Family Curculionidae Latreille, 1802
- *Otiorhynchus vargovitchi* Davidian, 2007. Troglobiont, described from the Beloskal'skaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Davidian, 2007).
- Family Elmidae Curtis, 1830
- *Limnius colchicus* Delève, 1963. Likely troglophilic, both larvae and adults encountered in the waters of the Dolgaya Cave near Khosta, Greater Sochi, Krasnodar Province. Penetrating inside the cave up to 1 km, but retaining the typical coloration (Palatov, Sokolova, 2015).
- Family Leiodidae Fleming, 1821
- *Catops subfuscus* Kellner, 1846. Troglophilic, recorded in a cave at Svetlaya Balka, Mostovskoy District, Adygea Republic, at Eki-Suara, Malokarachaevskiy District, Karachaevo-Cherkessia, and in a cave at Ispravnaya, Zelenchuk District, Karachaevo-Cherkessia (Perkovsky, 1991).
- *Choleva* sp. Subtroglophilic, recorded from the Labirintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1962).
- Family Pselaphidae Latreille, 1802
- *Bryaxis balneator* Besuchet et Kurbatov, 2007. Troglophilic, recorded from the Akhunskaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Besuchet, Kurbatov, 2007), but also inhabiting epigean biotopes.
- *Bryaxis kovali* Besuchet et Kurbatov, 2007. Troglophilic, recorded from the La-

birintovaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province; showing no visible adaptations to subterranean life (Besuchet, Kurbatov, 2007).

— *Seracamaurops komarovi* Hlaváč, Kodada et Koval, 1999 (Fig. 6F). Troglobiont, described from the Baribana and Gigantov (new data) caves in the Alek Massif, Greater Sochi, Krasnodar Province (Hlaváč et al., 1999).

Family Ptiliidae Heer, 1843

— *Ptenidium intermedium* Wankowicz, 1896. Troglophilic associated in its development with bat guano. Recorded from the Chortova Nora Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Koval, 2004a).

Family Scirtidae Fleming, 1821

— *Odeles* sp. Troglophilic, larvae found under stones in a stream in places with a weakened current in the Dolgaya Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Palatov, Sokolova, 2015).

Family Staphylinidae Lameere, 1900

— *Bisnius parcus* (Sharp, 1874). Troglophilic, recorded from the Chortova Nora Cave, Khostinsky City District, Greater Sochi, Krasnodar Province (Koval, 2004a).

— *Heinzia caucasica* Gusev et Koval, 2002. Troglophilic, described the Baribana Cave in the Alek Massif, Greater Sochi, Krasnodar Province, recorded also from the Sokolova (= Atsinskaya), Dolgaya and Vorontsovskaya caves in the same area; showing no visible adaptations to subterranean life, encountered in the Caucasus in epigean habitats as well (Gusev, Koval, 2002).

Order Diptera Linnaeus, 1758

Suborder Nematocera Schiner, 1862

Family Limoniidae Speiser, 1909

— *Limonia nubeculosa* Meigen, 1804. Troglophilic, repeatedly recorded from Transcaucasian caves: Bolshaya Kazachebrodskaya, Malaya Kazachebrodskaya, Akhunskaya, Shirokopokosskaya, Vorontsovskaya etc., all within Greater Sochi, Krasnodar

Province, etc. (Birstein, Lopashov, 1940; Zaitsev, 1948; Birstein, 1950; Koval, 2004b).

Family Sciaridae Billberg, 1820

— *Neosciara* sp. Troglophilic, recorded from the Bolshaya Kazachebrodskaya Cave, Adlersky City District, Greater Sochi, Krasnodar Province (Ljovuschkin, 1966).

Suborder Brachycera Zetterstedt, 1842

Family Heleomyzidae Beazzi, 1911

— *Heteromyza atricornis* Meigen, 1830. Troglophilic, recorded from the Bolshaya Kazachebrodskaya (= Verkhne-Mzymtinskaya), Akhunskaya and Chortova Nora caves, all within Greater Sochi, Krasnodar Province (Birstein, 1950; Koval, 2004a, b). Larvae dwelling in bat guano (Zaitsev, 1948).

Phylum Chordata Haeckel, 1874

Subphylum Vertebrata J.-B. Lamarck, 1801

Class Mammalia Linnaeus, 1758

Order Chiroptera Blumenbach, 1779

Caves play a vital role in the life-cycle of eight (out of 31 reported from the Russian Caucasus) bat species, which use them as hibernation, breeding and swarming sites. Another 16 species occur in caves and artificial undergrounds in some periods of the life cycle, but are not strictly dependent on them.

Family Rhinolophidae Gray, 1825

— *Rhinolophus euryale* Blasius, 1853. Seven distributional records of *R. euryale* were reported from the vicinity of Sochi, Krasnodar Province, Russia, including one nursery roost in a small cave near the Nizhnyaya Shilovka village (Gazaryan, 2016).

