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Currently important pathogenic *Listeria* species affecting animals and birds (review)

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ABSTRACT

Listeriosis is one of the most severe gastrointestinal diseases in the world. *Listeria* affect different groups of animals and birds. The pathogen has been detected in meat, milk, fish and fish products. The disease shows spring and autumn seasonality. It has been reliably established that *Listeria monocytogenes* is ubiquitous in the environment. *Listeria monocytogenes* is a facultative intracellular pathogen. Infection with *Listeria monocytogenes* causes an invasive disease in animals and humans, which is transmitted via the fecal-oral route from an animal to a human, from a mother to a fetus. The pathogenesis of *Listeria* infection has been well studied. The gastrointestinal tract is the site of the pathogenic *Listeria* species transit and spread. The infection incubation period is 20–30 days in animals and humans. The clinical course in different animal species, including birds, has a number of specific features. *Listeria* can cross the intestinal, placental and blood-brain barriers. The manifestations of listeriosis include encephalitis, meningitis, gastritis, meningoencephalitis, mastitis, abortions, endometritis, etc. Pathogenic *Listeria* species show hemolytic activity which non-pathogenic species (except *Listeria seeligeri*) lack. The review presents the up-to-date information on the classification of *Listeria*, the pathogenicity factors of *Listeria monocytogenes* as the major pathogen, the mechanisms of *Listeria* infection development in different animal species.

Keywords: review, *Listeria* spp., pathogenicity, biosafety, animals, birds, antibiotic resistance

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Актуальные патогенные виды листерии животных и птиц (обзор)

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РЕЗЮМЕ

Листериоз является одним из наиболее тяжело протекающих заболеваний пищеварительного тракта во всем мире. Листерии поражают различные группы животных и птиц. Возбудитель выявлен в мясе, молоке, рыбе и рыбопродуктах. Отмечается сезонность заболевания в весенний и осенний периоды. Достоверно установлено, что бактерия *Listeria monocytogenes* свободно обитает в окружающей среде. *Listeria monocytogenes* является факультативным внутриклеточным патогеном, заражение которым у животных и людей приводит к инвазивному заболеванию, передающемуся фекально-оральным путем от животного к человеку, от матери к плоду. Патогенез листериозной инфекции хорошо изучен. Желудочно-кишечный тракт является местом транзита и распространения патогенных листерий. Инкубационный период листериозной инфекции длится 20–30 дней у животных и людей. Клиническое течение у различных видов животных, и в том числе птиц, имеет ряд особенностей. Листерии успешно преодолевают кишечный, плацентарный, гематоэнцефалический барьеры. При листериозе отмечается энцефалит, менингит, гастрит, менингоэнцефалит, маститы, аборты, эндометриты и др. Патогенные виды листерий обладают гемолитической активностью, которая отсутствует у непатогенных видов (исключение – *Listeria seeligeri*). В обзоре представлена актуальная информация о классификации листерий, факторах патогенности *Listeria monocytogenes* как основного патогена, механизмах протекания листериозной инфекции у различных видов животных.

Ключевые слова: обзор, *Listeria* spp., патогенность, биобезопасность, животные, птицы, антибиотикорезистентность

