Palaeontologia Electronica
palaeo-electronica.org

Paleoparasitology in Russia, history and prospects

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ABSTRACT

The science of paleoparasitology refers to parasitic animals and plants existing both in the recent past (including human history) and more remote periods of life on Earth. The history of paleoparasitology and its development in Old and New World countries is well-known, however, in Russia, the history of this science has hardly been considered. The present paper offers a review of Pleistocene findings of fossil parasites, parasitizing both mammals and humans, recorded in Russia. New data on the latest research in this field is presented.

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Keywords: paleoparasitology; archaeoparasitology; mammals; ancient diseases; Russia

Submission: 10 October 2017 Acceptance: 5 September 2018

INTRODUCTION

Parasitology is a complex, multi-aspect biological subject involving morphological and anatomical studies of organisms, diseases caused by them, and host-parasite interactions (Pavlovskyi, 1946; Shevtsov, 1970). As a science, parasitology was formed in the nineteenth century (Akbaev, 1998). Before that, it was considered to be a part of invertebrate zoology and was tightly related to it. Parasites, their eggs, larvae, and pathological tissue changes caused by said parasites, are sometimes recorded in fossilized condition, therefore, one can speak about paleoparasitology – a science concerning ancient remains including fossil and archeological finds. The term "paleoparasitology" was first mentioned at the edge of 1970s-1980s in order to expand the definition of "paleopathology" – its first use was in a study of Brasilian archeological records using the so-called helminthological method (Ferreira et al., 1979; Araújo et al., 1981). Reinhard (1990) presumes that for the New World's archaeologists, the prefix "paleo-" solely refers to prehistoric cultures, populating American territory over nine thousand years ago, so using the term "paleoparasitology" in relation to

Serdyuk, Natalia V. 2018. Paleoparasitology in Russia, history and prospects. *Palaeontologia Electronica* 21.3.35A 1-15. https://doi.org/10.26879/826
palaeo-electronica.org/content/2018/2318-paleoparasitology-in-russia

later, "younger" archaeological objects would not be correct. He suggests the term "archaeoparasitology", which would encompass parasitological studies of archaeological records of different ages. Strictly speaking, both prefixes "archaeo-" άρχαίος and "paleo-" παλαιος are of Greek origin and similar meaning – "ancient". "Paleoparasitology" is regarded as a broader term, which can be applied to the studies of all parasitic plants and animals of both recent past (including human history) and other, more distant periods of life on Earth (Dittmar, 2009). It can be assumed that the relationship between paleoparasitology and archaeoparasitology (study of parasites in ancient humans and animals) is nearly the same as between parasitology itself and medical parasitology. Paleoparasitology investigates the entire diversity of fossil parasites whereas archaeoparasitology deals with the parasites in ancient people and animals. By analogy there are subdisciplines within parasitology and paleoparasitology, such as the study of fossilized parasitic worms – paleohelmintology – a subdiscipline, and the study of fossil arthropods and fossil protozoans – paleoarachnoentomology and paleoprotistology, respectively.

In the historical analysis of paleoparasitology and its establishment in the Old and New World, Western and Southeastern Asia is presented in analytical sketches (Araújo et al., 2015; Bouchet et al., 2003; Nezamabadi et al., 2011; Dittmar et al., 2012). However, these contributions do not cover the history of paleoparasitology in Russia. The present paper aims to fill this gap. There is a vast variety of parasitic organisms, however, our research will only focus on finding animals parasitizing other animals, particularly mammals. Paleoparasitology is a science even younger than parasitology itself. Its formation worldwide is tightly connected with archaeology and is directly implied by it (Callen and Cameron, 1960; Fry and Moore, 1969; Jones, 1982; Ruffer, 1910; Pike, 1967; Szidat, 1944). Specific research of fossilized animal parasites is rather a secondary phenomenon (Beltrame et al., 2011, 2014, 2015; Dalgleish et al., 2006; Fugassa et al., 2006; Huchet et al., 2013; Valim and Weckstein, 2012; Vullo et al., 2010; Wappler et al., 2004). Presently, however, the study of fossilized animal parasites is no longer secondary and continues to grow (De Baets and Littlewood, 2015; Leung, 2017).

In Russia, studies of fossilized animal parasites have become more popular. They were first mentioned in relation to the frozen carcass of the so-called Beryozovsky mammoth *Mammuthus primigenius* (Blumenbach, 1799), found in 1900 in the basin of the Kolyma river (Figure 1) (Balyanitskyi-Birulya, 1909; Zalenskyi, 1909).

