

**БИОЛОГИЧЕСКИЕ ОСОБЕННОСТИ И МЕДИЦИНСКАЯ
ЗНАЧИМОСТЬ БАКТЕРИЙ РОДА *LISTERIA***

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**BIOLOGICAL FEATURES AND MEDICAL SIGNIFICANCE OF THE
LISTERIA BACTERIA**

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Резюме

Бактерии рода *Listeria* широко распространены в окружающей среде, выделяются из почвенных и водных экосистем, продуктов питания, объектов внешней среды, циркулируют в организме. Некоторые их виды, прежде всего, *L. monocytogenes*, являются патогенными для человека и животных. Экологическая пластичность, стрессоустойчивость и толерантность листерий обуславливает их способность переходить от сапрофитного к паразитическому образу жизни и снова реверсировать к сапрофитизму при попадании в окружающую среду и выживать при различных ее условиях. При этом выявлено, что после размораживания и последующего культивирования листерий на свежих питательных средах отмечается выраженный гетероморфизм популяции, в том числе образование клеток протопластного типа, L-форм и извитых клеток-ревертантов, что усложняет их обнаружение и типирование в размороженных пищевых продуктах и требует применения таких методов обнаружения бактерий, как ПЦР и ИФА.

Известно, что непатогенные листерии, а также патогенные микроорганизмы, образующие биоценоз с *L. monocytogenes*, могут служить резервуаром детерминант патогенности и резистентности и быть переданы патогенным листериям путем горизонтального переноса, что обуславливает появление новых более вирулентных и патогенных, а также резистентных к антибиотикам штаммов. Кроме того, важнейшим механизмом адаптации *L. monocytogenes* к неблагоприятным факторам окружающей среды является их способность к образованию биопленок, существенно повышающих выживаемость и устойчивость к дезинфектантам. Сравнительно высокое геномное сходство между *L. monocytogenes* и некоторыми непатогенными видами листерий, в том числе *L. innocua*, и зачастую их сосуществование в сходных экологических нишах, может предоставить возможность для переноса генов устойчивости или вирулентности и обуславливает возможность создания у *L. innocua* резервуаров генов устойчивости, которые могут передаваться бактериям *L. monocytogenes*. В то же время, возможна

передача генов патогенности от *L. monocytogenes* к *L. innocua*, что предопределяет появление атипичных гемолитических патогенных штаммов, которые, учитывая более широкое распространение *L. innocua* в окружающей среде, могут представлять большую опасность для человека и животных.

Увеличение роли листерий в структуре инфекционных патологий человека и животных, изменчивость их морфологических, культуральных и биохимических свойств, а также постоянная модификация поверхностных антигенов листерий предопределяет необходимость совершенствования диагностики листериоза и требует создания новых иммунобиологических препаратов и современных схем для выделения и идентификации различных видов листерий.

В настоящем обзоре рассматриваются современные представления относительно распространенности и биологических свойств *Listeria* spp., факторов вирулентности и патогенности *L. monocytogenes*, а также методов идентификации листерий разных видов.

Ключевые слова: бактерии, листерии, листериоз, *L. monocytogenes*, *L. Innocua*, патогенность.

Abstract

Bacteria of the genus *Listeria* are widely distributed in the environment; they are isolated from soil and water ecosystems, food products, environmental objects, and circulate *in vivo*. *L. monocytogenes* are pathogenic for animals and humans. The ecological plasticity, stress resistance and tolerance of *Listeria* determines their ability to switch from a saprophytic to a parasitic life cycle and survive under various environmental conditions. After thawing and subsequent cultivation of *Listeria* on fresh nutrient medium, a pronounced populational heteromorphism is noted: formation of protoplast-type cells, L-forms and convoluted revertant cells, which requires the use PCR and ELISA for bacteria detection.

It is known that non-pathogenic *Listeria*, as well as pathogenic microorganisms forming a biocenosis with *L. monocytogenes*, can serve as a reservoir of pathogenicity and resistance determinants and be transferred to pathogenic *Listeria* by horizontal transfer, which leads to the emergence of new, more virulent and antibiotic-resistant strains. In addition, the most important adaptation mechanism of *L. monocytogenes* to adverse environmental factors is their ability to form biofilms markedly enhancing survival and disinfectant resistance. The relatively high genomic similarity between *L. monocytogenes* and some non-pathogenic *Listeria* species and often their coexistence in similar ecological niches, may provide an opportunity for the transfer of resistance or virulence genes. At the same time, the transmission of pathogenicity genes from *L. monocytogenes* to *L. innocua* is also possible, which predetermines the appearance of atypical hemolytic pathogenic strains, which, given the greater environmental prevalence of the latter can pose a great danger to humans and animals.

The increasing role of *Listeria* in the pattern of human and animal infectious pathologies, the variability of their morphological, cultivable and biochemical properties, as well as the constant modification of the surface *Listeria* antigens underlies a need to improve listeriosis diagnostics and requires creation of new immunobiological preparations and modern regimens for isolation and identification of various *Listeria* types.

This review discusses current views on *Listeria spp.* prevalence and biological qualities, virulence and pathogenicity factors of *L. monocytogenes*, as well as methods for identifying different *Listeria* species.

Keywords: bacteria, *Listeria*, listeriosis, *L. monocytogenes*, *L. innocua*, *pathogenicity*.

1 **1 Introduction**

2 It is known that bacteria of the genus *Listeria* can cause listeriosis, a severe
 3 infectious disease of humans and animals characterised by polymorphic clinical
 4 manifestations, high mortality (up to 20-40% among adults and more than 50% in
 5 newborns) [28] and often complicated by meningoencephalitis [97]. At the same
 6 time, while previously only *L. monocytogenes* was considered pathogenic for
 7 humans, the literature has recently begun to describe cases of listeriosis infection
 8 caused by other *Listeria* species, including *L. ivanovii* [66], *L. seeligeri* [140], *L.*
 9 *innocua* [103], *L. welshimeri* [43], and *L. grayi* [150].

10 In general, it is currently accepted that *L. monocytogenes* is the etiological
 11 agent of listeriosis in humans and many vertebrate species, including birds, whereas
 12 *L. ivanovii* causes infections mainly in ruminants [106].

13 The epidemic situation of listeriosis worldwide continues to worsen due to a
 14 number of reasons, including the unique plasticity of listeria and its ability not only
 15 to persist but also to multiply in infected products even at low temperatures (+4 - +7
 16 °C, typical of a refrigerator) [120], acidic environments [124], high salt
 17 concentrations [88], and under oxygen-deficient conditions (in vacuum-packed
 18 finished products) [45].

19 At the same time, one unfavourable external factor can increase the resistance
 20 of *Listeria* to others. For example, incubation of *L. monocytogenes* at low
 21 temperatures was found to increase its resistance to osmotic stress [115]. Similarly,
 22 high salt concentrations in the incubation medium can lead to cross-protection of *L.*
 23 *monocytogenes* against other causes of cell death including high temperature, acidity
 24 and oxidative stress [128]. It has been revealed that cultivation of *L. monocytogenes*
 25 under conditions of vacuum packing and low temperature (+6°C), regardless of the
 26 nutrient substrate, causes the formation of a capsule in the pathogen and the
 27 emergence of resistance to some antibiotics from the penicillin group [41]. In
 28 addition, under unfavourable conditions, *Listeria* are capable of forming biofilms
 29 that attach to abiotic or biological surfaces and serve as a survival strategy for the
 30 bacteria, allowing them to persist in unfavourable conditions, being protected from

31 the human immune system and various environmental factors (ultraviolet light,
 32 acids, drying, salinity, antimicrobial agents, disinfectants) [46].

33 The extremely high tolerance of *L. monocytogenes* to stress conditions causes
 34 a serious problem of listeriosis in the food industry, and the increasing role of listeria
 35 in the structure of infectious pathologies of humans and animals predetermines the
 36 need to improve the diagnosis, prevention and sanitary and epidemiological
 37 surveillance of listeriosis, which requires the creation of new immunobiological
 38 preparations and modern schemes for the isolation and identification of various
 39 *Listeria* species.

40 The present review discusses the current understanding of the prevalence and
 41 biological properties of *Listeria* spp. and the virulence and pathogenicity factors of
 42 *L. monocytogenes*, as well as methods of identification of *Listeria* species.