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INTRODUCTION

Microorganisms of the genus *Listeria* belong to the family *Listeriaceae*, the order *Bacillales*, the class *Bacilli* and the phylum *Firmicutes*. *Listeria* is a gram-positive bacterium genetically related to *Clostridium*, *Enterococcus*, *Staphylococcus*, *Streptococcus* and *Bacillus*. *Listeria* spp. are facultative anaerobic rods with a size of 0.4 × 1–1.5 μm, which do not form spores, have no capsule and are motile at 10–25 °C [1]. *Listeria* spp. are isolated from various environmental sources such as soil, water, wastewater, animal and human feces, food products. A number of researchers have found that the natural habitat of the bacterium is a decaying plant substrate. Transmission occurs through the fecal-oral route. In rural areas, ruminants are the main vectors of *Listeria* [2, 3, 4]. The genus *Listeria* is currently represented by the following species: *L. monocytogenes*, *L. innocua*, *L. ivanovii* (formerly known as *L. monocytogenes* serotype 5), *L. farberi*, *L. seeligeri*, *L. welshimeri*, *L. ilorinensis*, *L. rocourtiae*, *L. weihenstephanensis*, *L. marthii*, *L. grandensis*, *L. riparia*, *L. cossartiae*, *L. fleischmannii*, *L. portnoy*, *L. rustica*, *L. immobilis*, *L. booriae*, *L. thailandensis*, *L. goaensis*, *L. costaricensis*, *L. floridensis*, *L. aquatica*, *L. grayi*, *L. valentina*, *L. newyorkensis*, *L. swaminathanii*, *L. cornellensis* [5]. Two species, *L. ivanovii* and *L. monocytogenes*, are pathogenic for humans and animals [6]. The official discovery of *Listeria* was in 1924, when a group of researchers (E. G. D. Murray, R. A. Webb, M. B. R. Swann) in Cambridge, England, isolated *L. monocytogenes* as the etiological agent of a septicemic disease affecting rabbits and guinea pigs [7]. The first case of human listeriosis was reported in Denmark in 1929. *L. ivanovii* was first isolated from lambs in Bulgaria in 1955 [8]. Cases of *L. ivanovii* infection are rare; the bacteria of this species are mainly isolated from abortions and neonatal septicemias in sheep and cattle [9, 10, 11]. Although *L. seeligeri* is a non-pathogenic *Listeria* species, one human case of infection with this bacterium has been reported [12, 13].

Listeria spp. are widespread in nature, they have been isolated from more than 90 animal species, as well as from plants and a broad range of food products. These bacteria can persist in the animal body for a long time. Suppressing the growth of *Listeria* in the ready-to-eat products is still a challenge. The examination of the biological and environmental characteristics of *Listeria* is aimed at the prevention of *Listeria* infection and the control of this important food pathogen.

The novelty of the study is the systematization of the up-to-date data on the biological properties and classification of *Listeria*. The specific features of listeriosis in livestock and poultry are presented.

The work was carried out using analytical research methods and the RSCI, Scopus, Web of Science, Library Genesis, Sci-Hub, Google Scholar, PubMed, Cyberleninka databases.

The purpose of the review was to analyze and systematize current knowledge about pathogenic *Listeria* species, the classification of *Listeria*, the mechanism of the disease development and characteristic features of *Listeria* infection in different animal and bird species.

CLASSIFICATION AND BIOLOGICAL PROPERTIES OF *LISTERIA*

The bacteria of the genus *Listeria* are found on all continents. Soft cheeses and milk products, sausages, pastes, salads, smoked fish and, as a rule, ready-to-eat chilled industrially-made products are most often contaminated [14, 15, 16, 17]. *Listeria* is well adapted to survive on the surfaces of the food processing equipment. For example, *Listeria* tolerates high salt concentrations (> 10%) and relatively low pH values (< 5.0) and is able to reproduce at low temperatures [18, 19]. Listeriosis shall be differentiated from rabies, influenza, brucellosis, pasteurellosis, toxoplasmosis.

Pathogenic *Listeria* species show hemolytic activity which non-pathogenic species (except *L. seeligeri*) lack. The hemolysin gene (*hly*) has a key role in cell destruction [20]. The biological characteristics of some species of the genus *Listeria* are presented in Table 1 [21].

The classification of *L. monocytogenes* is based on the structure of the somatic (O) and flagellar (H) antigens, and all members of this species are divided into the following serovars: 1/2a, 1/2b, 1/2c, 3a, 3b, 3c, 4a, 4b, 4c, 4d, 4e and 7 [22].

Listeria monocytogenes is a facultative intracellular pathogen. Infection with *L. monocytogenes* causes an invasive disease in animals and humans, which is transmitted via the fecal-oral route from an animal to a human, from a mother to a fetus [23]. The pathogenicity factors of this bacterium species are shown in Table 2 [21].

Most of the information on the pathogenesis of listeriosis has been obtained on the basis of the interpretation of epidemiological, clinical and histopathological data in experimental infections in animals. The gastrointestinal tract is the main site of the entry and spread of pathogenic *Listeria* [17]. It is reported that the increased acidity of gastric juice can destroy a significant amount of *Listeria*. It is well known that *Listeria* infection incubation period in animals and humans is 20–30 days. *Listeria* spp. penetrating through the intestinal barrier are carried by lymph and blood to the mesenteric lymph nodes, liver, spleen [24].

