

Worldwide occurrence of *Yersinia* spp. within fattening pigs and wild boars

KARINA SUCHY¹, KATARZYNA MORKA², GABRIELA BUGLA-PŁOSKOŃSKA¹,
JAROSŁAW BYSTRÓŃ², JACEK BANIA²

¹Department of Microbiology, Faculty of Biological Sciences,
University of Wrocław, Przybyszewskiego 63, 51-148 Wrocław, Poland

²Department of Food Hygiene and Consumer Health Protection,
Wrocław University of Environmental and Life Sciences, C. K. Norwida 31, 50-375 Wrocław, Poland

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Suchy K., Morka K., Bugla-Płoskońska G., Bystróż J., Bania J.

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Summary

Yersiniosis is one of the most frequently reported zoonotic diseases in humans, primarily manifested with gastrointestinal symptoms. Its etiological agents are bacteria of the *Yersinia* genus, predominantly *Y. enterocolitica*. The reservoirs of these bacteria include animals such as pigs and wild boars, with the most common source of infection being the consumption of contaminated meat from these animals. This article presents a literature review covering the years 2011-2025, highlighting the ongoing issue of the presence of these bacteria in samples from pigs, wild boars, and their meat. Monitoring the presence of these pathogens in various hosts is crucial for understanding their carriage, transmission dynamics between animal hosts, and potential transmission to humans.

Keywords: *Yersinia* spp., *Yersinia enterocolitica*, fattening pigs, wild boars

Yersinia enterocolitica, a Gram-negative rod-shaped bacterium belonging to the *Yersiniaceae* family which, together with *Y. pseudotuberculosis* and *Y. pestis*, is a causative agent of human yersiniosis (1). *Y. enterocolitica* has been isolated worldwide, mainly from pigs but also from wild boars, sheep, horses, cattle, dogs, cats, ducks, amphibians and even beavers (11, 12, 17, 47, 89), with its reservoir encompassing a wide range of animals – including birds, fish, frogs, snails, oysters, and mammals – as well as environmental sources such as lakes, streams, soil, and vegetables (107).

The remaining species of the *Yersinia* genus were detected in the environmental samples, e.g. *Y. pekkanenii* was previously isolated from plants, water, soil samples indicating the environmental occurrence (65). *Y. kristensenii* and *Y. frederiksenii* have been isolated primarily from fresh water, sewage, soil, fish, wild rodents, domestic animals, food, healthy and sick humans (106). Only a limited amount of research on the isolation of *Y. pekkanenii*, *Y. kristensenii* and *Y. frederiksenii* from sick humans or potential pathogenicity has been published (41, 65, 94, 106). *Y. mollaretii* and *Y. bercovieri*, formerly classified as *Y. enterocolitica* biogroups 3A and 3B, have also been identified in environmental samples, including those from wild boars (15, 111).

Similarly, *Y. aldovae* and *Y. intermedia* have been isolated from raw and precooked pork meat, as well as from wild boar sources (91, 111).

Within the *Y. enterocolitica* specimen, biotypes 1A, 1B, 2, 3, 4, and 5 are distinguished by differences in biochemical characteristics and pathogenicity levels. Notably, there is an increasing frequency of reports regarding the acquisition of virulence genes such as *ail* or *ystB* by strains belonging to the 1A biotype (54, 84, 105, 113-115, 118). *Y. enterocolitica* is also classified into serotypes based on the O-antigen of lipopolysaccharides. A bioserotype combines biotyping (which differentiates strains based on biochemical properties, such as metabolism and virulence factors) with serotyping, providing a more detailed classification of *Y. enterocolitica* strains. Human yersiniosis is mainly transmitted via food-borne route, after eating contaminated food, most commonly pork, pork products and wild boar meat, as these animals act as reservoirs for the bacterium or cross-contaminated food without heat treatment. Animal yersiniosis is usually asymptomatic, however some manifestation of illness is possible in particular individuals of pigs or wild boars. A comprehensive literature search was conducted using databases such as PubMed, Google Scholar, and