43 **The prevalence and biological properties of species of the *Listeria* genus**

44 *Listeria* spp. are gram-positive flagellated bacilliform bacteria, facultative
 45 anaerobes that do not form spores and are motile at low temperatures [68], are widely
 46 distributed in the environment, isolated from soil and aquatic ecosystems, food, and
 47 environmental objects, circulate in the body, and some of their species are
 48 pathogenic for humans and animals [137].

49 Initially (until 2009), 7 species were identified in the genus *Listeria* (Pirie,
 50 1940): *L. monocytogenes*, *L. ivanovii*, *L. grayi*, *L. murrayi*, *L. innocua*, *L. seeligeri*,
 51 and *L. welshimeri*, of which *L. monocytogenes*, the main causative agent of
 52 listeriosis, poses the greatest threat to humans. In the last decade, due to the rapid
 53 development of sequencing technologies, 13 new species with diverse phenotypic
 54 and genotypic characteristics have been identified within the genus *Listeria*: *L.*
 55 *marthii* [83], *L. rocourtiae* [100], *L. fleischmannii* [47], *L. weihenstephanensis* [99],
 56 *L. riparia* [64], *L. grandensis* [64], *L. floridensis* [64], *L. cornellensis* [64], *L.*
 57 *aquatica* [64], *L. newyorkensis* [141], *L. booriae* [141], *L. costaricensis* [123] and *L.*
 58 *goaensis* [68]. In addition, two subspecies, subsp. *fleischmannii* and subsp.
 59 *colouradonensis*, have been established within the species *L. fleischmannii* [65].

60 Phylogenetic studies based on the 16S and 23S rRNA sequences revealed that
 61 the genus *Listeria* includes two evolutionarily formed lineages: *Listeria* sensu
 62 strictu, which includes *L. monocytogenes*, *L. innocua*, *L. welshimeri*, *L. seeligeri*, *L.*
 63 *ivanovii*, and *L. marthii*, and *Listeria* sensu lato, which unites *L. grayi*, previously
 64 considered nonpathogenic, and 12 new *Listeria* species discovered since 2009 [58,
 65 126]. All 6 species of *Listeria* sensu strictu share common phenotypic
 66 characteristics, such as the ability to grow at low temperatures and flagellar motility,
 67 whereas the 11 species of *Listeria* sensu lato represent three distinct monophyletic
 68 groups that can be recognised as separate genera [126]. These three putative genera
 69 of *Listeria* are immobile (except *L. grayi*), capable of nitrate reduction (except *L.*
 70 *floridensis*) and give a negative result in the Voges-Proskauer test (except *L. grayi*)
 71 [126]. Unlike all other *Listeria* species, species of the proposed new genus
 72 *Mesolisteria* cannot grow at temperatures below 7°C [126].

73 **The prevalence of *Listeria* in the environment**

74 The main source and reservoir of *Listeria* are environmental objects, primarily
 75 soil. *Listeria* is also excreted from plants, silage, dust, water bodies and sewage [26].
 76 There are 92 known animal species that serve as reservoirs or participate in the
 77 circulation of *Listeria*. The spread of the pathogen is particularly intensive during
 78 the period of rodent migration to places of their concentration (haystacks, hayfields).
 79 Rodents play a leading role in the transmission of *Listeria* to farm animals by
 80 contaminating feed and water [22]. Transmission of the pathogen between rodents
 81 in natural foci is supported by arthropods, including mites.

82 In addition, *Listeria* can be present in water in the environment, and therefore
 83 infection of animals through water is possible [33], including live fish, on whose
 84 body surface *Listeria* can multiply using the esculin of the mucus covering the scales
 85 as a food source [25]; cold smoking of fish creates specific conditions (salt, smoking
 86 solution) that favour *Listeria* multiplication [85]. *Listeria* can multiply in water and
 87 in soil microecosystems at low temperature with preservation of virulence of
 88 populations [37], which determines the spread and long-term persistence of *Listeria*
 89 in the external environment and economic objects.

90 Ecological plasticity and tolerance of *Listeria* stipulates their ability to switch
 91 from saprophytic to parasitic lifestyle and to reverse to saprophyticism again when
 92 introduced into the environment and survive under its various conditions. *Listeria*
 93 concentration has been found to increase in the external environment in autumn and
 94 spring, stabilise in winter and decrease in summer [7]. In addition, the ability of
 95 *Listeria* to actively multiply in melt water (at a temperature of 6°C) has been
 96 revealed, providing a 2-fold increase in bacterial mass [7]. At the same time, no
 97 significant changes in cell morphology in the population were observed when
 98 *Listeria* survived at low temperatures, including sub-zero temperatures, but after
 99 thawing and subsequent cultivation on fresh nutrient media, a pronounced
 100 heteromorphism of the *Listeria* population was observed, including the formation of
 101 protoplast-type cells, L-forms, and twisted revertant cells [5]. In this regard, the
 102 detection of *Listeria* in unfrozen food products requires, firstly, a long time for
 103 reversion in enrichment medium, and, secondly, there is a need to apply bacterial
 104 detection methods such as DNA diagnosis, PCR and ELISA.

105 The ability of *Listeria* to remain viable on food-contact surfaces in
 106 packinghouses has been revealed, which predetermines the likelihood of
 107 contamination of food products, including fruit, with a subsequent increase in the
 108 abundance of these bacteria as the products are stored [141]. In addition, there has
 109 recently been a steady increase in the proportion of multiple antibiotic-resistant *L.*
 110 *monocytogenes* strains worldwide [44], with additional pathogenicity factors [18].

111 In addition to abiotic factors, *Listeria* biology is also influenced by biotic
 112 environmental factors, including saprophytic microorganisms that contaminate food
 113 products, form common biocenoses with *Listeria*, and influence *Listeria* through
 114 exogenous metabolites or competition for nutrient substrates [36]. Nonpathogenic
 115 *Listeria*, as well as pathogenic microorganisms that form a biocenosis with *L.*
 116 *monocytogenes*, can serve as a reservoir of pathogenicity and resistance
 117 determinants and can be transmitted to pathogenic *Listeria* by horizontal transfer [9].

118 *L. monocytogenes* and *L. innocua* are the most common species of the genus
 119 *Listeria*, related in a strict sense [94] and often co-exist in environmental sites. It

120 was initially hypothesised that the two species evolved from a common ancestor but
 121 differ due to the loss of virulence genes in *L. innocua* [55]. It was later hypothesised
 122 that *L. innocua* evolved from the ancestors of four strains of the *L. monocytogenes*
 123 serogroup and may have retained some characteristics of its ancestor [116]. Atypical
 124 *L. innocua* was found to induce a protective immune response against *L.*
 125 *monocytogenes*, which is also in favour of a close genetic relationship between *L.*
 126 *innocua* and *L. monocytogenes* [111].

127 Genetically close to these two species is *L. welshimeri*, which is characterised
 128 by a smaller genome size compared to *L. monocytogenes*, suggesting similar
 129 evolutionary pathways of their genomes from a common ancestor [86]. However,
 130 the genome of the ancestor of *L. welshimeri* was more compact than that of *L.*
 131 *monocytogenes*, which led to the emergence of non-pathogenic species of *Listeria*
 132 spp. [86]. At the same time, the *prfA* virulence gene cluster present in the common
 133 ancestor of *Listeria* species was eventually lost in *L. innocua* and *L. welshimeri* [94,
 134 116].

135 The bacteria of *L. welshimeri* species are found in meat products and *L.*
 136 *seeligeri* in fish [17]. *L. innocua* is the predominant species in seawater, especially
 137 in coastal waters, compared to other *Listeria* species, which may cause
 138 contamination of fish, squid, crustaceans and other animals (seafood) and pose a risk
 139 to humans [74]. Bacteria of this species are often found in meat (frozen minced meat
 140 and semi-finished products, as well as smoked products ready for consumption), fish
 141 (salted, raw smoked fish, chilled and frozen semi-finished products), vegetables
 142 (onions, cabbage, potatoes, beetroot) stored in vegetable warehouses [17, 73], and
 143 are capable of adaptation in changing environmental conditions (survival in a wide
 144 range of temperature, humidity, pH of the environment), which significantly
 145 increases their chances of survival in different environmental conditions, causes
 146 their widespread active distribution and promotes the emergence of strains with
 147 atypical properties [59]. Thus, in addition to food products, *L. innocua* species are
 148 often present in silage and organs of rodents [17]. *L. innocua* have dual nature and
 149 are capable of both saprophytic and parasitic lifestyle depending on the habitat [15].