Table 1
Biological characteristics of some species of the genus *Listeria* [21]

Characteristics		*L. monocytogenes*	*L. innocua*	*L. ivanovii*	*L. seeligeri*	*L. welshimeri*	*L. grayi*
β-hemolysis		+	–	+	+	–	–
CAMP test (*Staphylococcus aureus*)		+	–	–	+	–	–
CAMP test (*Rhodococcus equi*)		±	–	+	–	–	–
Production of acid from	mannitol	–	–	–	–	–	+
	α-methyl-D-mannoside	+	+	–	–	+	+
	L-rhamnose	+	d	–	–	d	±
	soluble starch	–	–	–			+
	D-xylose	–	–	+	+	+	–
Hippurate hydrolysis		+	+	+			–
Nitrate reduction		–	–	–			±
Pathogenicity for mice		+	–	+	–	–	–

"+" – 90% or more of the strains are positive; "–" – 90% or more of the strains are negative; d – 11–89% of the strains are positive;
"±" – a variable variant; the absence of a result means that no tests for this parameter have been carried out.

An experimental study in mice (intravenous administration) has revealed that *L. monocytogenes* is rapidly removed from the bloodstream by resident macrophages of the spleen and the liver [25]. The major bacterial load is located in the liver, in which Kupffer cells are active. These macrophages destroy most of the engulfed bacteria. A number of authors believe that Kupffer cells initiate the activation of anti-listerial immunity by inducing the antigen-dependent proliferation of T lymphocytes and cytokine secretion [26]. Also, various scientific papers note the partial survival of *Listeria* cells after attack by macrophages, which actively grow over the next 2–5 days [27, 28, 29]. *Listeria* cells move by direct passage from hepatocyte to hepatocyte and disseminate in the liver parenchyma without coming into contact with the humoral immune system. The authors conclude that this explains the levelling of the role of antibodies in the antibody-*Listeria* interaction [30]. *L. monocytogenes* is a multi-system pathogen that affects a wide variety of animal and human tissues.

Table 2
Pathogenicity factors of *Listeria* monocytogenes [21]

Protein	Molecular weight, kDa	Gene	Function
prfA	27	*prfA*	Regulation of virulence gene transcription
Listeriolysin O	58	*hly*	Lysis of primary and secondary phagosomes
PICA (phosphatidylinositol-specific phospholipase C)	36	*plcA*	Phagosome lysis
Lecithinase	33	*plcB*	Lysis of secondary phagosome
Metalloprotease	57	*mpl*	Post-translational modification of lecithinase
ActA	67	*actA*	Polymerization of actin
Internalin, *inlB*	88.65	*inlA, inlB*	Induction of phagocytosis

BOVINE LISTERIOSIS

Cattle account for a greater number of pathogenic *Listeria* detections reported worldwide [31]. Bovine listeriosis most commonly manifests itself as encephalitis; miscarriages, septicemia with miliary abscesses are also noted. Foodborne transmission is the main mode of infection in cattle, particularly as a result of low-quality silage feeding, drinking of contaminated water. After ingestion, *Listeria* cells are disseminated via hematogenous spread to the viscera, nervous system and reproductive organs of pregnant cows. Another route of infection is through the abrasions of the skin or the conjunctiva during grazing or via the teats. When the central nervous system is affected, the pathological process localizes in the medulla oblongata and the pons [32, 33]. Damage to the respective nerve underlies the characteristic presentation: damage to the fifth cranial nerve (CN V) and the mandibular nerve leads to the inability to drink or eat and, consequently, to further disorders [34]; the sign of damage to CN IX and CN X is excessive salivation due to the swallowing difficulty; CN XII – the protrusion of the tongue; CN VIII – ataxia and circling, facial paralysis, including unilateral drooping of the lip, eyelid, ear; CN VI – strabismus. In advanced stages of the disease, the animal lapses into a coma and dies within a few days. Postmortem cerebral cortex lesions consist of the foci of necrosis infiltrated with neutrophils, macrophages, bacterial cells [35, 36]. Listeriosis shall be differentiated from rabies.