ScienceDirect to identify studies on the prevalence of *Y. enterocolitica* in pigs and wild boars. This review aims to provide a comprehensive overview of the prevalence of *Y. enterocolitica* and other *Yersinia* species in fattening pigs and wild boars based on studies published between 2011 and 2025. Given that pigs are recognized as the primary reservoir of *Y. enterocolitica* pathogenic to humans, and considering the significant wild boar population in Europe, synthesizing current prevalence data is crucial for evaluating the potential public health risk associated with these animal hosts (7, 12, 34, 35, 82).

Published data on the *Yersinia* spp. occurrence among pigs in the years 2011-2025

The presence of *Y. enterocolitica* in pigs is observed all over the world, accounting for increasing problems in food safety (43, 90, 120, 124). Fattening pigs (*Sus scrofa domestica*) are generally considered a symptomless reservoir for this bacterium, especially bioserotype 4/O:3 (24, 30, 43, 56-58, 75, 80, 90, 120, 124). Other biotypes (1A, 1B, 2, 3, 5) are much less common in

pigs but *Y. enterocolitica* strains of biotype 1A can pose a risk of yersiniosis since they cannot be considered completely avirulent. Moreover, *Y. enterocolitica* does not constitute hygiene criterion for pig carcasses according to the current pig meat inspection in European Union (27).

Due to its tropism for lymphoid tissue, *Y. enterocolitica* is more commonly detected in tonsillar than rectal samples; however, during the initial phase of infection, when bacterial dissemination remains localized, rectal swabs may yield higher detection rates (99). In pigs slaughtered at the age of 135 days or more, the tonsils may be a more significant source of *Y. enterocolitica* than faeces (43, 76). To characterize the carrier state in pigs it is necessary to confirm if during the sampling pigs were infected systemically or locally. In addition the younger pigs should be examined for *Y. enterocolitica* occurrence, which is the object of many papers concerning the *Yersinia* spp. prevalence. Table 1 presents data published during the last decade on the occurrence of *Yersinia* among slaughter pigs, collected in different countries, farms, and at different stages of