150 Bacteria of *L. monocytogenes* species were first isolated and described in 1911
 151 by the Swedish scientist G. Hulphers from purulent pus. Hulphers from a purulent
 152 nodule of the liver of a fallen rabbit [93], and a precise and detailed description of
 153 listeriosis was made in 1923 by E. Murray et al. [119]. The first documented culture
 154 of the pathogen in humans was isolated in France in 1921 by Dumont and Cotoni
 155 from a patient with meningitis, and its modern name was given in 1940 in honour of
 156 the English surgeon J. Lister, the founder of antiseptic methods. Despite the fact that
 157 *L. monocytogenes* is the main causative agent of listeriosis in humans, it is typical
 158 of the normal microflora of the middle and lower intestinal tracts of many animal
 159 and human species [54]; therefore, it may be excreted with faeces into the
 160 environment and subsequently contaminate soil, water, grass, etc.

161 The relatively high genomic similarity between *L. innocua* and *L.*
 162 *monocytogenes*, and sometimes their coexistence in similar ecological niches, may
 163 provide an opportunity for horizontal transfer of resistance or virulence genes [102].
 164 And, in particular, although antimicrobial resistance is less common in *L.*
 165 *monocytogenes* than in *L. innocua*, but *L. innocua* may form a reservoir of resistance
 166 genes that can be transferred between bacterial species, including transferring them
 167 to pathogenic *L. monocytogenes* [81]. In addition, the possibility of transferring
 168 antibiotic resistance genes to *Listeria* spp. from enterococci via transposons is also
 169 accepted [92].

170 **Biological properties of *L. monocytogenes*, *L. innocua* and *L. ivanovii***

171 Morphologically, *L. monocytogenes*, *L. innocua* and *L. ivanovii* are short,
 172 gram-positive, non-spore-forming bacilli of regular shape and are facultative
 173 anaerobes [26]. However, *L. monocytogenes* and *L. ivanovii* can transform into L-
 174 forms and parasitise intracellularly [26], showing the ability to survive in
 175 macrophages and infiltrate a number of normally non-phagocytic cells such as
 176 epithelial cells, hepatocytes and endothelial cells [139].

177 *L. monocytogenes* exhibits the ability to grow in a wide range of temperatures
 178 (1-45 °C, with the optimum temperature for their growth being 30-37 °C) and pH

179 (from 4.0-4.8 to 9.5-10.0) in the presence of NaCl (20%) and 15% CO₂ [11]. At
180 70 °C, *Listeria* die within half an hour and at 100 °C within 3-5 minutes [34].

181 *L. monocytogenes* is able to remain viable when stored in semi-liquid nutrient
182 medium and lyophilised under refrigerator conditions [4]. In this regard, dairy
183 products with a long shelf life, including soft cheeses, ice cream and butter, are the
184 most dangerous source of listeriosis, as they multiply at low temperatures and
185 accumulate dangerous doses of *Listeria* in milk [18]. In addition, *L. monocytogenes*
186 is detected not only in raw products, but also in cooked, uncooked and raw smoked
187 meat products, frozen, pickled and preserved seafood, as well as various semi-
188 finished products [144].

189 The high thermostability of *Listeria* is due to the presence of a complex of
190 genetic and biochemical mechanisms that allow them to adapt to changing
191 temperature conditions and survive in many environmental objects. One of the
192 mechanisms of thermoadaptation is the induction and repression of genes acting at
193 the isoenzyme level, regulating the launch of synthesis of "cold" and "heat"
194 isoenzymes. Moreover, the number of "cold" isoenzymes in *Listeria* significantly
195 exceeds the number of "thermal" isoenzymes, which makes *Listeria* facultative
196 psychrophiles. The most important mechanism of adaptation of *Listeria* to
197 unfavourable environmental factors is their ability to form biofilms, which
198 significantly increase survival and resistance to disinfectants [134].

199 The wide range of host organisms in which *L. monocytogenes* can reproduce
200 has caused antigenic heterogeneity of its outer envelope [23]. Thus, using molecular
201 typing methods, it is possible to distinguish within the species of *L. monocytogenes*,
202 three evolutionary lineages can be distinguished within the *L. monocytogenes*
203 species, characterised by different pathogenic potentials: Lineage I are strains
204 associated with epidemic outbreaks of listeriosis (serotypes 1/2b, 3b, 4b, 4d and 4e);
205 Lineage II are strains isolated during sporadic cases of listeriosis (serotypes 1/2a,
206 1/2c, 3a and 3c); Lineage III are strains rarely associated with cases of listeriosis
207 (serotypes 4a and 4c) and Lineage IV (4a, 4b, 4c) [107, 126, 131]. The most common
208 serotypes of *L. monocytogenes* in listeriosis patients are 4b, 1/2a, 1/2b [14]. At the

209 same time, about half of all cases of listeriosis in the world are caused by strains of
 210 serovar 4b, whereas serovariants 1/2a, 1/2b, 1/2c, and 3a are most often detected in
 211 infected products and natural environment [58, 104, 105].

212 At the same time, no regularities between the biological type of the host and
 213 the serovars of the isolated strains or the severity of the disease have been found. At
 214 the same time, it has been established that the course of the pathological process and
 215 host specificity are determined by listeriolysin and internalins A and B, which act as
 216 pathogenicity factors of *Listeria* [38, 126]. It has been found that DNA regions
 217 encoding *Listeria* pathogenicity factors are more frequently found in strains of
 218 serovar 4b [118].

219 Intraspecific cross-reactions are characteristic of *Listeria*: in particular, a
 220 culture containing DNA fragments characteristic of other serovariants was isolated
 221 within serovariant 4b [101]. In addition to intraspecies cross-reactions, *Listeria* also
 222 cross-reacts serologically with typhoid-paratyphoid bacteria and staphylococci [10].

223 The most genetically similar species to *L. monocytogenes* is *L. innocua*, which
 224 serves as an indicator of the possible presence of *L. monocytogenes* in products and
 225 can be pathogenic not only to animals [139], but also to humans [117].

226 The bacteria of *L. innocua* species are characterised by stability of phenotypic
 227 manifestations: morphology (short, randomly arranged bacilli, coccoid forms and
 228 ovoid bacteria that stain positively according to Gram stain), blue or bluish-green
 229 luminescence in oblique light, typical growth of colonies on nutrient media with a
 230 characteristic fermented milk odour, presence of catalase and absence of oxidase
 231 activity, motility at temperatures of 22°C and 37°C. Bacteria of this species are
 232 catalase-positive, most cultures show DNAase activity, and some strains are
 233 characterised by haemolytic activity [15]. In addition, bacteria of the *L. innocua*
 234 species are characterised by the presence of a gene encoding lecithinase, typical of
 235 *L. monocytogenes* [82], but not typical of *L. monocytogenes*, which retains
 236 lecithinase activity when cultured on nutrient medium containing lecithin, both in
 237 the presence and absence of activated carbon [21]. *L. innocua* is sensitive to

238 penicillins, aminoglycosides, carbapenems, fluoroquinolones, but resistant to
 239 nalidixic acid [15].

240 A peculiarity of *L. innocua* is the variability of biochemical activity. Thus,
 241 some experts [15] have established the ability of *L. innocua* to degrade glucose,
 242 salicin, rhamnose, mannose, maltose, esculin and fructose, along with the absence
 243 of degradation of urea, dulcitol, inulin, adonitol, raffinose, melibiose, starch and
 244 arabinose. The study of pathogenicity factors in some cultures of *L. innocua*,
 245 especially those isolated from fish, revealed haemolytic activity uncharacteristic for
 246 bacteria of this species [15], indicating the appearance of atypical strains and
 247 possibly due to the appearance of gene clusters similar to *L. monocytogenes* in the
 248 genome of *L. innocua* [59].

249 Although *L. monocytogenes* and *L. innocua* differ markedly in virulence, they
 250 are virtually indistinguishable by classical taxonomic criteria. Both species are
 251 actively motile and produce flagellin abundantly at 22°C. However, these species
 252 differ in motility and flagellin production at 37°C. At this temperature, *L.*
 253 *monocytogenes* strains are virtually immobile and produce little or no flagellin,
 254 whereas *L. innocua* strains are often motile and produce significant amounts of
 255 flagellin [95]. These data point in favour of differential regulation of flagellin
 256 production in *L. monocytogenes* and *L. innocua* at 37°C.

257 *L. monocytogenes* strains are characterised by the presence of both somatic O
 258 and flagellar H-antigens, whereas *L. ivanovii* (serotype 5) and *L. innocua* (serotype
 259 6) have only one somatic O-antigen each [42].