Currently, among the three subdisciplines of paleoparasitology, paleohelminthology appears to be the richest in terms of material. It is connected not only with well-established, tried, and true methods in this field but also with relatively good availability of fossil material suitable for helminthological analysis (Araújo et al., 2015). Fast entombment and preservation of the corpse enables us to obtain arachnoenthomological objects associated with their host (Vereschagin, 1975). However, these findings are extremely rare as after the death of their host, temporary ectoparasites eagerly seek a replacement host (Huchet et al., 2013). Parasitic paleoprotistology is a promising, up-and-coming subject (Côtê and Le Bailly, 2017; Faulkner and Reinhard, 2014). The development of biological subdisciplines, elaboration of new molecular and genetic techniques has lately allowed to set ambitious research goals in this area of paleoparasitology (Côtê and Le Bailly, 2017).

PALEOHELMINTHOLOGY

Russian paleohelminthology knows the occasions of both true and indirect presence of mature helminths in the intestines and eggs of fossilized excrement. The records of mature helminths are always associated with frozen carcasses of Pleistocene animals. Eggs can be found when the soil, filling in the visceral cavities, is being analyzed, or in fossil faeces.

An indirect indication to helminths is, supposedly, the presence of so-called "problematic bodies", found in a Beryozovsky mammoth. An adult male mammoth's carcass was discovered in 1901 by the Beryozovka river (right tributary of the Kolyma). The "sitting position" of the corpse facilitated good preservation of its extremities and soft tissues on the ventral surface. The remains were taken to Saint Petersburg to undergo scrutiny using all techniques available at the time. Presently, the exhibit is kept at the Zoological museum of Zoological Institute (ZIN) of Russian Academy of Sciences in St. Petersburg (Figure 2.1). Radiocarbon dating detected the finding's age as 31750±2500 years (Kuzmin et al., 2003).

The formations referred to as "problematic bodies" were located in the submucous membrane of the stomach (Figure 2.2). They differed from other tissues in composition, and a separate "body" (Figure 2.3) could be regarded either as a para-

FIGURE 1. Location of Paleoparasitological investigations (the map from http://kimkardashiani.blogspot.ru). The finds of parasites in Proboscidea: 1 – the Beryozovsky mammoth, 2 – the Kirgilaykh mammoth, 3 – the Shandrin mammoth, 4 – Berelekh mammoth cemetery, 5 – the Zhenya Mammoth; in Perissodactyla: 6 - the Selerikan horse, 7 – horse from Ukok burial; in Artiodactyla: 8 – the Indigirka bison; in Rodentia: 9 – the Indigirka ground squirrel, 10 – Egorov's narrow-skull vole. The finds of parasites at the archaeological sites: 11 – Caucasus dung deposits, 12 – Voymezhnoe, 13 – Zamostye-1, 2; 14 – Maray-1, 15 – Yarte-6, 16 – Nadym settlement, 17 – Ust-Voikar, 18 – Mangezeya, 19 – Zeleny Yar, 20 – Kikki-Akki, 21 – Vesakoyakha, 22 – Nyamboyto, 23 – Yaroslavl Kremlin.

site's egg or as an atypical (tumour) cell (Zalenskyi, 1909). As a conservative assumption, it can be suggested that it could have occurred from a pathological or parasitological process, and one can speak about granuloma associated with multiple stomach wall hemorrhages found in this mammoth. A pathoanatomical pattern similar to that in the mammoths, characterized by the formation of granulomata and stomach wall hemorrhages, can be observed in extant elephants affected by stomach nematodes (Basson et al., 1971; Graber, 1975; Fowler and Mikota, 2006; Soulsby, 1982; Strukov and Kaufman, 1989). Buildups of the same kind were later discovered in the famous baby mammoth Dima from Kirgilyakh (Ivanova, 1981).

However, the first real finding of fossil helminths on Russian territory took place a bit later. In 1946, Yu. N. Popov, a geologist, while exploring quaternary deposits, came across three entire mummified ground squirrel bodies in the permafrost layer in the Dirin-Yuryakh stream valley, the Elga river, and the Indigirka basin (Figure 1). The finding was described as a new species, *Spermophilus glacialis* Vinogradov, 1948, or the Indigirka ground squirrel (Vinogradov, 1948). Two mummies out of three were ethanol-preserved and taken to the ZIN of USSR Academy of Sciences (Figure 3). Their geological age was identified to be 10-12 thousand years old (Popov, 1947, 1948). The ground squirrels' internal organs appeared to be well-preserved; in the cecum, three female nematodes of the order Oxyurida were found. The nematodes were attributed to the genus *Syphacia,* while it turned out to be impossible to identify their species due to the specimens' poor preservation (Dubinin, 1948).

