УДК 576.895

PROFESSOR YURI SERGEEVICH BALASHOV: LEGACY OF AN OUTSTANDING PARASITOLOGIST

© 2021 E. I. Korenberg[a,*], O. Kahl[b]

[a]Gamaleya National Centre for Epidemiology and Microbiology,
Moscow, 123098 Russia
[b]Tick-radar GmbH, 10555 Berlin, Germany
**e-mail*: *edkorenberg@yandex.ru*

Received 16.10.2020
Received in revised form 30.10.2020
Accepted 02.11.2020

This paper is devoted to the contributions of the outstanding parasitologist Yuri S. Balashov. It is not biographical. Its purpose is to highlight selected aspects of Yuri S. Balashov's scientific legacy that the authors consider most important for an international readership. This should direct the attention of international researchers to his various scientific theses and concepts, some of which have been only published in Russian language, and should also open up a broader discussion. The scope of Balashov's scientific interests was remarkable, although he devoted special attention to the research of argasid and ixodid ticks (Argasidae and Ixodidae). The main results and conclusions of his tremendous work have been described here using mainly his own words. Only some explanations that may be required to increase the reader's understanding of the concepts, terms and thoughts of Yu. Balashov were made by the authors.

Keywords: parasitology, medical entomology, ecology, Argasidae, Ixodidae, ticks, natural foci

DOI: 10.31857/S0031184721010014

The life of Yuri Sergeevich Balashov (1931–2012), an outstanding parasitologist, has been described in special publications (Filippova, 2013; Medvedev, 2012; Medvedev et al., 2013). This paper is not biographical. Its purpose is to highlight the aspects of Balashov's scientific legacy that we consider most important. The scope of his scientific interests was remarkably broad, although he devoted special attention to the research of argasid and ixodid ticks (Argasidae and Ixodidae). Balashov was a prominent representative of the parasitology school founded by the Academician Yevgeny N. Pavlovsky, who developed the theory of natural focality of transmissible diseases (Pavlovsky, 1939; 1966) and whose ideas he expounded and further developed (Balashov, 1967; 1984a; 2003; Balashov et al., 1968). He greatly appreciated the biocenological and comparative parasitological concepts by Vladimir N. Beklemishev (1970) about parasitic systems and the life schemes of species, which he considered to be of high significance for the development of parasitology. This follows from Balashov's paper (1991) commemorating the centennial of Beklemishev's birth, where he expressed an idea that may stand for his "scientific signature" and serves as an epigraph to all his scientific activities: "It would be advantageous for parasitology to further develop the universal concept of parasitic systems that reflects the unity of all parasitic organisms as an ecological category. This concept stimulates the exchange of ideas between traditional parasitology and microbiology and creates prerequisites for developing our knowledge of the general principles of parasitism as a form of existence of living organisms" (Balashov, 1991, p. 189). It is in the light of such a broad general parasitological concept that Balashov analyzed crucial problems of medical entomology, the scientific branch treating medically significant arthropods, including the parasite–host relationships of arthropods and terrestrial vertebrates. He authored more than 200 scientific papers and several monographs (Balashov, 1967; 1972a; 1979; 1982; 1983; 1998; 2009). The publication of each of his books was a major event in parasitology, and many of them are quite comprehensive and have been milestones. However, it is the reading of these publications in a continuous chronological sequence that gives a holistic impression of Balashov's scientific legacy, demonstrating long-term consistency in his progression from particular studies to multifaceted generalizations in evolutionary parasitology. He did not abandon a given problem after addressing another one. They remained within the scope of his interests, and their range was growing broader and more complex over time. Here we attempt to recapitulate the results of this process, which in itself is fairly instructive, especially for young researchers working in an era where we emphasize research on the molecular and genetic level and less on the function of whole organisms, populations and ecosystems. The main results and conclusions of Balashov's tremendous work will be described here using mainly his own words. Any explanatory remarks or comments will be avoided where possible since they appear inappropriate in this context, although some of Balashov's views and postulates are obviously open to debate (Korenberg, 1999; 2010). Explanations that may be required to increase the reader's understanding of the concepts, terms and thoughts of Yu. Balashov will be made by the authors in footnotes or in square brackets.