— *Rhinolophus ferrumequinum* (Schreber, 1774) (Fig. 7B). This typical cave-dwelling species is abundant in the western Caucasus, whereas it is rather rare in the central part of the Caucasus due to the deficit of suitable underground chambers. Nursery roosts and hibernating groups have been found in the Caucasus only in underground chambers of different origin, mainly in karst caves. At least 65 among nearly 100 summer and winter records were made in the latter roost type.



Fig. 7. Some bats from the Russian Great Caucasus in nature. A — a Ringed European barbastelle, *Barbastella barbastellus* (Schreber, 1774), hibernating on the wall of a mine near Derbentskaya, Seversky District, Krasnodar Province; B — a winter aggregation of Greater Horseshoe bats, *Rhinolophus ferrumequinum* (Schreber, 1774), in a gypsum cave near Psebai, Mostovskoy District, Krasnodar Province; C — a colony of Bent-winged bats, *Miniopterus schreibersii* (Kuhl, 1817), in a limestone cave near Guamka, Apsheronsky District, Krasnodar Province; D — a maternity roost of Lesser mouse-eared bats, *Myotis blythii* (Tomes, 1857), in a cave near Karabudakhkent, Dagestan. All pictures by Suren Gazaryan.

Рис. 7. Некоторые летучие мыши с Большого Кавказа России в природе. А — широкоушка европейская (*Barbastella barbastellus* (Schreber, 1774)), зимующая на стене шахты близ станицы Дербентская (Северский район Краснодарского края); В — зимнее скопление большого подковоноса (*Rhinolophus ferrumequinum* (Schreber, 1774)) в гипсовой пещере близ поселка Псебай (Мостовской район Краснодарского края); С — колония обыкновенного длиннокрыла (*Miniopterus schreibersii* (Kuhl, 1817)) в известковой пещере близ поселка Гумака (Апшеронский район Краснодарского края); D — материнский насест остроухой ночницы (*Myotis blythii* (Tomes, 1857)) в пещере близ села Карабудахкент (Дагестан). Все фотографии Сурена Газаряна.

— *Rhinolophus hipposideros* (Borkhausen, 1797). The Lesser horseshoe bat is widely distributed across the region from the Utrish Peninsula in the West to the vicinity of Derbent in the Southeast. It hibernates in caves and other underground spaces, whilst maternity colonies overwhelmingly occupy above-ground roosts. In total, this bat has been reported from nearly 120 geographi-

cal locations in the Russian Caucasus, nearly half of which are caves.

— *Rhinolophus mehelyi* Matschie, 1901. The only maternity and hibernation roost in Russia has been known since 1972 in the Karabudakhkentskaya Cave in Dagestan, with the number of bats gradually depleting from 1000 in 1972 to 30–40 in 2008.

Family Vespertilionidae Gray, 1821

— *Barbastella barbastellus* (Schreber, 1774) (Fig. 7A). Barbastelles utilize caves and other underground shelters for hibernation and swarming. Of the ca 60 location records of the species, as many as 35 belong to caves. The hibernation colony in the Kanyon Cave, Krasnodar Province is the largest ever reported for the species, accumulating up to 8 thousand individuals in harsher winters. Another large winter aggregation of over 2,000 barbastelles was discovered in the Mayskaya Cave in Karachaevo-Cherkessia (Gazaryan, 1999, 2007a; Gazaryan, Panyutina, 2013).

— *Barbastella caspica* (Satunin, 1908). Amirkhanov (1980) reportedly found 6 individuals in two small caves near the Amushi and Tagada villages in Dagestan. The species was also recorded from caves in other parts of its distribution range.

— *Eptesicus serotinus* (Schreber, 1774). This species only occasionally hibernates in caves; several animals were found in the Kanyon Cave in winter, few serotines were also netted at the entrance to Babaylovskaya Cave in the Caucasian State Nature Reserve during swarming in August. In summer, resident males often occupy crevices and niches at the entrance parts of large caves and grottos.

— *Hypsugo savii* (Bonaparte, 1837). The species uses spacious caves and grottos as swarming sites. It was netted at the entrances to the neighbouring two caves in the Mzymta River valley near the city of Sochi: Bolshaya Kazachebrodskaya (Smirnov, 2001) and Dzykhrinskaya (= Lianovaya).

— *Myotis alcatheo* von Helversen et Heller, 2001. Several individuals were netted entering or flying out from the Fanagoriyskaya and Krasnoaleksandrovska (Takhira) caves, Krasnodar Province during swarming, one male was found hibernating in the Rozhnova Cave in Karachaevo-Cherkessia.