The next record of ancient helminths dates back to 1968; at a Selerikan allotment (the Indigirka basin), a partially preserved corpse of a male horse (stallion) *Equus lenensis* Russanov, 1968, was found in the permafrost and nicknamed the "Selerikan horse" (Figure 1). Its absolute age, based on the muscular tissue analysis, was 33800±2100 y.o.; based on plant remains in the stomach - 38590±1120 y.o. (Arslanov and Chernov, 1977). Its intestine loops were found to contain the "forage mass" (Vereshchagin and Lazarev, 1977), in which nematodes of the order Strongylida were discovered: four entire males, two males missing their heads, six separate heads, and two mid-body fragments. According to Dubinina's identification, the nematodes from the fossilized horse's stomach belonged to the species *Strongylus (Alfortia) edentatus* Looss, 1900, parasitizing contemporary equids (Dubinina, 1972).

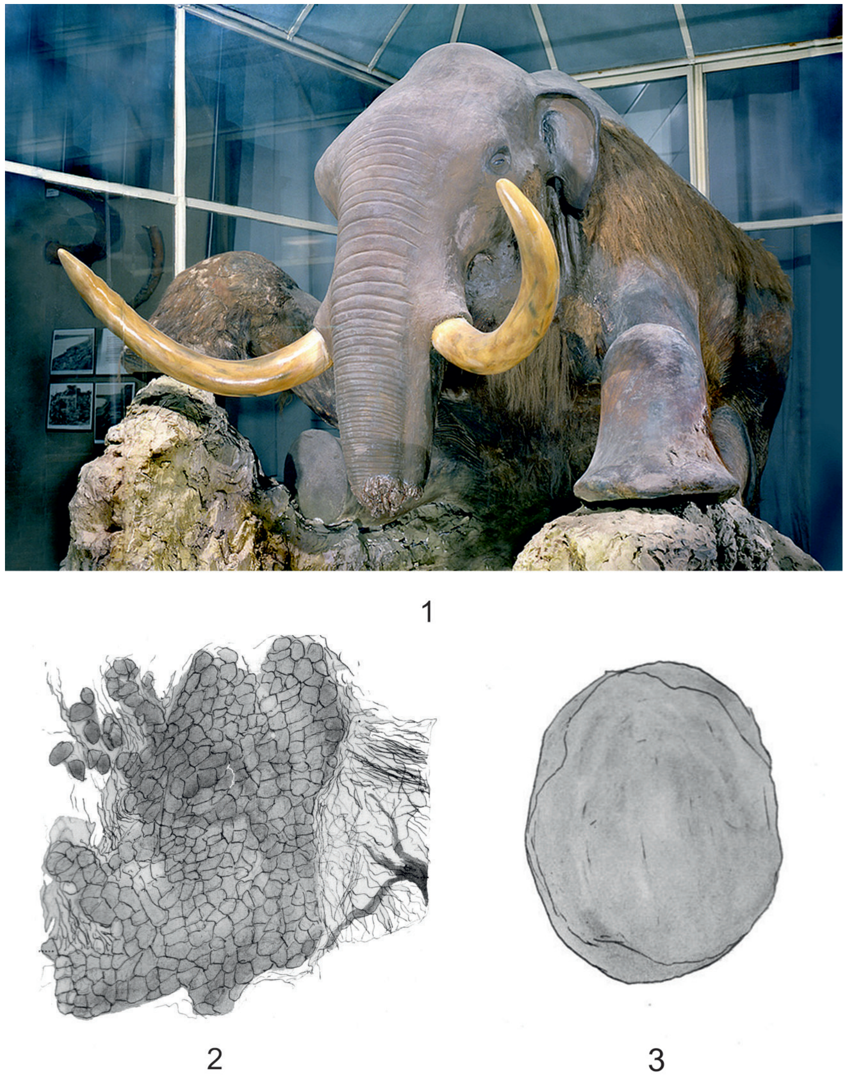

FIGURE 2. The Beryozovsky mammoth. 2.1 – the exhibit of Zoological museum in St. Petersburg (photograph by A.N. Tikhonov); 2.2 – the formation of “problematic bodies” located in the submucous membrane of the stomach of mammoth; 2.3 – a separate “body” (Zalenskyi, 1909, table V, figure 7). Reproduced with permission of ZIN RAS.