Biology and physiology of ticks

In the 1950s, Balashov initiated studies on elementary features of the biology and physiology of ixodid ticks (poorly known at that time), which was the basis for all his future research. The scope of the problems he addressed included the structure of tick mouthparts; the process of bloodsucking and changes in the integument during this process; the functions of dermal glands and adaptations to consuming large volumes of blood; the tick life cycle and changes in tick body weight in the course of bloodsucking and daily rhythmicity of tick detachment from the host after feeding; the structure of digestive organs as related to the process of digestion; excretory processes; gonotrophic relationships and spermatogenesis; and specific anatomical and physiological features of molting. The results of these studies provided a basis for the widely known monograph (Balashov, 1967) translated into English and published by the Entomological Society of America (Balashov, 1972a). This amazing monograph brought Balashov international recognition and became a desk book for several generations of medical entomologists worldwide. It is still an essential source for tick researchers today containing the precious results of countless studies in the laboratory and in the field. A special feature of his work is that it covered quite a large variety of argasid and ixodid species occurring in a huge area, in different climatic and biogeographical zones, the former USSR. He resumed, after about 20 years, in-depth studies on the structure of tick organs at an advanced methodological level. Together with his colleagues L. Amosova, V. Ivanov, S. Leonovich, and A. Reichel, he produced a series of publications on this matter, including the unique *Atlas of Electron-Microscopic Anatomy of Ixodid Ticks* (Balashov, 1979), which provided insight into specific features of different organs and mechanisms of their functioning in these arthropods. In one way or another, the results of these studies were also considered in Balashov's subsequent monographs (1982; 1998; 2009) as a factual basis for his theoretical generalizations. In particular, they allowed the conclusion that "the main difference [of digestion in argasid and ixodid ticks] to that in insects is that the host blood is digested mainly intracellularly, a process progressing slowly and asynchronously in different parts of the gut" (Balashov, 1999, p. 758). [He mentioned in an earlier publication (1972a, p. 272) that intracellular blood digestion in ticks was first described by Roesler (1934)]. This is also a highly relevant aspect when looking at ticks as vectors of pathogens.

Ixodid ticks take one blood meal in each postembryonic life stage. In contrast, argasid ticks have 2-4 nymphal instars with each taking a blood meal and also the adults feed several times. After feeding ticks pass through a series of different developmental phases, molting into a new phase after every next bloodmeal, or in case of the adult female sooner or later follower by oviposits. As a result, by feeding ticks in the laboratory Balashov was not only able to follow their complete life cycles but also to investigate all the various aspects of their biology in very different physiological states, an ideal basis for his comprehensive biological approach.

Beginning in the late 1950s, Balashov's attention was consistently attracted to problems of the ecology of ticks including their mobility, periodization of life cycles, and the effect of environmental factors on their abundance. The results of his first studies on the dynamics of reserve nutrients and the physiological age of activated unfed ticks provided a stimulus for research on improving methods for physiological age determination and analyzing population age structure as a whole, which was carried out by Balashov himself and other specialists for many years. Based on the analysis of specific ecological features and genetic differences between natural populations of *Ornithodoros tartakovskyi* ticks, Balashov noted that the results "...make one refuse to acknowledge that gene flow plays a significant role in the maintenance of species unity". Taking into account the low mobility of this tick and its hosts, he concluded that "elementary populations[1] occupy a space confined to a group of host burrows and may be largely isolated from neighboring populations located only a few hundred meters away". "Various landscape-geographic barriers creating unsuitable conditions for ticks break up the species range into a number of population groups in isolation from each other" (Balashov; 1971, p. 1800). He was the first to denote the hierarchy of units in the spatial population structure of certain tick species and to indicate the real landscape features (shown in maps) allowing these units to be distinguished.