Tab. 1. Occurrence of *Yersinia* spp. among pigs in the years 2011-2025

Year of publication	Year of Study	Source of isolation/type of samples/country	Occurrence	References
2011	2006	Tonsils of 212 fattening pigs sampled in Switzerland	<i>Y. enterocolitica</i> 4/O:3 n = 71/78 (91%) <i>Y. enterocolitica</i> 2/O:5,27 n = 6/78 (8%) <i>Y. enterocolitica</i> 2/O:9 n = 1/78 (1%)	(35)
2011	2004 2007-2009	In 2004 the blood samples of 900 fattening pigs, between July 2007 and June 2009 1500 blood samples from Lower Saxony, Germany	<i>Yersinia</i> sp. in 2004 n = 574/900 (63.7%) <i>Yersinia</i> sp. in 2007-2009 n = 966/1500 (64.4%) Altogether <i>Yersinia</i> sp. N = 1540/2400 (64.1%)	(3)
2012	No data	Fecal samples of 76 pigs monitored on a fattening farm over the 13 weeks of fattening period, Finland	<i>Y. enterocolitica</i> at week 2 n = 47/76 (61.8%) <i>Y. enterocolitica</i> at week 4 n = 67/76 (88.2%) <i>Y. enterocolitica</i> at week 6 n = 60/76 (78.9%) <i>Y. enterocolitica</i> at week 8 n = 17/76 (22.4%) <i>Y. enterocolitica</i> at week 10 n = 20/76 (26.3%) <i>Y. enterocolitica</i> at week 13 n = 11/40 (27.5%) Seroprevalence at week 13: 82%	(120)
2013	2007-2008	A total of 792 samples (480 swabs from tonsils and tongue, 120 swabs from slaughterhouse environment points, 72 swabs from market environment points, and 120 pork fragments) collected from two swine slaughterhouses and two respective markets in São Paulo State, Brazil	<i>Y. enterocolitica</i> in total n = 442/792 (55.8%) <i>Y. enterocolitica</i> 1A/nontypeable n = 92/442 (20.81%) <i>Y. enterocolitica</i> 1A/O:5a n = 10/442 (2.26%) <i>Y. enterocolitica</i> 1A/O:5b n = 18/442 (4.07%) <i>Y. enterocolitica</i> 1A/O:7 n = 1/442 (0.23%) <i>Y. enterocolitica</i> 1A/O:6 n = 1/442 (0.23%) <i>Y. enterocolitica</i> 4/O:3 n = 320/442 (72.40%) 122 biotype 1A strains were isolated from pork, markets, or slaughterhouses environments	(81)
2013	2008-2010	In 50 fattening pig herds in northern Germany, four pooled fecal samples and 10 swab samples from the pigs' direct and indirect environment, and flies, rodent droppings collected from each herd in the Weser-Ems region in the state of Lower Saxony in northwestern Germany	<i>Y. enterocolitica</i> in pooled feces n = 35/205 (17.1%) <i>Y. enterocolitica</i> in direct environment n = 21/260 (8.1%) <i>Y. enterocolitica</i> in indirect environment n = 2/170 (1.2%) <i>Y. enterocolitica</i> in flies/pests samples n = 2/65 (3.1%) <i>Y. enterocolitica</i> in pig herds n = 24/50 (48%)	(75)
2013	2005-2009	296 indoor pig fattening farms (conventional intensive production) in north-western Germany	<i>Yersinia</i> sp. in n = 192/296 (64.8%)	(55)
2014	2012	Tonsils from 7047 fattening pigs, representing 100 pig batches, in two Belgian slaughterhouses	<i>Y. enterocolitica</i> O:3 in pigs n = 2009/7047 (28.5%) <i>Y. enterocolitica</i> O:3 in batches farms n = 85/100 (85.0%) <i>Y. pseudotuberculosis</i> in farms n = 7/100 (7.0%)	(117)
2014	2012-2013	Meat samples from 1353 finishing pigs from 259 farms collected at slaughter, Finland	Pathogenic (Yop-positive) <i>Yersinia</i> spp. in meat juice samples n = 766/1353 (56.6%)	(28)