In 1971, in the vicinity of the Yana-Indigirka lowland, a hunter named Struchkov stumbled on a corpse of an extinct prehistoric bison *Bison priscus* Bojanus, 1827, which was subsequently nick-named the “Indigirka bison” or “Stryuchkov’s bison” (Figure 1). Its absolute age was identified to be 29500±1000 years (Lazarev, 2008). The body was seriously damaged by an ice wedge; in the abdomen, intestinal loops with desiccated contents were found to possess two preserved nematodes, later described as a new species *Ostertagia (Scrjabinagia) paleobisonica* Shakhmatova, 1988, from the order Strongylida (Shakhmatova, 1988). The holotype of *O. paleobisonica* is kept at the Zoological museum of the Institute of Systematics and Ecology of Animals, Siberian Branch of Russian Academy of Sciences (ISEA SB RAS) (Novosibirsk). V.I. Shakhmatova pointed out the resemblance between the newly discovered fossil species and the contemporary *Ostertagia bisonis* Chapin, 1925, from the American bison’s intestines (Chapin, 1925).

A large male mammoth (Figure 1) was found in 1972 beside the river Shandrin (Yakutia), its absolute age being 41750±880 years (Kuzmin et al., 2003). Inside the skeleton, in the area topographically corresponding to the abdominal cavity, frozen contents of the stomach and the intestines were preserved. Currently, the skeleton of the Shandrin mammoth is kept in the museum of the Institute of Archaeology and Ethnography, Siberian Branch of RAS (Novosibirsk), and the sublimated

FIGURE 3. *Spermophilus glacialis* Vinogradov, 1948 (photograph by F.N. Golenishchev). Reproduced with permission of ZIN RAS.

abdominal contents are at the Geological Museum of the Institute of Diamond and Precious Metal Geology, Siberian Branch of RAS (Yakutsk). In its intestine loops and stomach, contents of the larvae of nematodes were found (species attribution not indicated) (Vereschagin, 1975).

In June 1977, a calf mammoth's corpse, unique by its excellent, undamaged condition, was found in the Kirgilaykh river, the Kolyma tributary (Figure 1, Figure 4.1) (Vereshchagin, 1981). The geological age of the deposits housing the finding, is around 40 thousand years (Shilo et al., 1983). The frozen carcass was completely preserved, including the internal thoracic and abdominal organs. A detailed tissue study revealed some artefacts in the blood vessels. According to E.I. Ivanova (1981), round plates of 0,01-0,06 mm in diameter were numerous "parasite eggs" (Figure 4.2). An assumption was made that those multiple bodies (similar to the "problematic bodies" of the Beryozovsky mammoth) on the outer surface of the caudal vena cava were cysticerci of cestodes, which parasitize canines' intestines at mature stage. Also, a part of a parasitic worm body was found, sized 0.1-0.05 mm (species attribution not indicated). "A helminth fragment" (Figure 4.3) of the Kirgilaykh mammoth could be a part of a larva of an ancient parasitic nematode, as nematodes related to the blood stream are known to exist within some contemporary elephants (Alvar et al., 1959; Evans and Rennie, 1910; Seneviratna et al., 1967; White, 1980). But in order to prove or reject the presence of parasites in the Beryozovsky and Kirgilyakh mammoths, special histological studies and cutting-edge techniques are required.

In 1990, helminthological analysis was purposefully implemented into paleo-environmental research (Savinetsky and Khrustalev, 1990). Holocene deposits of animal feces from a rock location in North Caucasus were used (Figure 1). The results demonstrated a change in livestock rearing traditions during a fairly short time period (about 100 years). Subsequently, the results of coprological analysis were used in environmental and climatic studies (Khrustalev and Savinetsky, 1992; Savinetsky and Khrustalev, 2013).

In 2012, (at the Yenisei river mouth, Sopochnaya Karga cape), a partially preserved corpse of a young male mammoth – the so-called "Zhenya the mammoth" – was found in the Taymyr peninsula (Maschenko et al., 2015). This mammoth's internal organs were not preserved, its abdominal cavity being filled with loosely textured deposits, but there were structures morphologically similar to nematode and cestod eggs. The investigation of muscle tissues in this specimen by means of standard helminthological techniques failed to reveal any parasites (Glamazdin et al., 2014).

Studies of fossilized parasites allow not only to trace their phylogenetic lineages, parasitic formation in various groups and host-parasite interactions, but are also in demand in the field of archaeology. These records provide additional information regarding human diseases, nutrition, lifestyle, migrations, burial season, etc. All in all, archeoparasitological research commenced in Russia much later than anywhere else.