Parasite hosts as ecological niches

In this regard, it is quite logical that, from the late 1970s to the early 1980s, the need arose for Balashov to contemplate the diverse relationships between bloodsucking arthropods and their hosts. Developing Beklemishev's (1970) ideas on the evolution of parasite–host relationships and types of life schemes in bloodsucking and parasitic arthropods further, Balashov proposed his own concept of the origin and development of parasitism in different groups of arthropods, which we refer to as the evolutionary polyphyletic concept. Its essence

[1] An elementary population (or core population) is an element of the spatial structure of tick populations. This is an area with a higher number of ticks than the area that surrounds it. The population as a whole may have more than one core.

is that "... a long co-existence of arthropods and terrestrial vertebrates implies the possibility of emergence and dissolution of various forms of symbiotic relationships between them, including parasitism. The diversity of types of parasitism in insects and mites associated with its repeated and independent appearance. In particular therefore, blood sucking occurred in different families independently…" (Balashov, 2006a, p. 420; 2006b, p. 929). Based on this premise, Balashov (1982) proposed his "classification system of the types of parasitism in arthropods", which he continued to improve conceptually and terminologically over almost 40 years. In the final variant, this system included seven groups with different types of parasitism: (1) micro predators (free-living bloodsuckers), (2) nest-burrow ectoparasites with short feeding(s), (3) temporary ectoparasites with long feeding(s), (4) permanent ectoparasites, (5) intracutaneous parasites, (6) caviar parasites [egg or aviary], and (7) tissue parasites (Balashov, 2009, p. 33). He emphasized that "almost all conceivable instances of transitions from predation and schizophagy[2] to facultative ectoparasitism and from ectoparasitism to endoparasitism have occurred among arthropods parasitizing terrestrial vertebrates." Thus, there are no distinct boundaries between the different types of parasitism.

The term "type of parasitism" is regarded synonymous to the terms "type of life scheme" (Balashov, 1991, p. 190) and "life form" or "ecological group" (Balashov, 2006b, p. 930). At the same time, "it should be remembered that as ecological categories, these terms can combine species from phylogenetically unrelated taxa. Similar life patterns in many cases arose in the process of parallel evolution, although in some taxa comparative parasitological series may coincide with phylogenetics" (Balashov, 1991, p. 190). According to his ideas "... the concept of the type of parasitism is in no way identical to the concept of ecological niche[3], but much wider" (Balashov, 2002, p. 935), since each part of the host organism can be an ecological niche, which is mastered by certain parasites (Balashov, 2005, p. 444), and "the host organism is a set of many ecological niches for different species of parasites" (Balashov, 2009, pp. 227–228).

Evolution of hematophagy

Analyzing the relationships of bloodsucking arthropods with vertebrates, Balashov arrived at the conclusion that "hematophagy has evolved independently and asynchronously in several arthropod orders, families, and even genera" (Balashov, 1999, p. 759), "...but once emerged, it has largely determined subsequent directions in the evolution of bloodsuckers and particularly their co-evolution with vertebrate hosts" (pp. 751–752). "For the occurrence of hematophagy [among arthropods], the most important representatives had morphophysiological preadaptations to blood nutrition" (p. 758). "The necessity of piercing the skin of vertebrates and sucking the blood caused the convergent development of the oral apparatus of the piercing-sucking or cutting-sucking type" (p. 753). "Hematophagy in ixodid ticks could have arisen as early as 150–200 million years ago during the Triassic; in some groups of insects (lice, biting midges, fleas), during the Jurassic (145–200 million years ago); and in mosquitoes and flies (horseflies in particular), only during the Paleogene" (23–66 million

---

[2] Schizophagy: the ability to eat decaying animal or vegetable residues or suck out the contents of recently died arthropods, etc.