Year of publication	Year of Study	Source of isolation/type of samples/country	Occurrence	References
2015	2014	Samples of 156 pig tonsils and 156 mandibular lymph nodes collected from 13 farms in Croatia	<i>Y. enterocolitica</i> in tonsils n = 26/78 (33.33%) in 10/13 farms (77%) <i>Y. enterocolitica</i> in mandibular lymph nodes n = 8/78 (10.25%) in 6/13 farms (46%)	(124)
2016	2006-2007	Tonsils and intestinal samples from 388 healthy fattening pigs collected monthly between September 2006 and August 2007, Finland	<i>Y. enterocolitica</i> in tonsils n = 234/388 (60.3%) <i>Y. enterocolitica</i> in pig intestinal samples n = 94/356 (26.4%)	(90)
2016	2013	336 samples collected at primary production, slaughter and meat processing from five conventional fattening pig farms and one common slaughterhouse, Lower Saxony, Germany	<i>Y. enterocolitica</i> in pooled fecal samples n = 4/36 (11.1%) <i>Y. enterocolitica</i> in tonsils of fattening pigs n = 6/50 (12.0%) <i>Y. enterocolitica</i> in cecal content n = 2/50 (4.0%) <i>Y. enterocolitica</i> in meat samples n = 2/50 (4.0%) <i>Y. enterocolitica</i> in primary production stage n = 4/36 (11.1%) <i>Y. enterocolitica</i> in slaughter stage n = 8/250 (5.3%) <i>Y. enterocolitica</i> in meat processing stage n = 2/50 (4.0%)	(78)
2016	2013-2014	201 pigs at slaughter belonging to 67 batches, Northern Italy	<i>Y. enterocolitica</i> 4/O:3 in pig tonsils n = 55/201 (27.4%) <i>Y. enterocolitica</i> in batches n = 38/67 (56.7%) <i>Y. enterocolitica</i> in farms n = 36/61 (59.0%) <i>Y. pseudotuberculosis</i> in pig tonsils n = 4/201 (2.0%) <i>Y. pseudotuberculosis</i> in batches n = 4/67 (6.0%) <i>Y. pseudotuberculosis</i> in farms 3/61 (4.9%)	(16)
2019	2012-2014	Blood samples from 1116 pigs from 57 indoor fattening pig farms in southern Finland, 653 pigs tested twice during the fattening period	Pathogenic <i>Yersinia</i> spp. in pigs n = 738/1116 (66.1%) Pathogenic <i>Yersinia</i> spp. in farms n = 50/57 (87.7%) Seroprevalence at the beginning of the fattening period n = 198/653 (30.3%) Seroprevalence at the end of the fattening period n = 472/653 (72.3%)	(27)
2019	No data	Tonsils of 266 sows from 115 farrowing farms collected from two slaughterhouses, Finland	<i>Y. enterocolitica</i> 4/O:3 in sows n = 16/266 (6.0%) Seroprevalence in sows 77.1%	(53)
2022	2020-2021	200 slaughtered pig tonsils from 11 pig farms at six slaughterhouses, 30 pig carcasses sampled at five slaughterhouses, Latvia	<i>Y. enterocolitica</i> in tonsils n = 84/200 (42.0%) <i>Y. enterocolitica</i> 4/O:3 in tonsils n = 70/200 (35.0%) <i>Y. enterocolitica</i> 1A in tonsils n = 14/200 (7.0%) <i>Y. enterocolitica</i> 4/O:3 in carcasses n = 4/30 (13.0%)	(116)
2022	No data	Tonsils from 234 fattening pigs from slaughterhouses, 128 samples of retail pork cuts and minced pork, Croatia	<i>Y. enterocolitica</i> in tonsils n = 101/234 (43.2%) <i>Y. enterocolitica</i> in retail samples n = 0/128 (0.0%)	(125)
2022	2018-2019	960 tonsils from 960 pig carcasses after their evisceration collected at three slaughterhouses, Serbia	<i>Y. enterocolitica</i> in tonsils n = 100/960 (10.4%)	(7)
2023	2016-2021	790 tonsil and fecal samples from 601 pigs, Bulgaria	<i>Y. enterocolitica</i> in pigs n = 40/601 (6.7%)	(5)

fattening and slaughter, depending on the study. The prevalence data come from Switzerland, Germany, Finland, Brazil, Belgium, Croatia, Italy, Latvia, Serbia and Bulgaria. In Finland the prevalence of *Y. enterocolitica* in 388 tonsil samples collected monthly between September 2006 and August 2007 was 60.3% (n = 234/388) and its prevalence in 356 intestinal samples was 26.4% (n = 94/356) (90). Nathues et al. confirmed also the occurrence of *Y. enterocolitica* in the German pig herd environment (75). Morka et al. in 2021 (64) confirmed that pigs are an important host for *Y. enterocolitica* 4/O:3 carrying virulence genes which suggests possible implications in food safety due to the pig asymptomatic carriage (no clinical symptoms nor gross pathological lesions are visible). The same paper presented less diversity of pig strains in terms of virulotypes and VNTR/PFGE (Variable Number of Tandem Repeats and Pulsed-Field Gel Electrophoresis) profiles in contrast to wild boar strains (64).