260 **Biological properties of other *Listeria* species**

261 Phenotypic properties of other species of the genus *Listeria*: *L. ivanovii*, *L.*
 262 *grayi*, *L. murrayi*, *L. seeligeri*, *L. welshimeri* are not sufficiently defined, and in some
 263 respects are similar to *L. monocytogenes* bacteria, which may lead to inaccurate
 264 identification. Thus, it is known that the new *Listeria* species do not differ from *L.*
 265 *monocytogenes* and are short bacilli of regular shape with rounded ends, sometimes
 266 almost cocci, gram-positive, capsules and spores do not form, they are not resistant
 267 to acid, aerobes, facultative anaerobes, chemoorganoautotrophs, but in the external

268 environment are chemolithoautotrophs, catalase-positive, oxidase-negative, exhibit
 269 motility at 20-25 °C [8].

270 Bacteria of *L. marthii* species grow well on conventional nutrient media in the
 271 temperature range of 1-45°C, the optimal temperature is 30-37°C. They are motile,
 272 form an umbrella of 3-5 mm in semi-liquid agar at 20-30°C and do not form it at
 273 37°C. Nonhemolytic, hydrolyse esculin, produce hydrogen sulfide, tolerant to
 274 sodium chloride, positive for methyl red, ferment D-glucose, lactose and maltose;
 275 do not ferment D-xylose, D-mannite, sucrose and L-rhamnose, reduce nitrates,
 276 active against urease, form indole and hydrolyse gelatin. On dense media, after
 277 incubation for 24 hours at 37°C, colonies 0.2-0.8 mm in diameter, smooth, bluish-
 278 green, translucent, slightly raised with a fine surface texture and a smooth edge grow.
 279 The type strain is FSL S4-120T [83].

280 Colonies of *L. rocourtiae* species after 48 h of cultivation at 30°C grow on
 281 trypticase-soya agar 0.5-1.0 mm in diameter, round, translucent, convex with a fine
 282 surface texture and a smooth edge. They reduce nitrate and manite, do not exhibit
 283 haemolytic activity, are able to degrade to acid ribose, D-xylose, galactose, glycerol,
 284 erythritol, adonite, D-glucose, D-fructose, D-mannose, L-sorbose, rhamnose,
 285 dulcitol, inositol, mannitol, sorbitol, methyl-D-glucoside, N-acetylglucosamine,
 286 amygdalin, arbutin, salicin, cellobiose, maltose, lactose, melibiose, starch, trehalose,
 287 glycogen and D-raffinose. It does not ferment L-xylose, D-arabinose, L-arabinose,
 288 methyl-D-mannoside, sucrose, inulin, melecitose, L-fructose, xylitol, D-turanose,
 289 D-fructose, D-tagatose, D-arabitol, 5-ketogluconate or 2-ketogluconate. The type
 290 strain is CIP 109804 (DSM 22097) [100].

291 The bacteria of *L. fleischmannii* species are typical short bacilli arranged
 292 singly or in short chains (0.4-0.6 mm diameter and 0.7-1.2 mm length). On nutrient
 293 agar at 37°C after 24 hours, colonies grow 0.4-1.0 mm in diameter, translucent,
 294 round, with a low convex surface and smooth edges. Immobile, although they
 295 contain the flagellin flaA gene. Reduce nitrate, hydrolyse hippurate and esculin, and
 296 produce hydrogen sulphide. The main differentiating character that distinguishes
 297 this species from others is the unique ability to ferment D-mannite and D-xylose.

298 The species *L. fleischmannii* is non-haemolytic, does not invade Caco-2 cells and
 299 does not contain *Listeria* virulence genes on pathogenic islet 1. The type strain is
 300 LU2006-1T (DSM 24998) [47]. Based on molecular genetic studies, the species *L.*
 301 *fleischmannii* was divided into subspecies according to genomic characteristics: *L.*
 302 *fleischmannii* subsp. *fleischmannii* and *L. fleischmannii* subsp. *colouradonensis*
 303 [65].

304 Bacteria of the subspecies *L. fleischmannii* subsp. *fleischmannii* are
 305 characterised by an optimal growth temperature of 30-37 °C, are immobile at 25 °C,
 306 are non-haemolytic, reduce nitrate, and degrade D-xylose to acid, D-arabitol, L-
 307 rhamnose, α -methyl-D-glucoside, D-ribose, turanose, sucrose and melecitose, and
 308 do not ferment glucose-1-phosphate, inositol, arylamidase, α -mannosidase and D-
 309 tagatose. The typical strain is LU2006-1 [65].

310 Bacteria of the subspecies *L. fleischmannii* subsp. *soloradonensis* are
 311 characterised by similar phenotypic features to the subspecies *L. fleischmannii*
 312 subsp. *fleischmannii*, but differ from it in their inability to ferment sucrose,
 313 melecitose, and turanose, but ferment inositol. The type strain is TTU M1-001 [47,
 314 65]. The genomes of both subspecies of *Listeria fleischmannii* contain putative
 315 enhancin genes; a mosquitocidal toxin has been identified in the genome of *Listeria*
 316 *fleischmannii* subsp. *colouradonensis*, suggesting possible adaptation to insect
 317 habitation [47, 65].

318 Bacteria of *L. weihenstephanensis* species are non-haemolytic bacilli 0.4-
 319 0.5 mm in diameter and 2.0-4.5 mm in length with rounded ends; colonies 1.0-
 320 2.5 mm in diameter, translucent, whitish, round, smooth, slightly convex with
 321 slightly irregular edges grow on trypticase-soya agar. The optimum temperature for
 322 their growth is 28-34°C, they do not grow at 38°C, their mobility is weak at 15-
 323 30°C, the optimum pH is 7-8. Isolates can grow in broth at 3°C for 10 days in
 324 anaerobic conditions. They grow well in nutrient broth containing 6.5 % NaCl. Test
 325 positive with methyl red, negative with Voges-Proskauer and CAMP test, do not
 326 hydrolyse urea and do not form indole and hydrogen sulphide, reduce nitrate to
 327 nitrite. Do not ferment α -mannosidase, arylamidase, D-ribose, 1-phosphate-glucose

328 and D-tagatose. Esculin, D-arabitol, D-xylose, L-rhamnose and methyl-D-
 329 glucopyranoside are fermented [99]. After 14 days of anaerobic incubation, acid
 330 formation is noted from glycerol, D-ribose, D-xylose, D-glucose, D-fructose, D-
 331 mannose, L-rhamnose, inositol, D-mannite, and methyl-D-glucopyranoside, N-
 332 acetylglucosamine, amygdalin, arbutin, aequulin, salicin, cellobiose, maltose,
 333 lactose, trehalose, starch, glycogen, xylitol, gentiobiose, D-arabitol and potassium
 334 5-ketogluconate. Not able to degrade erythritol, D-arabinose, L-arabinose, D-
 335 galactose, L-xylose, D-adonite, L-sorbose, methyl-b-D-xylopyranoside, dulcitol, D-
 336 sorbitol, methyl-D-mannopyranoside to acid, melibiose, sucrose, inulin, melezitose,
 337 raffinose, turanose, D-lyxose, D-tagatose, D-fucose, L-fucose, L-arabitol, potassium
 338 2-ketogluconate and potassium gluconate [99].

339 Bacteria of *L. floridensis* species are morphologically bacilli with rounded
 340 ends, 0.6×1.3-1.9 mm in size, unable to grow at temperatures below 7 °C. The
 341 optimum temperature for their growth is 37-41 °C; they do not show motility at
 342 temperatures of 4, 22, 30 and 37 °C. The species *L. floridensis* is the only species of
 343 the genus *Listeria* lacking motility and unable to reduce nitrate, characterised by
 344 negative Voges-Proskauer reaction and CAMP test. The typical strain is FSL S10-
 345 1187 [64].

346 The bacteria of *L. aquatica* species are 0.6-0.7 × 1.5-2.4 mm in size, like *L.*
 347 *floridensis* are unable to grow at temperatures below 7 °C, and the optimal
 348 temperature for them is 37-41 °C, are not motile at 4, 22, 30 and 37 °C, and show
 349 negative Voges-Proskauer reaction and CAMP test. Unlike *L. floridensis*, they
 350 reduce nitrate but do not reduce nitrite, do not ferment maltose but are able to
 351 ferment D-tagatose. The typical strain is FSL S10-1188 [64].