[3] In ecology, the concept of "ecological niche" is a set of all environmental factors that determine the possibility of the existence of a given species in nature. According to Balashov (2009, p. 351), "ecological niche determines the place and role of a parasite in the community. It includes parameters of the parasite's habitats, its interactions with the host organisms, and the external environment".

years ago) (p. 751). According to Balashov (2009, p. 347) the concept of parasitism means "permanent or temporary cohabitation of different species, in which one of them uses another species (host) as a source of food or habitat". Moreover, "the categories of parasitism and hematophagy applied to Insecta and Acarina do not always coincide" (Balashov, 2009, p. 210), because "hematophagy is not necessarily associated with parasitism. Among Diptera it [hematophagy] is peculiar to many groups actively attacking vertebrates but not living on their body. In turn, not all parasitic arthropods are hematophagous and many feed on wool, feathers, skin particles, secretions of skin glands and other parts of the host organism" (Balashov, 1999, p. 761). "Parasitism apparently evolved repeatedly and independently in different groups of the Acarina, the initial stages of transition to parasitism progressing in the dwellings of prospective hosts" (Balashov, 2000, p. 937). In Balashov's opinion, free-living bloodsuckers are not "fully functional components of parasite communities"[4] (Balashov, 2002, p. 936). He particularized the vague notion of "parasite specificity" and, in addition to conventional host specificity, introduced new concepts of phylogenetic and ecological specificity, substantiating them as follows: "The specificity of parasites in the choice of hosts may be conditioned both by affiliation of the latter with certain taxonomic groups (phylogenetic specificity) and by ecological factors, in cases where a parasite can live on unrelated host species inhabiting the same biotopes or occupying similar ecological niches[5] (ecological specificity)" (Balashov, 2001, p. 475). These considerations led Balashov to analyze the origins of parasitic and bloodsucking arthropods and their coevolution with host species, which explained almost any of their morphological and biological features as well as the underlying speciation processes. This problem was analyzed in most detail for the group of ixodid ticks. In Balashov's opinion, "proixodids might have initially fed on various arthropods or their dead bodies and then shifted to hematophagy on vertebrates" (Balashov, 2006a, p. 416). "Paleontological and zoogeographic data provide evidence for the Mesozoic origin of ixodid ticks" (Balashov, 1989, p. 457). "The common ancestral group of the Argasidae and the Ixodidae must have existed long before the Cretaceous", in the Early Mesozoic, and "...became segregated into an individual evolutionary branch in the Triassic" and "...transition to parasitism in the common ancestors of the recent Ixodidae and Argasidae could have occurred during the Late Paleozoic or Early Mesozoic (about 200–250 million years ago), under tropical climate conditions" (Balashov, 2004, pp. 913, 915, 919). "The parasitic relationships of the ancestors of the Ixodidae with mammals formed by the Middle Mesozoic or even earlier" (Balashov, 1989, p. 457). "At an early stage of its evolutionary development, after transition to hematophagy, the proixodoid lineage divided into two main branches: the ancestors of the Argasidae and the Ixodidae" (Balashov, 1999, p. 750). "Two recent genera, *Carios* and *Aponomma*[6], already existed as early as in the Cretaceous (65–100 million years ago), and species of the genera *Amblyomma, Ixodes*, *Hyalomma,* and *Ornithodoros* appeared during the Eocene (30–40 million years ago)" (Balashov, 2004, p. 913).

Thus, Balashov considered that the group of ixodid ticks had formed prior to the breakup of Pangaea into Gondwana and Laurasia. Judging from specimens found in Paleogene ambers, the formation of the genera *Amblyomma* and *Ixodes* also occurred before this

[4] Balashov (2009, p. 347) called the term "community of parasites" (parasitocenosis) as a set of parasitic individuals of various species living on one host individual.

[5] See note 3.

[6] *Carios* is an argasid genus or subgenus (depending on the taxonomic concept). Some species of the former ixodid genus *Aponomma* have been placed into the genus *Amblyomma,* and the remaining Australian *Aponomma* species, into the genus *Bothriocroton* (Klompen et al., 2002).