The infection of *Y. enterocolitica* in pig herds is dynamic and varies with the age of the animals and farming conditions. Nesbakken et al. (76) conducted studies assessing the presence of *Y. enterocolitica* at different time points in the life of pigs, based on samples collected from feces, tonsils, and blood. Young piglets up to approximately 60 days of age (before weaning) do not show the presence of *Y. enterocolitica*, with infection beginning around day 80. The highest percentage of bacteria excreted in feces is observed at approximately 130 days of age, after which the number declines; however, *Y. enterocolitica* remains detectable in the tonsils until slaughter (76). In the other study conducted by Vilar et al. (119) pigs were divided into five age groups: younger than 1 month, 1-2 months, 2-3 months, 3-5 months, and older than 5 months. The prevalence of *Y. enterocolitica* in these groups was observed as follows: 0.0% (n = 0/38), 22.3% (n = 48/215), 44.2% (n = 144/326), 36.4% (n = 106/291), and 20.2%

($n = 25/124$), respectively. In contrast, seroprevalence increased gradually across these groups from 4% to 71% in the oldest pigs. In sows, fecal prevalence was 5% ($n = 24/486$), while seroprevalence reached 67.3% ($n = 72/107$) (119). Virtanen et al. (120) in 2012 monitored fecal prevalence in a group of pigs every two weeks over a 13-week feeding period. The pigs entered the fattening unit at approximately 12 weeks of age. After two weeks *Y. enterocolitica* prevalence was 61.8% ($n = 47/76$); at 4 weeks, 88.2% ($n = 67/76$); at 6 weeks, 78.9% ($n = 60/76$); at 8 weeks, 22.4% ($n = 17/76$); at 10 weeks, 26.3% ($n = 20/76$); and at 13 weeks, 27.5% ($n = 11/40$). The highest prevalence was observed at 16-18 weeks of age, after which detectability in feces significantly decreased. However, seroprevalence after 13 weeks reached 82% (120). Gürtler et al. (43) examined fecal samples from pigs at 3 days, 3 weeks, 10 weeks (after weaning), 14 weeks (after transfer to the fattening department), and 20 weeks (during the final weeks of the fattening period). *Y. enterocolitica* was first observed in 14-week-old pigs, with a prevalence of 2.8% ($n = 15/537$), while in the final weeks of fattening, fecal prevalence reached 19.6% ($n = 96/491$) (43). The authors suggest that the absence of bacteria in young piglets may result from passive immunity transferred by sows with milk. Additionally, young piglets have limited contact with other animals, which may reduce the risk of infection. The infection may be attributed to the weakening of passive immunity after weaning and increased exposure to *Y. enterocolitica* in the environment, particularly through contact with infected pigs. Furthermore, stress associated with transport and relocation may suppress the immune system and increase susceptibility to infection. Additional risk factors include the absence of bedding and the use of well water instead of municipal water. Effective strategies for reducing contamination include implementing an „all-in/all-out” system, which restricts contact between different pig groups and minimizes bacterial transmission, as well as limiting the number of piglet suppliers to lower the risk of introducing *Y. enterocolitica* into herds (43, 76, 119, 120).

The asymptomatic carriage of *Y. enterocolitica* among animals, especially pigs,

is caused by bacterial ability to modulate the host's immune response. The *Y. enterocolitica* 1B/O:8 bioserotype stimulates macrophages to secrete cytokine IL-8 at significantly high levels, whereas the 4/O:3 and 2/O:9 bioserotypes induce IL-8 secretion at much lower levels IL-8 is responsible for inducing neutrophil and other granulocyte to migration in the site of infection, which triggers inflammation leading to elimination of the pathogen (21, 101, 102). IL-10, produced by macrophages, B and T cells and dendritic cells, is responsible for the suppression of the inflammatory response in an effective elimination of the causative agent (101). Bioserotypes 4/O:3, 1B/O:8, 2/O:9 of *Y. enterocolitica* are able to induce increased secretion of IL-10, therefore, the inflammatory response is reduced and chances of *Y. enterocolitica* cells to survive are significantly higher. The above interactions between *Y. enterocolitica* and the immune system may explain the common asymptomatic *Y. enterocolitica* carriage by pigs (101).