352 Bacteria of *L. riparia* species are straight bacilli with rounded ends, measuring
 353 0.5-0.7×2.3-3.7 mm. Like *L. floridensis* and *L. aquatica*, they do not grow at 7 °C
 354 and below, their optimum temperature is 37-41 °C, are not motile at 4, 22, 30 and
 355 37 °C, and show negative Voges-Proskauer reaction and CAMP test. Similar to *L.*
 356 *aquatica* and unlike *L. floridensis*, they reduce nitrate and do not reduce nitrite. The
 357 main differential characteristic from other species of the genus *Listeria* is the ability

358 to ferment L-rhamnose, mannose, D-galactose and L-arabinose. The typical strain is
359 FSL S10-1204 [64].

360 The species *L. cornellensis* is represented by straight sticks with rounded ends,
361 measuring 0.4-0.7×2.4-3.8 mm. The optimum temperature for their growth is 30-
362 37 °C, they are not motile at 4, 22, 30 and 37 °C, exhibit negative Voges-Proskauer
363 reaction and CAMP test. They reduce nitrate and do not reduce nitrite. Phenotypic
364 traits resemble the species *L. grandensis*. The typical strain is TTU A1-0210 [64].

365 Phenotypically similar to *L. cornellensis* are bacteria of *L. grandensis* species,
366 which morphologically are straight bacilli with rounded ends, 0.6-0.7×2.0-3.1 mm
367 in size. Their optimum growth temperature is 30-37 °C, and they are immobile at
368 temperatures of 4, 22, 30 and 37 °C. Voges-Proskauer reaction and CAMP test are
369 negative. Reduces nitrate and does not reduce nitrite. The type strain is TTU A1-
370 0212 [64]. In addition, *L. cornellensis* and *L. grandensis* are the only species of
371 *Lisretia* unable to cleave L-rhamnose. At the same time, *L. cornellensis* differs from
372 *L. grandensis* species in its weak lactose cleavage [64].

373 Bacteria of *L. newyorkensis* species are immobile at all temperatures, able to
374 grow in the temperature range of 4-41 °C, the optimal temperature for their growth
375 is 30-37 °C. Able to reduce nitrate but do not ferment nitrite. Show positive reaction
376 with methyl red, Voges-Proskauer test negative, unable to ferment xylitol, D-
377 fructose, α -mannosidase, D-arabitol, but do ferment D-galactose, D-ribose and L-
378 arabinose. The typical strain is FSL M6-0635 [152].

379 Bacteria of the species *L. booriae* are non-haemolytic bacilli, non-motile at all
380 temperatures and capable of growth between 4-41 °C, the optimum temperature for
381 growth is 30-41 °C. They differ from other species in their ability to ferment D-
382 arabitol, melibiose and L-arabinose. The typical strain is FSL A5-0281 [152].

383 The species *L. costaricensis* shows the greatest similarity in the structure of
384 16S rRNA genes with the type strain *L. floridensis* (98.7 %), which allowed us to
385 assign it to the same branch as *L. fleishmannii*, *L. floridensis* and *Listeria sensu lato*.
386 The typical strain is CLIP 2016/00682 [123].

387 *L. goaensis* are short non-spore-forming gram-positive immobile bacilli,
 388 oxidase-negative, catalase-positive and exhibit the ability to α -haemolysis on dishes
 389 with 5% agar with sheep and horse blood [68].

390 Thus, bacteria of the genus *Listeria* are ubiquitous and have a wide adaptive
 391 capacity that allows them to adapt to existence in different environments and, at the
 392 same time, to acquire various uncharacteristic properties. In this regard, knowledge
 393 of phenotypic features of biological properties of different *Listeria* species may be
 394 useful in determining approaches to the detection of epidemically dangerous *Listeria*
 395 from a variety of environmental objects.

396 **Pathogenicity factors of *L. monocytogenes***

397 Currently, *L. monocytogenes* serves as a model system for studying the main
 398 aspects of intracellular pathogenesis, as its ability to parasitise in the cytosol of
 399 mammalian cells, to use the actin-based motility system and to spread from cell to
 400 cell, avoiding contact with the humoral immune system [150], to overcome three
 401 principal protective barriers on the way of spreading in the body has been
 402 established: to penetrate through intestinal enterocytes, entering the blood and
 403 lymph, and to overcome the blood-brain barrier and placental barrier [63]. At the
 404 same time, *L. monocytogenes* is able to penetrate into target cells by phagocytosis,
 405 including it in those cells for which it is not characteristic, and, as a result, to affect
 406 various cell types, suppressing at the initial stages of infection the Th1-type immune
 407 response, which is the main one for the elimination of intracellular parasites, which
 408 significantly complicates the organism's fight against this pathogen [1].

409 The most typical features of *L. monocytogenes* are an exceptionally large
 410 number of surface proteins, an abundance of transport proteins, in particular proteins
 411 designed for carbohydrate transport, and a variety of regulatory proteins [50].

412 Surface proteins play an important role in the interactions of the
 413 microorganism with the environment, including target cells during infection of the
 414 host organism. In this case, the main virulence factors of *L. monocytogenes* are such
 415 surface proteins as internalins A and B, necessary for penetration into eukaryotic
 416 cells, and actA, which plays a key role in actin-based motility [50].

417 Pathogenicity islands identified in the *L. monocytogenes* genome are LIPI-1
 418 (prfA, hly, plcA, plcB, mpl and actA) regulated by the PrfA protein [78], LIPI-2
 419 (inlABCJ) [151], LIPI-3 (llsAXAXGHHBYDP) [57] and LIPI-4 (licABC,
 420 lm900558-70013 and glvA) [154]. It has been found that the presence of the
 421 pathogenicity island LIPI-3 in the genome of the bacterium causes a high level of its
 422 virulence and is often accompanied by the development of the meningoencephalic
 423 form of the disease [3].

424 The pathogenesis of *L. monocytogenes* requires the coordinated expression of
 425 six genes, namely prfA, plcA, hly, mpl, actA and plcB, which are mainly localised
 426 to the pathogenicity island LIPI-1 [150] regulated by the transcription regulator PrfA
 427 [56]. The processes activated by PrfA are crucial for the infection cycle of *L.*
 428 *monocytogenes*. They include phagosome lysis with release of bacteria into the
 429 cytoplasm and actin-dependent intercellular mobility of bacteria [77]. For example,
 430 the prfA gene encodes the transcription activator prfA, which directly or indirectly
 431 induces the transcription of more than 140 genes, including the other five genes
 432 found in LIPI-1 [129]. The plcA and plcB genes encode phospholipases C, which in
 433 combination with listeriolysin O (LLO) protect bacteria from cytoplasmic
 434 phagosomes [143]. The mpl gene encodes a zinc-metalloprotease required for pro-
 435 plcB maturation [134], and the actA gene product is a multifunctional virulence
 436 factor [149].

437 Auxiliary, or minor, virulence factors of *L. monocytogenes* are the products
 438 of 13 genes, 5 of which are associated with bacterial adhesion to and/or invasion into
 439 mammalian cells. The iap (invasion-a-associated p protein) gene encodes the
 440 extracellular protein p60, which has murein hydrolase activity and is required for
 441 bacterial division and invasion into target cells [150]. The lpeA gene encodes a
 442 protein that belongs to the lipoprotein receptor associated antigen I (LraI)
 443 superfamily. LraI proteins, in turn, are associated with the bacterial surface and
 444 include several adhesion proteins of many gram-positive pathogenic bacteria, such
 445 as the adhesins PsaA, also typical of *Streptococcus pneumoniae*, FimA, typical of
 446 *Streptococcus parasanguinis*, and EfmA, also characteristic of *Enterococcus*

447 *faecium* [110]. The *lpeA* gene also encodes the extracellular domain of SBP
 448 ("Streptococcal solute binding proteins"), which in *L. monocytogenes* binds Zn²⁺ and
 449 Mn²⁺ and mediates entry into eukaryotic cells, including hepatocytes and
 450 macrophages [135].

451 The *lpsA* gene encodes a protein of the same name, which is a type II signal
 452 peptidase required for *lpeA* maturation [136], with genetic defects in *lpsA* causing
 453 improper maturation of *lpeA*, subsequent loss of its proper surface localisation and
 454 ultimately a significant weakening of *L. monocytogenes* virulence.