breakup, no less than 180–190 million years ago. “The genera *Haemaphysalis* and *Dermacentor* apparently evolved after the breakup of the single landmass into the northern and southern halves, with the former genus being formed under conditions of moist subtropical climate and forests of Southeastern Asia, and the latter in a temperate climate of steppe or mountain landscapes. The genera *Rhipicephalus* and *Hyalomma* appear to be younger, with the former having evolved in Africa during the period of its isolation in the Paleogene and the latter in the deserts of Western Asia prior to the formation of its land connections with Africa and the Arabian Peninsula” (Balashov, 1993, p. 935). Polyphagy[7] and oligophagy of ixodids have caused limited or no phylogenetic parallelism with hosts in their evolution. “Restrictions in the distribution of some species are usually explained by the direct effect of unfavorable environmental factors on the non-parasitic phases rather than by the absence of suitable hosts” (Balashov, 1989, p. 457). The analysis of parasite-host relations in other arthropod groups eventually led Balashov to an extremely important conclusion, which is formulated as follows: “Coevolution in its pure form is peculiar only in a few taxa of parasitic arthropods” and, therefore, “... it has been an important, but not the only way of their speciation” (Balashov, 2009, p. 230).

Reproductive isolation of ticks

A few of Balashov’s publications are devoted to the problem of interspecific hybridization and reproductive isolation in some ixodid tick species (Balashov et al., 1998), still a very relevant topic. It has been established experimentally that hybridization can happen between closely related species of ticks. In particular, hybrid female ticks of the ricinus/persulcatus group of the first generation (F1) oviposited after engorgement, but the next generation (F2) did not produce fertile offspring. According to Balashov (1998), there is reproductive isolation, which is due to the genetic incompatibility of ticks of different species.

Natural focality of diseases

The implications drawn from all the above accounted for Balashov’s broad general parasitological and biocenological approach to the problem of the natural focality of diseases, which always remained in the focus of his attention. Balashov’s particular contribution to the study of the epizootiology of various arthropod-borne pathogens and their invasions is described in his last monograph (Balashov, 2009). Here we limit ourselves to considering only some of his general conclusions, definitions, and concepts that we regard as fundamentally important. Unfortunately, they are often disregarded in papers today. Balashov’s initial premise, formulated more than 45 years ago, was that “a focus of infection is a fine self-regulating system whose individual components are connected by feedback loops” (Balashov, 1972b, p. 175). Having analyzed feedback connections in an ixodid tick-vertebrate parasitic system, he arrived at the conclusion that “the high stability of such systems is attributable to moderate intensity of immune reactions in the hosts and relatively low numbers of ticks feeding on them” (Balashov, 1992, p. 185). He further explains that this stability “is provided by complex parasite–host interactions at the stage of feeding. As a result of such interactions, the vertebrate host is sensitized to antigens of vector saliva and develops anti-tick resistance. In nature, however, the main hosts do not have absolute resistance, despite regular contact with ticks” (p. 194). Such balanced relationships also prevail between ixodid ticks and

[7] In this context, polyphagy means that there are many different hosts, which is characteristic of at least some parasitic stages in the life cycle of all members of given genus or a particular species.

agents of transmissible infections, so that “pathogens cause minimum harm to tick vectors and can persist in their bodies almost lifelong, retaining the ability to be transmitted both to vertebrate hosts and within the tick population” (Balashov, 1995, p. 337). Furthermore, “the eventual location of microorganisms in certain organs or cells of the vector depends on the possibility for them to penetrate the system of organ envelopes and membranes as well as on the suitability of certain cells for the existence of those pathogens” (Balashov, 1984b, p. 30). “Actually, ixodid ticks can be part of several different natural foci within one ecosystem” (Balashov, 1972a, p. 338), but the circle of tick hosts is wider than the circle of animals that are susceptible[8] [without the influence of any other factors] to a particular pathogen (Balashov, 1972b). Vectors of infection as well as reservoir hosts of pathogens may be of different levels: principal (main), accessory (secondary), or incidental. It was very timely that Balashov (2009) once again made a point of these elementary notions of epizootiology, which had almost fallen into oblivion.