The detection rate of *Yersinia* spp. in animals is highly dependent on the sampling site, the age of the individuals, and the selected isolation and cultivation methods, particularly when using selective-differentiating media. The standardization of data remains challenging due to the geographical distribution of *Y. enterocolitica*, diverse research methodologies, and variations in laboratory capabilities (32, 103). While ISO10273:2017 provides a standardized method for detection, its limitations, such as overgrowth of accompanying flora, have led many researchers to explore alternative methods, including PCR and antibody detection. Differences in the detection of *Y. enterocolitica*, depending on the applied method, were

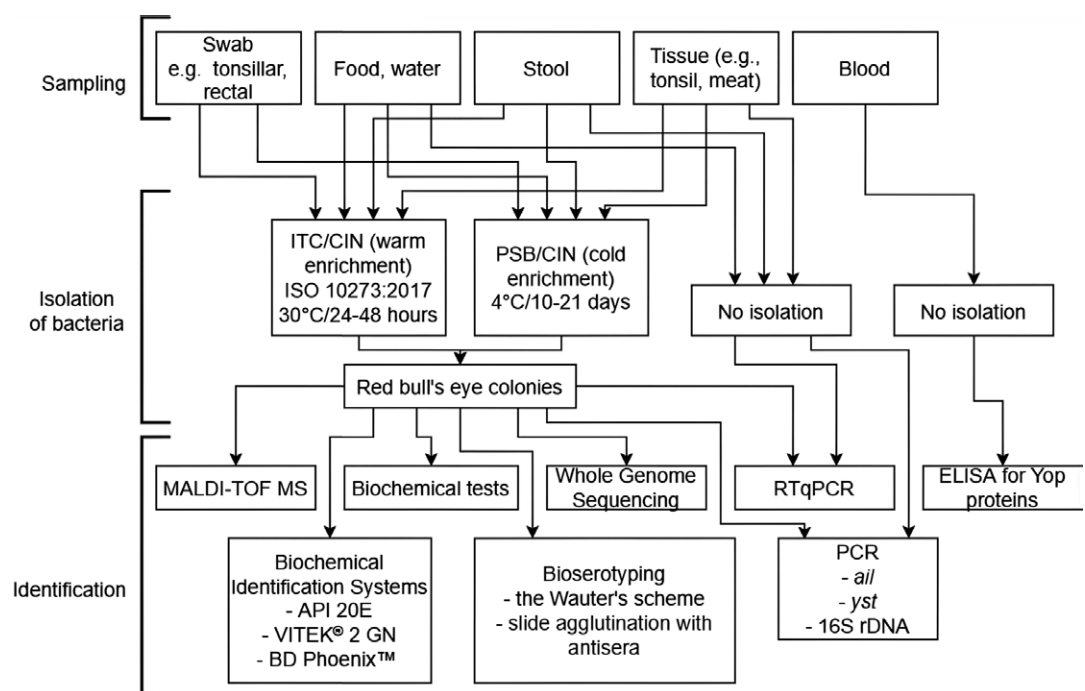


Fig. 1. Selected sample types and methods used in *Y. enterocolitica* detection (4, 8, 13, 20, 61, 77, 100, 108, 112, 123)

observed in the study by Fredriksson-Ahomaa in 2007 (31). Traditional culture methods are time-consuming and exhibit low efficiency, with a detection rate of 35% in porcine tonsils. In contrast, real-time PCR is a significantly faster and more sensitive technique, detecting the pathogen in 88% of cases. However, since it detects only the genetic material, it often excludes further characterization of the strain, as no live bacteria are present. Additionally, in the analysis of raw pork samples, PCR identified bacteria in 7% of cases, whereas culture methods produced negative results for all tested samples (31). In a 2018 study on the presence of *Y. pseudotuberculosis*, 503 samples were tested using the PCR method, and 32 were positive. All PCR-positive samples were analyzed using cultivation, but colonies were successfully isolated from only 10 out of 32 samples (93). Furthermore, access to detailed bioserotype classification is often limited, even in studies investigating *Yersinia* spp. occurrence in human populations. A schematic summary of selected steps involved in *Y. enterocolitica* detection, including sample types, isolation approaches, and identification methods, is presented in Figure 1.