455 The *lap* gene encoding a protein of the same name (Listeria adhesion protein
 456 p) promotes adhesion to intestinal epithelial cells and facilitates extraintestinal
 457 dissemination of bacteria [51]. Specifically, the *lap* gene product interacts with its
 458 cognate host cell receptor, heat shock protein 60 (Hsp60) on the apical side and
 459 causes dysfunction of the epithelial barrier, which favours translocation of *L.*
 460 *monocytogenes* across it [71]. *Lap* is an alcohol acetaldehyde dehydrogenase
 461 (*lmo1634*) present in both pathogenic and non-pathogenic *Listeria* species [91].
 462 However, *lap* exhibits virulent properties only in pathogenic *Listeria* due to the lack
 463 of secretion and surface reassociation of *lap* in non-pathogenic species [52, 91]. The
 464 interaction of *lap* with the host cell receptor Hsp60 leads to activation and nuclear
 465 translocation of nuclear factor- κ B (NF- κ B), which causes activation of myosin light
 466 chain kinase (MLCK) [71]. Activated MLCK phosphorylates myosin light chain
 467 (MLC), which predisposes cellular redistribution of tight junction proteins (claudin-
 468 1 and occludin) and adhesive junction protein (E-cadherin) and opening of the
 469 intercellular junction [71]. Consequently, *L. monocytogenes* performs efficient
 470 translocation across the intestinal barrier by activating the Lap-Hsp60-NF- κ B-
 471 MLCK axis [70].

472 The *fbpA* gene encodes an adhesin containing fibronectin-binding domains;
 473 this protein provides adhesion to target cells, especially hepatocytes [127].

474 The genome of *L. monocytogenes* also contains genes encoding enzymes that
 475 protect bacteria from the host immune system or increase their survival in the cytosol
 476 of infected cells. For example, the *pdgA* and *oatA* genes (peptidoglycan-N-

477 deacetylase and O-acetylase, respectively) may be required for resistance to host
478 lysozyme. Mutations in these two genes result in increased sensitivity of
479 peptidoglycan to lysozyme inducing attenuation of *L. monocytogenes* virulence
480 [133].

481 The *lplA1* gene encodes a lipooligase that promotes cytosolic replication of
482 *Listeria* in target cells [96].

483 The *gtcA* gene encodes an enzyme that catalyses glycosylation of teichoic
484 acid in the envelope of *L. monocytogenes*, which mediates key features of
485 pathogenicity: proper anchoring of the main surface virulence factors (Ami and
486 InlB); resistance to antimicrobial peptides and reduced susceptibility to antibiotics
487 [114].

488 The *prsA2* gene encodes a peptidylprolyl-cis-trans isomerase that promotes
489 proper protein folding, which is essential for the maturation and secretion of some
490 proprotein virulence factors (such as phospholipase C PC-PLC) of *L.*
491 *monocytogenes*, and the *lplA1* gene is required for intracellular survival of *Listeria*
492 [76].

493 The *clpC*, *clpE* and *clpP* genes encode proteases that presumably act as
494 mediators of the stress response and promote intracellular replication [150].

495 Hypervirulent isolates of *L. monocytogenes*, in addition to the pathogenicity
496 islet LIPI-1, also contain islets LIPI-3 and LIPI-4 [112]. Moreover, the LIPI-3 islet
497 contains genes encoding listeriolysin S, a second haemolysin that enhances *L.*
498 *monocytogenes* survival in polymorphonuclear neutrophils, whereas LIPI-4 encodes
499 a cellobiose phosphotransferase system [61] that enhances invasion into the central
500 nervous system, along with maternal-neonatal infection. In addition, the
501 pathogenicity islet LIPI-3 contains genes encoding important virulence factors,
502 namely internalins. These include the operon *InlA*, which promotes invasion of
503 epithelial and other cells, and *inlC*, which is involved in intercellular spread [60].
504 Hypervirulent strains of *L. monocytogenes* containing LIPI-3, having a bactericidal
505 function, have been found to promote intestinal colonisation and can modulate the
506 host microbiota [132].

507 Along with genes encoding pathogenicity and virulence factors, the genome
 508 of *L. monocytogenes* is characterised by the presence of SSI-1 (lmo0444, lmo0445,
 509 pva, gadD1 and gadT1) [130] and SSI-2 (lin0464 and lin0465) stress tolerance
 510 islands [87]. It was found that SSI-1 predetermines bacterial resistance to acids, salts,
 511 and growth in food [130], whereas SSI-2 predetermines survival under alkaline
 512 conditions and oxidative stress [57, 87].

513 It has also been shown that the presence in the *L. monocytogenes* genome of
 514 the lin gene correlates with resistance to the macrolide clarithromycin, the sul gene
 515 – to the sulfonamide bisseptol, the fosX gene – to fosfomycin, the aad, ant, and aph
 516 genes – to amikacin, and alleles 1, 8, 15, 18, and 28 of the pbp-like gene – to beta-
 517 lactams [3].

518 An important specific feature of the genomes of the genus *Listeria*, probably
 519 also related to the ability of these bacteria to colonise a wide range of ecosystems, is
 520 the presence of a large number of genes encoding various transport proteins [50]. As
 521 in most bacterial genomes, the predominant class of transport proteins in *Listeria* is
 522 ABC-transporters. Moreover, 26% of the genes encoding *Listeria* transport proteins
 523 are responsible for carbohydrate transport mediated by the phosphoenolpyruvate-
 524 dependent phosphotransferase (PTS) system, which allows bacteria to utilise
 525 different carbon sources. Furthermore, in many bacteria studied so far, PTS is a key
 526 link between metabolism and regulation of catabolic operons [146].

527 Thus, the genome of *L. monocytogenes* is characterised by the presence of a
 528 large variety of genes responsible for invasion into target cells of the host organism,
 529 survival in them, resistance to antibiotics and disinfectants, which determines the
 530 high pathogenicity and virulence of bacteria of this species.

531 **Methods of identification of different *Listeria* species**

532 The increasing role of *Listeria* in the structure of human infectious pathologies
 533 makes it necessary to improve the diagnosis, prevention, and sanitary and
 534 epidemiological surveillance of listeriosis, which predetermines the creation of new
 535 immunobiological preparations and modern schemes for the isolation and
 536 identification of *L. monocytogenes* in accordance with international standards [30].

537 In addition, it has been established that *L. monocytogenes* is characterised by
538 variability in morphological, cultural and biochemical properties, which causes
539 difficulties in the laboratory diagnosis of listeriosis. In particular, it has been
540 revealed that storage of food products at +22°C and seafood and dairy products at
541 +6°C may change the pathogenic properties of *Listeria* and, in particular, the loss of
542 haemolytic activity and decreased production of lecithinase, which is important for
543 the differentiation of *L. monocytogenes* from other nonpathogenic *Listeria* species
544 [41].

545 Currently, morphological, bacteriological, biochemical, serological and
546 molecular biological methods are used to diagnose listeriosis.

547 Morphological diagnosis of listeriosis is based on the detection during autopsy
548 of granulomas (listeriomas) in internal organs in the form of whitish, greyish or
549 yellowish nodules ranging in size from a poppy seed to a millet grain, which are
550 most often found in the liver, colon, pharynx, oesophagus, lungs, spleen and brain
551 [26]. In the initial stages, listeriomas represent a small focus of inflammation, in the
552 centre of which a large number of partially phagocytised *Listeria* are found among
553 decaying leukocytes. Further the number of leucocytes in the focus increases, and in
554 its peripheral parts an admixture of fibrin is found. At later stages of the process on
555 the periphery of the focus there are small overgrowths of granulation tissue,
556 consisting mainly of macrophages, which can gradually completely replace the area
557 of necrosis. *Listeria* is practically undetectable in the granulation tissue [153].

558 The biochemical methods of *L. monocytogenes* differentiation are based on
559 catalase positivity, motility at 18-25°C and immobility at 37°C, the ability to
560 hydrolyse esculin and not to exhibit lecithinase activity, typical of *Listeria*
561 parasitising inside the cell, when cultured on nutrient media containing lecithin [21].

562 The presence of the gene encoding lecithinase is typical not only for *L.*
563 *monocytogenes*, but also for *L. seeligeri* and *L. ivanovii*, but not for *L. innocua* [82].
564 At the same time, *L. monocytogenes* is characterised by induction of lecithinase
565 activity when activated charcoal is added to the nutrient medium, whereas *L. ivanovii*
566 is characterised by lecithinase activity irrespective of the presence of activated

567 charcoal in the incubation medium, and *L. seeligeri* is characterised by the absence
 568 of lecithinase activity irrespective of the presence of activated charcoal in the
 569 incubation medium [21], which is most likely due to interspecific differences in the
 570 regulation of the expression of pathogenicity factors. One of the reasons for the
 571 increased production of lecithinase and other pathogenicity factors in *L.*
 572 *monocytogenes* is the activation of the positive regulator of pathogenicity factor
 573 expression PrfA [137], which is highly homologous in *L. monocytogenes*, *L.*
 574 *ivanovii*, and *L. seeligeri*, but differs by 3 amino acid residues in these species,
 575 possibly affecting its functionality.