“Several conditions must be met to join a new parasitic community: First, the establishment of contact with a host; second, morphophysiological suitability of the host for the parasite; and third, the ability of the parasite to occupy its ecological niche and coexist with other arthropod species living on the same host. The results of these interactions determine the specific occurrence in nature of certain parasite species. Violation of one of these conditions prevents the colonization of a new host” (Balashov, 2002, p. 938). Therefore, “even in cases of frequent transcontinental transfer of ticks by birds migrating between Europe, Africa, and Asia, migrants are usually incapable of establishing themselves in new regions” (Balashov, 2004, p. 917). Here, these words concern arthropod vectors, but they are equally applicable to agents of infections and invasions with natural focality.

Today, despite the distinct progress in our knowledge of ticks and tick-borne pathogens we still cannot but agree with Balashov’s statement made more than 35 years ago: “Unfortunately, we are still very far from understanding the holistic picture of the complex interactions of pathogens of vector-borne infections with the arthropod vectors, which ultimately determine the possibility of further circulation of the pathogenic agent in nature or its death in the deadlock of infection” (Balashov, 1984a, p. 334).

Obviously, Balashov’s scientific legacy includes ideas that can serve as starting points for further research on the problems of medical entomology and therefore deserve in-depth and comprehensive ongoing analysis.

ACKNOWLEDGEMENTS

The authors express their deep gratitude to Professor Pat Nuttall (Department of Zoology, University of Oxford, UK) for constructive advice on the structure of the article.

REFERENCES

Balashov Yu.S. 1967. Bloodsucking Ticks (Ixodoidea) – Vectors of Diseases of Man and Animals. Leningrad, Nauka, 319 p. [in Russian]

Balashov Yu.S. 1971. Genotypic differences between natural populations of *Ornithodoros tartakovskyi* ticks (Ixodoidea, Argasidae). Zoologichesky Zhurnal 50 (12): 1795–1802. [in Russian].

Balashov Yu.S. 1972a. Bloodsucking ticks (Ixodoidea) – vectors of diseases of man and animals. Miscellaneous Publications of the Entomological Society of America 8 (5): 159–376.

[8] The term “susceptibility” in the biological and medical literature means the ability of a given host species to respond to the introduction of a pathogen by the development of an infectious process, regardless of its outcome (Kucheruk, Rosický, 1983).

Balashov Yu.S. 1972b. Pathogenicity of transmissible disease agents for arthropod vectors. In: Petrishchev PA (ed.) Achievements and Prospects for Future Development of the Theory of Natural Focality of Human Diseases. Moscow, Meditsina, 162–179 pp. [in Russian].

Balashov Yu.S. (ed.) 1979. Atlas of Electron-Microscopic Anatomy of Ixodid Ticks. Leningrad, Nauka, 256 p. [in Russian].

Balashov Yu.S. 1982. Parasite-Host Relationships of Arthropods with Terrestrial Vertebrates. Leningrad, Nauka, 316 p. [in Russian].

Balashov Yu.S. (ed.) 1983. An Atlas of Ixodid Tick Ultrastructure. Translation Special Publication of the Entomological Society of America, Maryland, 289 p.

Balashov Yu.S.1984a. Yevgeny N. Pavlovsky's ideas of modern parasitology. Zoologichesky Zhurnal 63 (3): 325–337 [in Russian].

Balashov Yu.S. 1984b. Role of specific morphological features of bloodsucking arthropods in transmission of infectious agents. Parazitologicheskii Sbornik (Collected Papers in Parasitology). Leningrad, Nauka 32: 22–42 [in Russian].

Balashov Yu.S. 1989. Coevolution of ixodid ticks and terrestrial vertebrates. Parazitologiya 23 (6): 457–468 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/1989/prz_1989_6_1_Balashov.pdf

Balashov Yu.S. 1991. The significance of V.N. Beklemishev's concepts of parasitic systems and ecological groups of species for the development of parasitology. Parazitologiya 25 (3): 185–195 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/1991/prz_1991_3_1_%D0%92alash%D0%BEv.pdf

Balashov Yu.S. 1992. Peculiarities of the parasitic system ixodid tick–vertebrate animal. Parazitologiya 26 (3): 185–197 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/1992/prz_1992_3_1_%D0%92alash%D0%BEv.pdf

Balashov Yu.S. 1993. Importance of continental drift in the distribution and evolution of ixodid ticks. Entomologicheskoe Obozrenie 72 (4): 929–936 [in Russian]. [Balashov Yu.S., 1994. Importance of continental drift in the distribution and evolution of ixodid ticks. Entomological Review 73: 42–50.]