— *Myotis bechsteinii* (Kuhl, 1817). Single hibernating individuals were found in the karst caves Fanagoriyskaya and Kanyon.

Swarming Bechstein's bats were netted at the entrances to the caves Malaya and Bolshaya Kazachebrodskaya (Tsytsulina, 1998; Smirnov, 2001), and Dzykhrinskaya (= Lianovaya), Akhunskaya and Fanagoriyskaya, all within the Krasnodar Province. — *Myotis blythii* (Tomes, 1857) (Fig. 7D). With ca 110 record locations, the Lesser Mouse-eared Bat occurs literally everywhere in montane ecosystems of the region. As everywhere within their range, these bats occupy both underground and above-ground roosts in summer, although hibernate only in caves and other underground sites. Large maternity colonies comprising hundreds of females are sustainably present in the caves Karabudakhkenskaya (Dagestan) and Samorodnaya (Karachaevo-Cherkessia); a mass winter aggregation amounting to over 2,000 bats is known from the Shubi-Nykass Cave in North Ossetia (Gazaryan, 2007b).

— *Myotis brandtii* (Eversmann, 1845). Brandt's bat is common in woodland areas across the region and the absence of any records from Dagestan is apparently related to insufficient research efforts. Among 26 record locations in the Russian Caucasus, seven belong to the following caves: Fanagoriyskaya, Kanyon, Babaylovskaya and Tru-52 in the Krasnodar Region, Mayskaya and Pogrebok in Karachaevo-Cherkessia, and Anglo-Russkaya in the Adygea Republic. During the swarming time, *M. brandtii* was abundant among bats netted at the entrances to these caves, even though only single solitarily hibernating Brandt's bats were found there in the winter.

— *Myotis dasycneme* (Boie, 1825). One young female was found on 8 November 2003 in the Gunkina-4 Cave in Karachaevo-Cherkessia (Gazaryan, 2004), but the occurrence has since been revealed nowhere else in the region. Consequently, we tend to associate this single record with a vagrant bat.

— *Myotis daubentonii* (Kuhl, 1817). Until the end of the 20th century, the species had

been considered as extremely rare or even a recent colonist in the Caucasus and Transcaucasia. However, after extensive field-work the former putative status was reassessed to common and abundant across the region (Gazaryan *et al.*, 2008). Although it was recorded at 82 locations in the Russian Caucasus, only several hibernation sites containing modest (up to 10 animals) numbers of Daubenton's bats have been found so far. Daubenton's bats do not aggregate in large clusters in the Caucasus and only sole animals could be observed in the caves Fanagoriyskaya, Ared, Kanyon and Chernorechenskaya, Krasnodar Region, as well as in several mines.

– *Myotis davidii* Peters, 1869. One genetically identified specimen of this species was collected in the Razvalka mine near Pyatigorsk, Stavropol Province. See Benda *et al.* (2016) for details.

– *Myotis emarginatus* (Geoffroy, 1806). Similar to the Greater Horseshoe Bat, the distribution of this species in the Caucasus is limited by the availability of suitable underground maternity sites. The species has not been found in the Eastern Caucasus and reported only twice from the central part of the region, including one record in a small cave near the Babugent settlement (Kabardino-Balkaria). Other 21 record locations lay in karstic areas of the Western Caucasus within the Krasnodar Province and Adygea Republic. Maternity colonies were reported from the Khadzhokhskaya (now abandoned by bats), Dedova Yama, Teshebskaya, Svetlaya, Mordvinovskaya and Ared caves; hibernating individuals were recorded in the Ambitsukova, Fanagoriyskaya, Kabaniy Proval, Ared and Dedova Yama caves.

– *Myotis mystacinus* (Kuhl, 1817). The distribution of *M. mystacinus* in the region and its dependence on caves is unclear due to difficulties in a morphological identification of this species in its contemporary sense. Genetically identified specimens were collected in the Fanagoriyskaya Cave (Benda *et al.*, 2016).

– *Myotis nattereri* (Kuhl, 1817). Recorded from 27 sites in the Russian Caucasus, this bat has rarely been found in caves and undergrounds. Few individuals were captured as they swarmed in the Akhunskaya, Pervomayskaya, Babailovskaya, Fanagoriyskaya and Kanyon caves, Krasnodar Province. In the latter two caves, single Natterer's bats were also found during winter. Nine pregnant females were netted on 4 June 2007 as they swarmed at the entrance to Kamennye Sarai Cave, Stavropol Province.

– *Nyctalus noctula* (Schreber, 1774). Roosting behaviour unusual for this species was first reported in 1980 for the Proval Cave, Stavropol Province (Gazaryan, Kazakov, 2002), in 2008 this colony remained in the cave. Only adult males used this cave in summer, whereas females were found there only between September and May.