The genital form of listeriosis in cows presents as abortions in the last trimester of gestation. In case of fetal infection, newborn animals develop meningitis and subsequently die [37].

The authors also note the seasonality of bovine listeriosis, with the number of cases increasing in winter and spring and decreasing in summer [32].

PORCINE LISTERIOSIS

In pigs (the young ones), listeriosis most often manifests itself as septicemia and is less common than in other animal species. Encephalitis and miscarriages are rarely reported [38]. Hepatic necrosis is a characteristic morphological feature of listerial septicemia in newborn piglets [39, 40]. The first case of listeriosis in piglets was reported in Russia in 1936 by T. P. Slabospitsky, who named the pathogen *L. suis* [41]. In sows, *L. monocytogenes* localizes in the tonsils, from where it then enters the gastrointestinal tract. Porcine listeriosis cases are more frequently detected in winter and spring. The symptoms of central nervous system disturbance in young animals with listerial encephalitis are incoordination, weakness and apathy, followed by death. Meningoencephalitis in pigs is characterized by a sudden decrease in appetite, neurological disorders (trembling, partial paralysis, urinary incontinence, seizures), elevated body temperature [42]. Histopathological examination reveals severe monocytic infiltration, many blood vessels show perivascular constriction [43, 44]. The largest outbreak of listerial meningoencephalitis in pigs was reported in India, in which 27 of 75 pigs died [45].

OVINE LISTERIOSIS

Ovine listeriosis is caused by *L. monocytogenes* serotypes 1/2 and 3, as well as by *L. ivanovii*. Ovine listeriosis (circling disease) was first reported in New Zealand in 1929. The frequency of infection in sheep is higher (up to 30%) than in cattle (up to 15%). Ovine listeriosis manifests itself as encephalitis, gastrointestinal septicemia with hepatitis, splenitis, pneumonitis and abortions more commonly occurring in the last trimester of gestation. Encephalitis is the most common form of listeriosis diagnosed in sheep [46]. Lambs aged 5 weeks may develop septicemia, older lambs develop encephalitis. *Listeria* infection in adult sheep presents as a central nervous system disorder (meningoencephalitis), refusal to eat or drink, elevated temperature, teeth grinding, paralysis of the muscles of mastication, excessive salivation caused by the inability to swallow due to damage to the cranial nerve, circling movements (circling disease). In advanced stages, muscular incoordination develops, which is followed by the animal's inability to walk; death occurs within 2–3 days after the onset of the first symptoms. Histological examination reveals microgranulomas and microabscesses in the brainstem. Listerial encephalitis in sheep is most common in late autumn, winter and early spring. After hematogenous spread to the uterus, *L. monocytogenes* is detected within 48 hours in the fetus and the amniotic fluid. Initially, pregnant ewes develop purulent metritis. The clinical symptoms resolve after the abortion, and the ewes begin to feel much better. Morbidity in ewes ranges from 1 to 20%, with mortality of lambs being high. Septicemia is most frequent in newborn lambs and follows 2–3 days after oral infection. It is characterized by high temperature, loss of appetite, diarrhea. Death may occur as a result of extensive liver damage, pneumonia; the mortality rate is much lower for the septicemic form of listeriosis than for the encephalitic one. The factors contributing to the pathogenicity of *Listeria* are overcrowding, stress and feed quality [47, 48].

Listeria ivanovii is a recognized etiological agent of abortions in sheep [48]. Ovine listeriosis cases caused by *L. ivanovii* and characterized by abortions make up 8%. Factors predisposing to infection with *L. ivanovii* are the same as for *L. monocytogenes* and include stress, decreased immunity, feeding of poor-quality feed, contact with infected animals, etc. [49, 50].