Thus, helminthological analysis was applied in studying Russia's archaeological sites and records (Figure 1). From 1988 to 1991, comprehensive research of Paleolithic encampments and type-sites of the Volga-Oka interstream area were carried out (Sidorov et al., 1993). Fossil excrement of unclear (dog or human) origin was found at three sites – Voymezhnoe 1, Zamostie 1, and Zamostie 2 (Aleshinskaya et al., 1997; Engovatova, Khrustalev, 1996). A helminthological study showed that infection by broad tapeworm *Diphyllobothrium latum* (L., 1758) and cat liver fluke *Opisthorchis felineus* (Rivolta, 1884), covered both people and dogs.

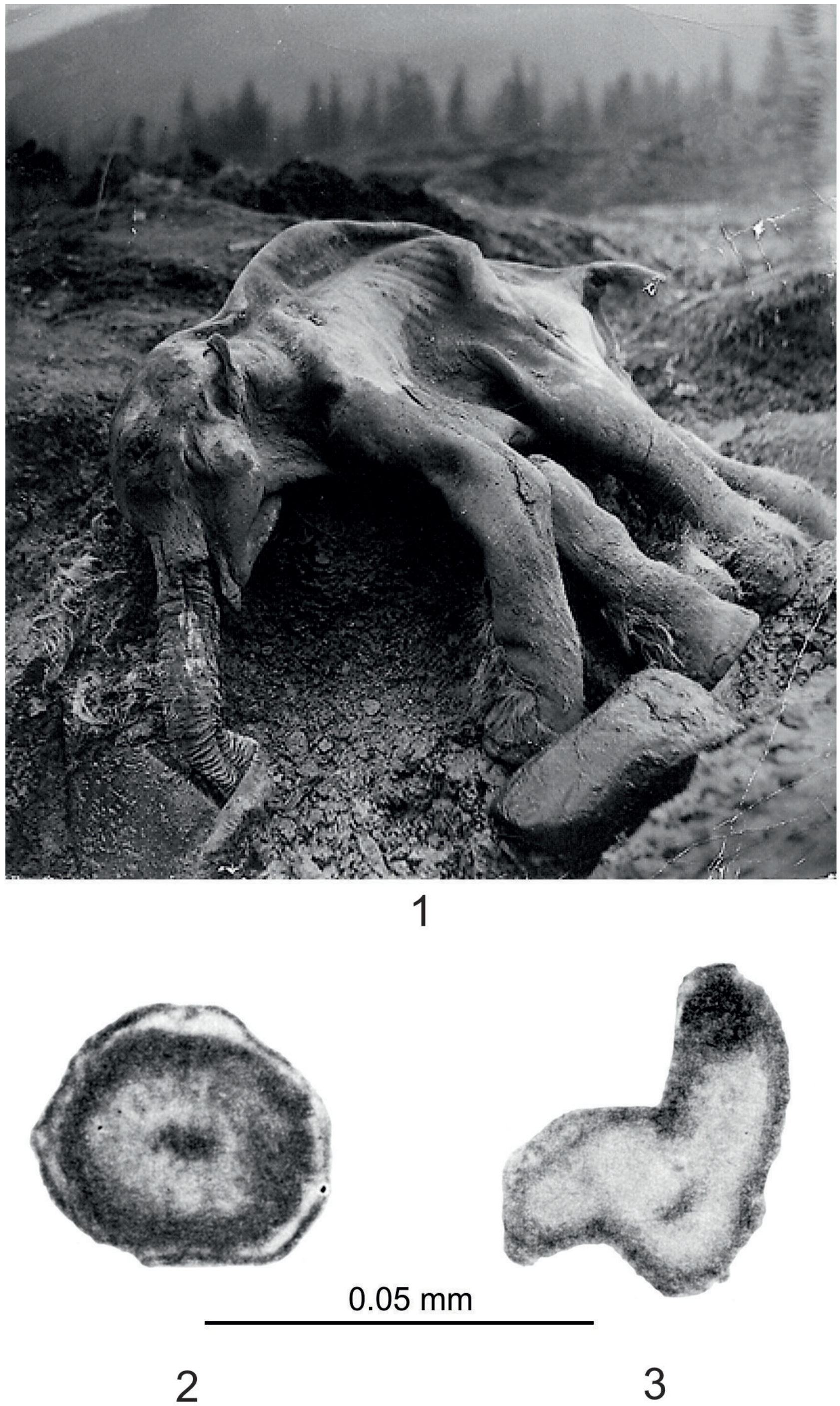

FIGURE 4. The mammoth calf Dima (Kirgilaykh mammoth): 4.1 – photograph taken at the discovery site (photograph by A.V. Lozhkin); 4.2 – "parasite eggs" in the blood vessels of Kirgilaykh mammoth, 4.3 – "a helminth fragment" (Ivanova, 1981, figures 15 and 16, p. 143). The figure was modified by the author.