Balashov Yu.S. 1995. Relationships of ixodid ticks (Ixodoidea) with agents of transmissible diseases of vertebrates. Parazitologiya 29 (5): 337–352 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/1995/prz_1995_5_1_Balashov.pdf

Balashov Yu.S. 1998. Ixodid Ticks: Parasites and Vectors of Infections. St. Petersburg, Nauka, 287 p. [in Russian].

Balashov Yu.S. 1999. Evolution of haematophagy in insects and ticks. Entomologicheskoe Obozrenie 78 (3): 749–763 [in Russian]. [Balashov Yu.S.: 1999. Evolution of Haematophagy in Insects and Ticks. Entomological review 79 (8): 943–954.]

Balashov Yu.S. 2000. Evolution of nidicolous parasitism in insects and acarines. Entomologicheskoe Obozrenie 79 (4): 925–940 [in Russian]. [Balashov Yu.S. 2000. Evolution of nidicolous parasitism in insects and acarines. Entomological review 80 (9): 1103–1114.]

Balashov Yu.S. 2001. Specificity of host–parasite relations between arthropods and terrestrial vertebrates. Parazitologiya 35 (6): 473–489 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/2001/prz_2001_6_1_Balashov.pdf

Balashov Yu.S. 2002. Species diversity of insect and acarine parasite communities on mammalian hosts. Entomologicheskoe Obozrenie 81 (4): 930–943 [in Russian]. [Balashov Yu.S. 2002 Species diversity of insect and acarine parasite communities on mammalian hosts. Entomological review 82 (8): 1035–1046.]

Balashov Yu.S. 2003. Academician E.N. Pavlovsky's school of thought in parasitology in the Zoological Institute RAS. Parazitologiya 37 (4): 249–258 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/2003/prz_2003_4_1_Balashov.pdf

Balashov Yu.S. 2004. The main trends in the evolution of ticks (Ixodida). Entomologicheskoe Obozrenie 83 (4): 909–923 [in Russian]. [Balashov Yu.S. 2004. The main trends in the evolution of ticks (Ixodida). Entomological review 84 (7): 814–824.]

Balashov Yu.S. 2005. Ecological niches of ectoparasites. Parazitologiya 39 (6): 441–456 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/2005/prz_2005_6_1_Balashov.pdf

Balashov Yu.S. 2006a. The origin and evolution of parasitism on terrestrial vertebrates in insects, mites, and ticks. Parazitologiya 40 (5): 409–424 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/2006/prz_2006_5_1_Balashov.pdf

Balashov Yu.S. 2006b. Types of parasitism of acarines and insects on terrestrial vertebrates. Entomologicheskoe Obozrenie 85 (4): 918–936 [in Russian]. [Balashov Yu.S. 2006b. Types of parasitism of acarines and insects on terrestrial vertebrates. Entomological review 86 (8): 957–972. https://doi.org/10.1134/S0013873806080112]

Balashov Yu.S. 2009. Parasitism of Ticks and Insects on Terrestrial Vertebrates. St. Petersburg, Nauka, 358 p. [in Russian].

Balashov Yu.S., Grigorieva L.A., Oliver J. 1998. Reproductive isolation and interspecific hybridization of ixodid ticks of the *I. ricinus – I. persulcatus* group (Acarina, Ixodidae). Entomologicheskoe Obozrenie 77 (3): 713–722 [in Russian].

[Balashov Yu.S., Grigorieva L.A., Oliver J. 1998. Reproductive isolation and interspecific hybridization of ixodid ticks of the *I. ricinus – I. persulcatus* group (Acarina, Ixodidae). Entomological review 78 (4): 500–508.]

Balashov Yu.S., Gutsevich A.V., Derbeneva-Ukhova V.P., Shipitsyna N.K. 1968. Medical and veterinary entomology in the USSR. Entomologicheskoe Obozrenie 47 (2): 298–316 [in Russian].