Published data on the occurrence of *Yersinia* spp. among wild animals, particularly wild boars, from 2011 to 2025

The wild boars (*Sus scrofa*) serve as a reservoir for *Y. enterocolitica*, although this role appears to be underestimated. Since the increase of game meat consumption has been noted there is a need of enhanced surveillance and studies on the prevalence of *Y. enterocolitica* in wild boars. There is also a growing trend of outdoor pig farming, which, combined with high wild boar densities, may increase the risk of pathogen transmission between wild boars and fattening pigs, as well as in the opposite direction. All studies indicate that wild boars continue to serve as a reservoir for biotype 1A (9, 15, 60, 111). However, the presence of the *ail* gene in this biotype suggests horizontal gene transfer, as the *ail* gene is typically found in *Y. enterocolitica* strains of bioserotype 4/O:3, which are common in pigs. This highlights the potential for genetic exchange between wild boars and pigs. It is important to note that *Y. enterocolitica* transmission can also occur in the opposite direction, which may pose a risk to wild boars (84, 121). Moreover, wild boars are known to be susceptible to diseases commonly affecting fattening pigs (52). Unfortunately, the role of wild boars in *Y. enterocolitica* carriage is poorly understood (82, 110). Additionally, due to certain specific characteristics, the isolation and identification of *Y. enterocolitica* isolates from wild boars requires more effort compared to isolates from other sources. Factors such as animal age, season of sampling, lymphatic and/or fecal carrier state, and high genetic diversity – resulting from the wild-living nature of wild boars, where anthropogenic

influence is lower compared to industrial farming – along with the close phylogenetic relatedness of species within the *Yersinia* genus, may affect the accuracy of species identification. In the case of environmental or less-characterized strains, such as those isolated from wild animals, the lack of representative mass spectra in commercial databases may lead to misidentification or inconclusive results (15). This highlights the necessity of employing diverse isolation and identification methods to reveal biochemical differences and to prevent overgrowth by other bacterial species (15, 31, 32, 100, 103, 112).

The considerable population of wild boars in Poland and other countries highlights the need for monitoring the presence of *Yersinia* in these animals, as they may play a significant role in the epidemiology of this pathogen. In Poland occurrence of *Y. enterocolitica* and other species within the *Yersinia* genus among wild animals has been confirmed (9, 11, 12, 108, 109). Currently, we do not have reliable information on the exact population size of wild boars in Poland – the methods used to estimate the wild boar population in Poland include tracking, drive hunts, and observation logs recorded during field surveys (83). The estimates presented in the 2024 *Statistical Yearbook of Forestry* indicate a population of 52.9 thousand wild boars in 2023 and 55.8 thousand in 2024. However, these figures are significantly underestimated, as evidenced by the number of wild boars hunted during the 2023/2024 season – 173.7 thousand – which suggests that more boars were culled than counted. The lack of accurate data, caused by unreliable counting methods, results in an unclear understanding of the scale of the issue.

According to the PubMed source the prevalence of *Yersinia* spp. within wild boars has been published worldwide since 2001. In a 2002 study, 131 wild boars (*Sus scrofa leucomysta*) captured in Japan between 1994 and 1995 were examined for *Yersinia* spp. and *Listeria* spp. *Y. pseudotuberculosis*, *Y. enterocolitica*, *Y. frederiksenii* and *Y. aldovei*, were isolated in 37% (n = 49/131) of the wild boars. However, no human pathogenic biotypes of *Y. enterocolitica* were isolated (45). Hayashidani et al. (45) indicated only that wild boar could be a reservoir for *Y. pseudotuberculosis* in Japan. Takahashi et al. (111) examined 54 wild boars hunted in Japan from November 2014 to June 2016. A total of 69 *Yersinia* strains were isolated from 40 wild boars, with a prevalence of 74%. These strains belonged to eight *Yersinia* species, with *Y. enterocolitica* being the most frequently detected (39/69; 56.5%). The second most common species was *Y. kristensenii*, with 14 isolates. Among the *Y. enterocolitica* isolates, 38 belonged to biotype 1A, while one was classified as biotype 3VP.