As a preventive measure, vaccination with live attenuated strains of *L. monocytogenes* takes place. For example, in Germany and Greece, immunization of sheep with an attenuated vaccine based on serovars 1/2a and 4b reduced the incidence of listeriosis and abortions as compared with the control group. The results of field tests showed that the immunized ewes delivered more lambs free from *Listeria* (92.4 vs 69.7%) and of higher birth weight (2.2 vs 1.8 kg) than lambs from the control unvaccinated ewes. Besides, *L. monocytogenes* was not isolated from the milk samples from the vaccinated ewes, in contrast to the control group, in which *Listeria* was detected in 31.9% of milk samples [47].

In the event of an outbreak, several strains of the same or different *Listeria* serotypes may be isolated. DNA fingerprinting, phage typing, pyrolysis mass spectrometry are used as additional diagnostic methods to confirm the diagnosis [51].

CAPRINE LISTERIOSIS

Clinical listeriosis in goats is similar to that in sheep and manifests itself as septicemia, abortion, encephalitis [52]. The mechanism of the disease development is as follows: pathogenic *Listeria* penetrates into the goat body through the gastrointestinal tract, which leads to a transient bacteremia and further spread to the central nervous system, viscera, as well as to the placenta. Depression, decreased appetite and milk yield, diarrhea, elevated body temperature (41 °C) are the first signs of septicemia. In pregnant does, *L. monocytogenes* penetrates through the placenta into the fetus and subsequently causes late miscarriages [53].

A number of researchers note that meningoencephalitis is the most frequently reported form of listeriosis in goats. Early signs of listerial encephalitis in goats are excessive salivation, ear droop, tongue protrusion, absence of rumination [54]. Some researchers also point out that goats are more susceptible to listeriosis than sheep [52]. For example, during an outbreak of listeriosis in Iraq, the morbidity (30.0 vs 16.7%) and mortality (21.2 vs 14.9%) were higher in goats than in sheep [55]. *Listeria* isolations from goats are more frequent in winter and spring.

AVIAN LISTERIOSIS

Avian listeriosis was first reported in 1935 [56]. Wild ducks, turkeys, pheasants, geese are asymptomatic carriers of *Listeria*. Birds become *Listeria*-infected orally by pecking feces, soil, carcasses. Listeriosis is much less common in birds than in sheep, goats and cattle [57, 58, 59]. Listeriosis in birds can also develop as a secondary infection associated with viral diseases, as well as with salmonellosis, coccidiosis, worm infections, tick-borne encephalitis, lymphocytosis, enteritis and others that contribute to a decrease in immunity [60]. One of the distinguishing features of avian listeriosis is septicemia characterized by focal necrosis of viscera, particularly the liver and the spleen. At the same time, a number of authors note cardiac lesions such as vascular occlusion, pericarditis and increased amounts of pericardial fluid. The septicemic form of listeriosis produces the following conditions: splenomegaly, peritonitis, nephritis, ulcers in the ileum and caecum, necrosis of

the oviduct, generalized pulmonary edema, conjunctivitis, enteritis. In acute cases of the septicemic form of listeriosis, all internal organs are affected. Birds show practically no overt clinical signs other than emaciation and die on days 5–9 of the disease [59, 61].

Listerial meningoencephalitis is far less common in birds. It is characterized by the disturbances of the central nervous system such as incoordination, tremors, torticollis, dropped wings, unilateral or bilateral toe paralysis [62], which later lead to death. Necropsy reveals congestion and necrotic foci in the brain [63, 64].

Chicken embryos and young chickens are the most susceptible to listeriosis [61, 65, 66]. In day-old chicks, *Listeria* is most frequently detected in the caecum, liver, spleen and cloacal swab samples [63].

Thus, the incubation period of listeriosis depends on the overall clinical picture. In animals and birds, the infection occurs in the septicemic, encephalitic, abortive forms. Pathogenic *Listeria* species are important etiological agents of animal and bird diseases that lead to severe consequences and economic damage [67]. To date, listeriosis remains an urgent issue and does not receive sufficient coverage in the public space.

CONCLUSION

Listeria spp. are distributed globally in a wide variety of domestic and wild animals, as well as in humans, and possess a zoonotic potential.

The analysis of scientific publications has made it possible to summarize data on the mechanisms and routes of transmission, pathogenicity factors of *Listeria*, their serological diversity, localization in the body of susceptible animals, the forms of listeriosis in cattle, pigs, sheep, goats and birds.

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