In 2011, V.A. Zakh and coauthors presented coprological data obtained at the Maray-1 encampment of the so-called Krasnoozerskaya culture ("culture of the red lake", ninth to sixth centuries B.C.) in the Ishim river basin (western Siberia). The authors believe that the feces belonged to dogs living at the site alongside people. A study of the feces revealed the presence of cat liver fluke eggs as well as those of *Strongyloides papillosus* (Wedl, 1856) and an ascarid (no indication of species).

Moreover, the presence of demodectic ticks (with no indication of species) was reported (Zakh et al., 2011).

Various research methods were used in comprehensive archaeological studies of encampments in the northern part of western Siberia (Yamal Peninsula); at Yarte-6 (mid eleventh – early twelfth century), Nadym settlement (late twelfth – early eighteenth century), Ust-Voikar (late eighteenth – early twentieth century) and Mangezeya (seventeenth century), archaeoparasitological investigations took place (Vizgalov, 2013). In fossilized dog feces found at Yatre-6 site multiple cat liver fluke egg shells were recorded. Mangezeya appeared to possess the most diverse representation of helminths fauna: eggs of cat liver fluke, broad tapeworm, whipworm *Trichocephalus* sp., toxocara *Toxocara canis* (Werner, 1782) and common liver fluke *Fasciola hepatica* L., 1758 were located there. It is worth noting that nowadays the cat liver fluke does not occur at Yamal territory, yet it is present in the Ob-Irtysh basin. Presumably, the ancient inhabitants migrated with their dogs which contracted helminthic infections while at the Ob-Irtysh basin (Vizgalov, 2013). Also, the fluctuations of this parasite's range cannot be excluded so the matter requires future investigations.

In 2013, the team of the Institute of Problems of Northern Development, Siberian Branch of RAS, when excavating at the North Selkup burial ground Kikki-Akki (seventeenth – nineteenth century) located in Tyumen region, took specific effort to select soil (core) samples from nine human burial sites. The samples were taken from the pelvic-sacral part of the tomb (Slepchenko and Ivanov, 2015). In 2014, when excavating a medieval (twelfth – thirteenth century) burial site Zeleny Yar (lower Ob' region, Priuralsky district), soil and substrate were also sampled in the part where children had been buried (Slepchenko et al., 2015). In 2014, pelvic samples from the skeletons of late nineteenth – early twentieth century burial grounds Vesakoyakha VI, Vesakoyakha VII and Nyamboyto belonging to Tazov Nenets people (Slepchenko et al., 2016). These efforts resulted in obtaining information on the cat liver fluke and broad tapeworm infections in the population of Yamalo-Nenets Autonomous district.

PALEOARACHNOENTOMOLOGY

Russian paleontological arachnoentomology is abundant in terms of findings. The presence of a parasitic infestation can be direct (when parasites themselves are found next to their hosts) and indirect (finding parasites without hosts or recording free-living stages of a parasite and comparing them with contemporary forms) (Nagler and Haug, 2015). Arachnoentomological objects, buried together with their hosts, are quite rare in the fossil record.

One of the three Indigirka ground squirrels from the abovementioned quaternary location of the Dirin-Yuryakh stream had some lice egg shells and two male lice in their abdominal hair, on the ventral side. The lice were described as a new species, *Neohaematopinus relictus* (Dubinin, 1948). The new louse species is morphologically closer to species parasitizing contemporary ground squirrels from the genus *Spermophilus*; they can sometimes be found on other representatives of the squirrel family (Dubinin, 1948). Also, a leather beetle larva and the tibia of an unknown beetle were discovered. Unfortunately, nothing is known about what happened to this material further.

In 1968, the ZIN of USSR Academy of Sciences obtained five vole mummies from the Indigirka basin. The animals were attributed to Egorov's narrow-skull vole (Baranova and Feigin, 1980). The finding's geological age appeared to be 37700±2000 years (Garutt and Yuriev, 1966). The well-preserved fur contained dried mites, lice, and lice eggs. One of the voles was found to possess a mole mite of the genus *Hirstionyssus* (fam. Hirstionyssidae); the second one – a male and a female individual of *Myocoptes* (fam. Listrophoridae); nine mites of the family Myobiidae and two lice of the genus *Hoplopleura* (fam. Hoplopleuridae); the third animal had four mites of the genus *Hyperlaelaps* (fam. Laelaptidae), five Myobiidae ticks, and four *Hoplopleura* lice; the fourth vole was infested by 64 *Hoplopleura* lice (Sosnina, 1972). Acariformes mites are represented by the following species: *Myocoptes japonensis japonensis* Radford, 1955, and *Radfordia hylandi* Fain et Lukoschus, 1977 (Dubinina and Bochkov, 1996). Both the morphological study and parasitological analysis of the fossilized vole mummies suggested their placement into the American species *Microtus miurus* Osgood, 1901, keeping the subspecific status (Golenishchev, 2008).