576 The increase in the production of pathogenicity factors (particularly
 577 lecithinase) by *L. monocytogenes* in the presence of activated charcoal is associated
 578 with its adsorption and, consequently, the elimination of the autorepressor product
 579 produced by *Listeria* itself from the incubation medium [75]. In this connection, the
 580 restoration of *Listeria's* ability to produce lecithinase upon addition of the sorbent to
 581 the incubation medium should not depend on the composition of the cultivation
 582 medium. At the same time, in the studies of some specialists a significant difference
 583 in the induction of lecithinase activity on different media, including media of the
 584 same name, produced by different manufacturers, was found, which may be due to
 585 the following reasons. Firstly, the components of the medium can influence the
 586 adsorption capacity of carbon, in particular, even trace amounts of detergents can
 587 reduce the adsorption properties of carbon. Secondly, the increase in lecithinase
 588 activity when a sorbent is added to *Listeria* incubation medium may be due not only
 589 to an increase in the amount of lecithinase produced, but also to an increase in its
 590 lecithinase activity depending on the influence of external factors, the concentration
 591 of which in the medium may vary.

592 Differentiation of species of the genus *Listeria* based on motility at certain
 593 temperatures is complicated by the fact that some strains of *L. innocua* showed
 594 motility at both 37°C and 20°C, while some strains of *L. welshimeri* remained
 595 immobile at room temperature [21].

596 Another biochemical feature of bacteria of the genus *Listeria* is the ability to
597 hydrolyse 4 carbohydrates (mannitol, rhamnose, raffinose and D-xylose), but this
598 ability cannot be used to differentiate *L. monocytogenes* from *L. innocua* [21].

599 Other methods of bacteriological identification of *Listeria*, which allow
600 differentiating pathogenic and non-pathogenic species, often give contradictory
601 results. In particular, the β -haemolysis characteristic of *L. monocytogenes* on blood
602 agar is weakly expressed in some strains, and some strains show no haemolytic
603 activity at all [21].

604 To date, bacteriological confirmation of listeriosis is the only reliable way to
605 make a final diagnosis [42], which necessitates the development of new approaches
606 for isolating, typing, and identifying virulent strains of *Listeria* in order to identify
607 the most significant of them in human infectious pathology.

608 At the same time, the duration of investigations by bacteriological methods
609 varies from 3-4 days for negative results to 10-11 days to confirm a positive result.
610 In addition, the detection of *L. monocytogenes* in animal products by microbiological
611 methods is often difficult due to the high concentration of competitive microflora,
612 the presence of *Listeria*-inhibiting food components and the generally low level of
613 *L. monocytogenes* in samples [122]. Finally, the bacteriological characterisation of
614 *Listeria* in clinical samples is sometimes difficult due to the variability of *Listeria*
615 and its tendency to form coccoid forms [21], predisposing cases of false
616 identification of *Philococcus*, *Corynebacterium* and *Enterococcus* as *L.*
617 *monocytogenes* and vice versa. At the same time, the parallel use of biochemical
618 methods, and, in particular, the typical for *L. monocytogenes* induction of lecithinase
619 activity in the incubation medium in the presence of sorbents makes it possible to
620 reliably identify *L. monocytogenes* from lecithinase-producing *Enterococcus* spp.
621 and *Escherichia coli*, whereas the absence of lecithinase activity in the medium
622 without sorbents distinguishes *L. monocytogenes* from staphylococci.

623 Although serological methods are adjunctive in the diagnosis of listeriosis,
624 they are often effective and provide relatively rapid results, ease of reaction, and the
625 ability to test a variety of biomaterial.

626 Serological reactions used for the diagnosis of listeriosis include enzyme-
 627 linked immunosorbent assay (ELISA), agglutination reaction (RA), complement
 628 binding reaction (CBR), indirect haemagglutination reaction (IHGR), and indirect
 629 immunofluorescence reaction (NIRF). Blood and cerebrospinal fluid can be used as
 630 test material, and the result is considered positive when the antibody titre is from
 631 1:250 to 1:5000 [32].

632 In the laboratory diagnosis of listeriosis, two serological methods are most
 633 often used: complement binding reaction with inactivated cytoplasmic antigen and
 634 indirect haemagglutination reaction with erythrocyte antigenic diagnosticum [2],
 635 which are not highly specific. In general, serological diagnosis of listeriosis is not
 636 sufficiently effective due to false-positive results, the diverse antigenic structure of
 637 the bacterium, the antigenic affinity of *Listeria* with other microorganism species,
 638 and the technical conditions of the reactions [34].

639 Most serological methods for the detection of *Listeria* are based on the use of
 640 monoclonal antibodies, which was the first method for typing *L. monocytogenes*
 641 serotypes [72]. However, this method is time-consuming and has a low differential
 642 capacity [98]. Therefore, molecular typing methods have become increasingly
 643 popular for *Listeria* typing [72], including ribotyping, multi-target enzyme
 644 electrophoresis (MLEE), pulsed-field gel electrophoresis (PFGE), and multi-target
 645 sequencing (MLST) [90]. Meanwhile, PFGE is considered the gold standard method
 646 for determining *Listeria* subtypes because of its differential ability, reproducibility
 647 and repeatability [109].

648 The first monoclonal antibodies for the detection of *Listeria* showed
 649 specificity to a common flagellar H-antigen typical for *L. monocytogenes*, *L. ivanovi*,
 650 *L. innocua*, *L. weishimeri* and *L. seeligeri*, but not for 30 cultures of other species,
 651 including staphylococci and streptococci [80]. Subsequently, a genus-specific panel
 652 of monoclonal antibodies developed by B.T. Butman et al. Butman et al. [53],
 653 including 15 specific antibodies showing affinity to thermostable rhodospecific
 654 protein with molecular mass from 30,000 to 38,000 Da and not cross-reacting with
 655 21 species of other microorganisms, including streptococci. Two monoclonals from

656 this panel were subsequently used to create a commercial immunoenzyme test
657 system (*Listeria* – EEK) for the detection of *Listeria* spp. [62], which has found
658 widespread use as an additional, but not alternative, method for the detection of
659 *Listeria* spp. in food [138].

660 At the same time, polyclonal antibodies used in the immunofluorescence
661 method and monoclonal antibodies are currently not practically used for the
662 diagnosis of listeriosis and retain practical significance only in livestock facilities
663 for the prevention of listeriosis in animals and service personnel [39].

664 Currently, serological methods used in clinical laboratory diagnostics and
665 aimed at detecting specific antibodies to listeria have been developed. One of the
666 relatively specific serological methods is the detection of antibodies to listeriolysin
667 O, the terminal polypeptide fragment of the recombinant molecule of which is the
668 most specific when screening sera of listeriosis patients compared to other protein
669 antigens [84]. At the same time, experts recommend using this serological method
670 only to detect non-invasive asymptomatic forms of the disease in epidemic outbreaks
671 of listeriosis [53]. When analysing the sera of donors and patients with listeriosis, it
672 is advisable to detect antibodies to the protein antigens of *Listeria* (*irpA*, *InlB* and
673 *actA*) associated with pathogenicity [24, 84]. Specific antibodies to *Listeria* antigens
674 are detected in the blood from the second week of the disease and persist for several
675 years after recovery.

676 At the same time, it is known that *Listeria* serovars and serotypes are not
677 speciospecific and may be common to different *Listeria* species regardless of their
678 pathogenicity for humans. In particular, *L. monocytogenes* is characterised by one
679 or more common antigenic determinants with *Listeria* species other than *L.*
680 *welshimeri*. In this regard, serovar identification alone, without the use of other
681 methods, does not accurately identify listeriosis [50].

682 Thus, serological methods for diagnosing listeriosis have a number of
683 disadvantages, including low specificity (*Listeria* antigens are very similar in
684 structure to antigens of other microorganisms, so false-positive or false-negative
685 results are often obtained), the possibility of detecting not the pathogen itself, but

686 only antibodies to it, low reliability of the results, false-negative reactions in severe
 687 immunodeficiency states even in very severe course of listeriosis, and the possibility
 688 of performing the analysis of listeria antigens. In general, the results of serological
 689 tests provide certain information about a patient's possible contact with the pathogen,
 690 but do not allow diagnosing listeriosis with a high degree of accuracy even when
 691 several serological methods are used, including due to the antigenic affinity of
 692 *Listeria* with staphylococci, enterococci and erysipeloid [20].