– *Pipistrellus pipistrellus* (Schreber, 1774). A group of 30–40 hibernating pipistrelles was found in a deep crevice inside the Kamennye Sarai Cave, Stavropol Province on 20 December 2009. This is the only documented evidence of this species hibernating in Russian caves.

– *Plecotus auritus* (Linnaeus, 1758). Twenty-six of ca 60 records of this species in the region belong to underground sites, including 20 karst caves, where it was found both during the hibernation and swarming seasons. The largest number of the brown long-eared bats netted at one roost did not exceed 15 animals, and only solitary individuals could usually be found in winter shelters.

– *Plecotus macrobullaris* Kuzyakin, 1965. The sole record in an underground site was made in a mine at Razvalka Mountain, Stavropol Province on 21 December 2009. However, we anticipate future findings of this species in natural underground roosts.

Family Miniopteridae Dobson, 1875

– *Miniopterus schreibersii* (Kuhl, 1817) (Fig. 7C). Among the Russian representatives of Chiroptera, Schreiber's Bent-wing bat shows the highest rate of dependence on caves and is very selective in terms of their

size, accessibility and microclimate. Hence, it inhabits only the Western Caucasus with its vast karst areas, and is not distributed eastward to the Central and Eastern Caucasus; 34 record locations in the Adygea Republic, Krasnodar Province and Karachaevo-Cherkessia are available. All known records pertain to natural caves, with two exceptions when four individuals were observed in abandoned mines and one animal was found roosting under a bridge. The largest colonies (up to 5,000 bats) occupy spacious horizontal caves with large entrances, which make them exposed to disturbance by visitors and susceptible to vandalism and intentional killing. For these reasons, bats forsook some of the previously reported cave roosts and many colonies have depleted in numbers since the first extended survey (Gazaryan, Ostapenko, 1999). To avoid possible further decline and disturbance, we abstain from listing the names of these roosting sites.

Family Molossidae Gervais, 1856

– *Tadarida teniotis* (Rafinesque, 1814). This species does not inhabit caves in the strict sense of this term, but colonies could be found in ceiling crevices of rocky overhangs, where these bats may also swarm. Under such circumstances the free-tailed bats were found in a large grotto at the valley of the Cherek River in Kabardino-Balkaria (Gazaryan, Tembotova, 2007).

V. Conservation of caves and hypogean species

Some of the karst cavities in European Russia are protected as objects of nature reserve stock, with various statuses allotted. Yet no dedicated animal life conservation is being performed in such caves. For example, the Shulgan-Tash (= Kapovaya) Cave in Bashkortostan (= Bashkiria), southern Cisuralia, is part of the Shulgan-Tash Federal State Nature Reserve as an object of the national historical and cultural legacy of the palaeolithic epoch. However, this very cave also hosts a few troglobiont spring-

tails and mites, as well as a number of troglophiles amongst earthworms, spiders, beetles and flies (see above). In 1973, the Bolshaya Azishskaya and Fanagoriyskaya caves, both in the Krasnodar Province, were allotted the status of nature monuments. A good number of karst cavities are situated inside nature reserve stock objects of higher rank. Thus, numerous caves are located within the Sochi National Park or Caucasian Biosphere State Nature Reserve. Yet many caves like Shulgan-Tash, Bolshaya Azishskaya, Vorontsovskaya, Bolshaya Kazachevodskaya etc., despite their protection statuses, are subjected to economic/excursion activities, this clearly rendering a negative effect on the biotas they host.

A number of cave animal species in European Russia are listed in regional red data books. Thus, the Red Data Book of the Moscow Region contains the amphipod crustacean *Synurella ambulans* (F. Müller, 1847). The Red Data Book of the Krasnodar Province lists several cave mollusks, crustaceans and many insects, while that of the Adygea Republic a few insects as well, all largely highly local endemic troglobionts (e.g. Turbanov et al. (2016a, b, c) and references therein). A number of bat species are likewise listed in several regional red data books. The main emphasis is thereby put on the conservation of caves as geological bodies, but not as shelters to the biotic components they support.

VI. Conclusion

As a result, the subterranean biota of European Russia, including that of the northern Caucasus, but excluding that of Crimea, presently comprises at least 389 species or subspecies (some still unidentified) from 229 genera (a few still unidentified), 150 families, 75 orders, 48 classes and 25 phyla, among which 96 species or subspecies represent presumed stygo- or troglobionts. The taxonomically most diverse phylum is Arthropoda which encompasses the bulk of the fauna, in particular due to crustaceans, beetles and collembolans. Whereas the troglofauna of northern Russia is completely devoid of such strongly cave-adapted animals, in the

Urals, Cis-Urals and central Russia there are a few, but the richest hypogean list in the region concerns the northern Caucasus, especially its western part where karst is particularly abundant.

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