The fossilized horse from the location Selerikan (the Indigirka river basin) mentioned above was found to possess fragments of the armour, or testa of a moss mite Orobatidae, which apparently had accidentally gotten into its intestines with food (Dubinina, 1972).

FIGURE 5. The woman mummy from Ukok and her reconstruction. The photo was modified by the author (photograph by K.A. Bannikov, V.P. Mylnikov and reconstruction by D.V. Pozdnyakov).

Quite often flies' puparia can be found alongside skeletal remains (Gautier, 1974; Gautier and Schumann, 1973; Germonpre and Leclerq, 1994; Heinrich, 1988; Lister, 2009). Even though one cannot exclude in-life (vital) myiases in ancient animals, it is much more likely that the pupae populated the location after the animal's death. Thus, puparia findings (without species identification) have been reported in Russia for the woolly mammoth from Berelekh (Yakutia) (Figure 1) (Vereshchagin, 1977).

The most interesting discovery was that of a stomach botfly *Cobboldia russanovi* Grunin, 1973, found in the so-called Shandrin mammoth (Grunin, 1973). The first description of the stomach botfly was made on the basis of eleven larvae (eight entire ones, two larvae missing their anterior segments and one missing posterior segments) of the third stage *C. russanovi* removed from the superficial layer of the frozen stomach contents monolith of the Shandrin mammoth. The holotype and the paratype of *C. russanovi* is kept at the Zoological museum in Saint Petersburg, a paratype is also available at the Zoological museum of the ISEA SB RAS (Novosibirsk).

Arachnoentomology's role in the studies of people's lifestyles and daily draft is not the last one as it helps to clarify the season of entombment. For the first time, such an investigation took place in the mid-1990s. In 1993, a burial site of Pazyryk culture (V-III centrury B.C.) with a preserved female mummy was discovered in the high alpine permafrost deposits at Ukok plato, Altai (Figure 5) (Polosmak, 1994). Six horses were buried together with the woman. One of the horses had two third-stage larvae of the large stomach botfly *Gasterophilus intestinalis* De Geer, 1776, in its frozen stomach contents (Figure 6) (Shokh, 2000). Knowing the rates of contemporary botfly larvae development, the researchers assumed that the entombment had taken place in June, which was later proven by the botanical evidence (Polosmak, 2013).

On the grounds of the so-called Round-log town (territory of Yaroslavl Kremlin), a communal grave of the XIII century was found. The remains were shown to contain Calliphoridae flies puparia, which led to an assumption that the entombment took place much later than the people had died. According to the radiocarbon analysis, the people died during an attack by Tatar-Mongols in February 1238 but were not buried until late May – early