693 The diagnosis of listeriosis can be suspected or made if there is a reliable
 694 difference in antibody titres in paired sera of patients with a characteristic clinical
 695 picture (RA with coloured diagnostics, RBC, NIRF, RNAS), cerebrospinal fluid
 696 (NIRF, PCR, ELISA, microscopy) and bacteriological examination by enrichment
 697 with charcoal immunoglobulin sorbent [13, 39, 42].

698 At the same time, serological methods of laboratory diagnostics of listeriosis
 699 remain the main methods in the practice of Russian bacteriologists and allow
 700 establishing the presumed diagnosis with further confirmation by bacteriological
 701 methods [40]. At the same time, the slide agglutination method is relatively simple
 702 and reliable, requiring the availability of agglutinating listeriosis sera, the
 703 improvement of methods for obtaining which is very important at present.

704 One of the relatively fast, highly effective methods for the detection of *L.*
 705 *monocytogenes* is the molecular biological method of PCR and enzyme
 706 immunoassay [27] using the highly specific chromogenic medium ALOA-agar [48].

707 The specificity and high sensitivity of PCR have been confirmed on various
 708 strains of pathogenic *Listeria*, but poor lysis of some *Listeria* strains, apparently
 709 related to the structure of the cell wall, may give false-negative results [21]. In this
 710 regard, some specialists recommend PCR using listeria cells added to the reaction
 711 mixture without pretreatment with lytic enzymes [67]. In addition, the multi-targeted
 712 variable number of tandem repeats assay (MLVA), a PCR-based typing method that
 713 characterises bacteria by detecting tandem repeats at several specific loci in the
 714 bacterial genome, is quite informative [79, 108].

715 Matrix Assisted Laser Desorption/Ionisation Time of Flight (MALDI-TOF)
 716 is a relatively effective method for the identification of *L. monocytogenes* [12]. At
 717 the same time, there are reports in the literature that species identification of *Listeria*
 718 species by MALDI-TOF is not always correct, which may be due to the influence of
 719 various factors, such as cultivation conditions, the composition of nutrient media,
 720 and the level of polymorphism of strains taken for research [89, 125].

721 Real-time polymerase chain reaction is a comparatively fast and practical
 722 alternative to the microbiological method for the detection of *Listeria* [35].
 723 Therefore, the development of species-specific PCR methods for the detection of the
 724 *L. monocytogenes* genome is an urgent task. For PCR identification of *L.*
 725 *monocytogenes*, various genes are used as targets: 16S and 23S rRNA, *prs*, *gyrB*,
 726 *rpoB*, *hly*, *inlA* and *inlB*, *plcA*, *iap*, etc. [17, 21, 69, 113, 121, 147]. At the same
 727 time, the real-time PCR method does not allow distinguishing viable bacterial cells
 728 from non-viable ones; therefore, positive results obtained using this method must
 729 necessarily be confirmed by a traditional microbiological method [35].

730 To determine the serological affiliation of *Listeria* cultures, according to the
 731 world classification, it is recommended to use the multiplex PCR method based on
 732 the correlation between the serogroup affiliation of an isolate and the presence of
 733 specific open reading frames in its genome [9, 16], which makes it possible to
 734 identify the diversity of *L. monocytogenes* cultures and differentiate the strains of
 735 epidemic significance and danger to humans [39].

736 To obtain *Listeria* isolation media, it is necessary to study the optimal
 737 conditions for their growth and reproduction and to determine the optimal
 738 concentrations of nutrient elements. *Listeria* have been found to grow on simple
 739 nutrient media, capable of reproduction in a wide range of temperatures (4-45 °C),
 740 pH (5.0-9.0), and humidity, in the presence of 20% NaCl and 15% CO₂ [29, 49]. The
 741 high metabolic plasticity of *Listeria* determines the possibility of their transition
 742 from the saprophytic phase to the parasitic phase and vice versa; optimal cultivation
 743 conditions are necessary to preserve the virulent properties of *Listeria*, which is
 744 important for the accumulation of full biomass [29]. At the same time, the cultivation

745 conditions (composition of nutrient media, temperature and incubation time)
 746 influence the polymorphism of *Listeria*, which complicates the estimation of the
 747 results of bacteriological analysis and may lead to errors in diagnosis [5]. In
 748 particular, the prolonged stay of *Listeria* in cold storage predetermines the presence
 749 of most of the microorganisms at the L-transformation stage, which requires a long
 750 time of their reversion in enrichment media for the detection of pathogens [5]. In
 751 this regard, accurate diagnosis of *Listeria* requires the use of methods such as DNA
 752 diagnosis, PCR and ELISA [5].

753 At the same time, accelerated methods such as ELISA, PCR, DNA-DNA and
 754 DNA-RNA hybridisation, radioimmunological methods, and the use of
 755 chromogenic nutrient media are the most suitable for the detection of *L.*
 756 *monocytogenes* in perishable products, which are characterised by high speed of
 757 analysis, sensitivity and specificity, and low consumption of nutrient media. High
 758 sensitivity and specificity in detecting *L. monocytogenes* has been shown for the test
 759 system LOCATE® *Listeria*, in which highly specific monoclonal antibodies to
 760 thermostable O-antigens or somatic antigens of the *Listeria* cell wall are used as
 761 antibodies [6]. Proteomics methods involving mass spectrometric analysis of
 762 proteins are also used to diagnose listeriosis [31].

763 2 Conclusion

764 Throughout their long evolution, pathogenic *Listeria* have developed a set of
 765 unique mechanisms that allow them, along with a saprophytic lifestyle, to switch to
 766 intracellular parasitisation, avoiding contact with the humoral immune system and
 767 suppressing at the initial stages of infection the Th1-type immune response, which
 768 is essential for the elimination of intracellular parasites. In addition, *L.*
 769 *monocytogenes* is able to switch on phagocytosis in those cells for which it is not
 770 usually characteristic, which predetermines the possibility of its invasion of a wide
 771 range of target cells and significantly complicates the course of listeriosis.

772 Ecological plasticity and tolerance of listeria determine their ability to change
 773 from saprophytic to parasitic way of life and to reverse back to saprophyticism when
 774 they enter the environment and survive under different environmental conditions. At

775 the same time, non-pathogenic *Listeria*, as well as pathogenic microorganisms
776 forming a biocenosis with *L. monocytogenes*, can serve as a reservoir of
777 pathogenicity and resistance determinants and be transmitted to pathogenic *Listeria*
778 by horizontal transfer. Thus, the high degree of genetic relatedness of *L.*
779 *monocytogenes* with *L. innocua* makes it possible for *L. innocua* to create reservoirs
780 of resistance genes that can be transferred to *L. monocytogenes*, including virulence
781 genes. In addition, pathogenicity genes can be transferred from *L. monocytogenes* to
782 *L. innocua*, which predetermines the emergence of atypical haemolytic pathogenic
783 strains, which, given the greater prevalence of *L. innocua* in the environment, may
784 pose a greater threat to humans and animals.

785 The constant evolution of pathogenic *Listeria* and their acquisition of new
786 surface antigens, in turn, complicate the laboratory diagnosis of listeriosis and
787 differential typing of *Listeria* in the food industry and require the development of
788 new immunobiological preparations, culture media and modern schemes for the
789 isolation and identification of *L. monocytogenes*.

ТИТУЛЬНЫЙ ЛИСТ_МЕТАДААННЫЕ

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Блок 3. Метаданные статьи

**БИОЛОГИЧЕСКИЕ ОСОБЕННОСТИ И МЕДИЦИНСКАЯ
ЗНАЧИМОСТЬ БАКТЕРИЙ РОДА *LISTERIA***

**BIOLOGICAL FEATURES AND MEDICAL SIGNIFICANCE OF THE
LISTERIA BACTERIA**

Сокращенное название статьи для верхнего колонтитула:

БАКТЕРИИ РОДА *LISTERIA*

LISTERIA SPP BACTERIA

Ключевые слова: бактерии, листерии, листериоз, *L. monocytogenes*,
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Keywords: bacteria, *Listeria*, listeriosis, *L. monocytogenes*, *L. innocua*,
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