Beklemishev V.N. 1970. Biocenological Foundations of Comparative Parasitology. Moscow, Nauka, 502 p. [in Russian].

Filippova N.A. 2013. Yuri Sergeevich Balashov, 25 December 1931–28 September 2012. Journal of Parasitology 99 (5): 927–929. https://www.jstor.org/stable/41982118

Klompen H., Dobson S.J., Barker S.C. 2002. A new subfamily, Bothriocrotoninae n. subfam., for the genus *Bothriocroton* Keirans, King & Sharrad, 1994 status amend (Ixodida: Ixodidae), and the synonymy of *Aponomma* Neumann, 1899 with *Amblyomma* Koch, 1844. Systematic Parasitology 53: 101–107. https://doi.org/10.1023/A:1020466007722

Korenberg E.I. 1999. Book review: Yu.S. Balashov, Ixodid Ticks: Parasites and Vectors of Infections, Nauka, 1998. Zoologichesky Zhurnal 78 (11): 1257–1259 [in Russian].

Korenberg E.I. 2010. Book review: Yu.S. Balashov, Parasitism of Ticks and Insects on Terrestrial Vertebrates, Nauka, 2009. Zoologichesky Zhurnal 89 (1): 121–125 [In Russian].

Kucheruk V.V., Rosický B. 1983. Diseases with natural foci: basic terms and concepts. Journal of Hygiene, Epidemiology, Microbiology, and Immunology 27 (4)s: 353–364.

Medvedev S.G. 2012. In memoriam of Yuri Sergeevich Balashov, 1931-2012. Acarina 20 (2): 199–200. https://elib.utmn.ru/jspui/bitstream/ru-tsu/12774/1/Medvedev2012_Balashov_orbituary.pdf

Medvedev S.G., Filippova N.A., Leonovich S.A. 2013. In memory of Yuri Sergeevich Balashov (25. XII. 1931–28. IX. 2012). Parazitologiya 47 (3): 185–196 [in Russian]. https://www.zin.ru/journals/parazitologiya/content/2013/prz_2013_3_1_Medvedev.pdf

Pavlovsky E.N. 1939. On the natural foci of infectious and parasitic diseases. Bulletin of the USSR Academy of Sciences 10: 98–108 [in Russian].

Pavlovsky E.N. 1966. Natural Nidality of Transmissible Diseases. Urbana, Illinois, University of Illinois Press, 261 p.

Roesler R. 1934. Histologische, physiologische und serologische. Untersuchungen über die Verdauung bei der Zeckengattung *Ixodes* Latr. Zeitschrift für Morphologie und Ökologie der Tiere 28 (3): 297–317. https://www.jstor.org/stable/43261463

ПРОФЕССОР ЮРИЙ СЕРГЕЕВИЧ БАЛАШОВ: НАСЛЕДИЕ ВЫДАЮЩЕГОСЯ ПАРАЗИТОЛОГА

Э. И. Коренберг, О. Кал

Ключевые слова: паразитология, медицинская энтомология, экология, Argasidae, Ixodidae, клещи, природный очаг инфекции

РЕЗЮМЕ

Статья посвящена научным достижениям выдающегося паразитолога Ю.С. Балашова. Это не биография. Цель данной статьи – осветить некоторые аспекты научного наследия Ю.С. Балашова, особенно те, которые, по мнению авторов, наиболее важны для интернационального читателя. Это должно привлечь внимание исследователей разных стран к различным научным трудам и концепциям, часть которых была опубликована только на русском языке, и способствовать их более широкому обсуждению. Масштаб научных интересов Балашова был поразителен, хотя основное внимание он уделял исследованию аргасовых и иксодовых клещей (Argasidae и Ixodidae). Главные результаты и заключения его обширных работ описаны в основном с использованием его собственных слов и выражений. Авторам принадлежат только некоторые объяснения, предназначенные для лучшего понимания читателем концепций, терминов и мыслей Ю.С. Балашова.