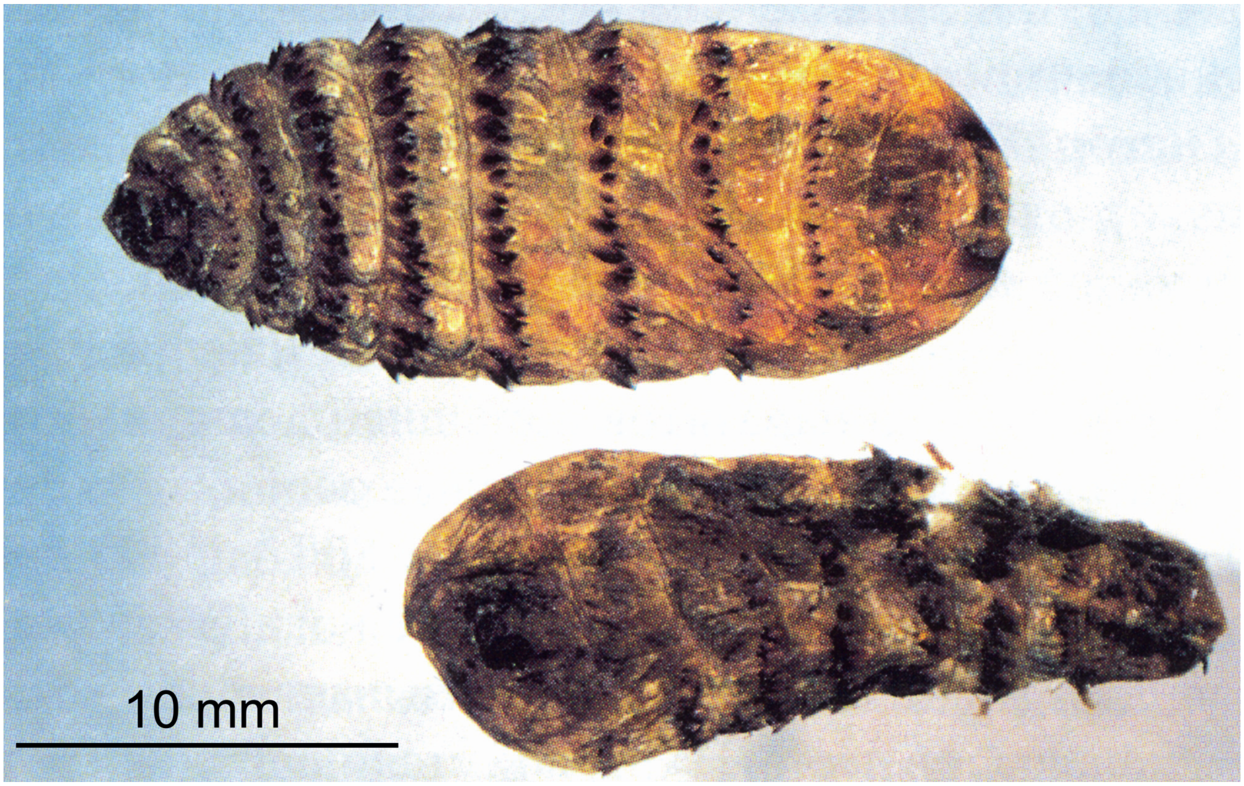

FIGURE 6. The bots of *Gastrophilus intestinalis* De Geer, 1776 from horse stomach, Ukok burial (Shokh, 2000, figure 278, p. 253). The photo was modified by the author.

June of that year (Engovatova et al., 2012). Human hairs from the abovementioned burial site of the Nadym settlement (twelfth – early eighteenth century) in the Yamal tundra forest were found to be infected by the head louse *Pediculus humanus capitis* De Geer, 1778 eggs (Vizgalov, 2013).

PALEOPROTISTOLOGY

The third area of paleoparasitology – paleoprotistology – is rapidly advancing all over the world (Frías et al., 2013). It is well known that parasitic Protozoa and their cysts are not always traceable in the contemporary material (Gavrilova and Proskuryakova, 2015; Konyaev et al., 2015; Eckmann, 2003; Todozakova and Medkova, 2016). Nevertheless, molecular methods have successfully been applied in such kinds of research to identify leishmaniasis (Zink et al., 2006), amoebiasis (Gonçalves et al., 2004; Le Bailly and Bouchet, 2006), trypanosomiasis (Guhl et al., 1999; Madden et al., 2001; Arajuo et al., 2007; Aufderheide et al., 2004), and giardiasis (Gonçalves et al., 2002; Le Bailly et al., 2008). Molecular techniques have been applied not in archaeological researches only. They have been used for studying ancient protozoans of fossilized animals as well (Beltrame et al., 2014; Wood et al., 2013). Molecular methods are also useful in Russian contemporary parasitology (Bychkov et al., 2007; Votyntsev et al., 2015; Morozov, 2011; Morozov and Kuznetsova, 2014). Paleontological and archaeological samples and specimens await their researchers.

CONCLUSION

The history of fossil parasite studies in Russia is similar to that worldwide: originally, the investigations were sporadic but as the interest to this branch of parasitology increased, the studies expand and become more comprehensive. Sampling for parasites is now goal-oriented, both in archaeology and paleontology. From large objects, visible with the naked eye (worms, arthropods), paleoparasitology shifts to microorganisms (Sarcomastigophora, Ciliates, Sporozoa). In turn, archaeologists were given additional tools for paleoreconstructions: the lifestyles, households, nutrition of prehistoric and ancient people, their migrations, and environment.

ACKNOWLEDGEMENTS

The author deeply appreciates the kind collaboration of Prof. V.V. Malakhov, a corresponding member of the Russian Academy of Sciences, Head of the Department of Invertebrate Zoology of the Faculty of Biology, Moscow State University named after M.V. Lomonosov, for fruitful discussions in preparation of the present paper. I would like to acknowledge Dr. K. De Baets for useful comments on an earlier draft of this manuscript. I would also like to thank anonymous reviewer for his helpful comments on an earlier version of the manuscript. The research was supported by the Russian Science Foundation (project 14-50-00036).

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