In Europe the reservoir role of wild animals, especially wild boars, was determined in Poland (9, 10, 108), Switzerland (35, 36), Germany (2, 4, 93), Sweden (96-98),

Tab. 2. Occurrence of *Yersinia* spp. among wild boars in the years 2011-2025

Year of publication	Year of study	Source of isolation / type of samples / country	Occurrence	References
2011	2007-2008	Tonsils from 153 wild boars sampled in Switzerland	<i>Y. enterocolitica</i> 2/0:5, 27 n = 3/153 (2.0%) <i>Y. enterocolitica</i> 2/0:9 n = 4/153 (2.6%) <i>Y. enterocolitica</i> 4/0:3 n = 5/153 (3.3%) <i>Y. enterocolitica</i> NT n = 2/153 (1.3%) <i>Y. enterocolitica</i> in total n = 18/153 (11.8%) <i>Y. pseudotuberculosis</i> 0:1 n = 3/153 (2.0%) <i>Y. pseudotuberculosis</i> 0:2 n = 1/153 (0.7%)	(35)
2014	2010-2011	319 tonsils, ileocaecal lymph nodes and faecal samples collected from 88 wild boars, Sweden	<i>Y. enterocolitica</i> in tonsils n = 19/175 (10.9%) <i>Y. enterocolitica</i> in ileocaecal lymph nodes n = 4/56 (7.1%) <i>Y. enterocolitica</i> in faecal samples n = 1/88 (1.1%) <i>Y. enterocolitica</i> in total n = 24/319 (7.5%)	(96)
2015	2012-2013	302 rectal swabs obtained from 151 wild boars shot in Poland	<i>Y. enterocolitica</i> in total n = 40/151 (26.5%) <i>Y. enterocolitica</i> 1A n = 34/40 (85.0%) <i>Y. enterocolitica</i> 1B n = 3/40 (7.5%) <i>Y. enterocolitica</i> 2 n = 2/40 (5.0%) <i>Y. enterocolitica</i> 4 n = 1/40 (2.5%)	(9)
2015	2012-2013	Tonsils collected from 111 wild boars in Lower Saxony, Germany	<i>Y. frederiksenii</i> n = 2/111 (1.8%) <i>Y. enterocolitica</i> 1A n = 17/111 (15.3%) <i>Y. enterocolitica</i> 1B n = 2/111 (1.8%)	(4)
2015	2013	The samples collected from 20 wild boars shot in North-East Poland	<i>Y. enterocolitica</i> n = 11/20 (55%)	(10)
2016	2011-2014	434 wild boars hunted mainly in North-Eastern Poland	<i>Y. enterocolitica</i> n = 176/434 (40.6%)	(108)
2016	2011-2012	The 490 blood and 72 tonsillar samples of 505 wild boars, northern Spain	<i>Yersinia</i> sp. in blood samples n = 257/490 (52.5%) <i>Yersinia</i> sp. in tonsil samples n = 37/72 (51.4%) <i>Y. enterocolitica</i> in n = 24/72 (33.3%) <i>Y. pseudotuberculosis</i> in n = 18/72 (25.0%)	(6)
2018	2015-2016	Tonsil samples collected from 503 wild boars, northeast Germany	<i>Y. pseudotuberculosis</i> positive animals by PCR n = 32/503 (6.4%) <i>Y. pseudotuberculosis</i> positive animals by cultural detection n = 10/503 (2.0%)	(93)
2018	2014-2016	354 samples (136 samples from tonsils, 25 samples from submandibular lymph node, 14 samples from other tissue from the throat region, 90 samples from mesenteric lymph node and 90 samples from faeces) from 90 wild boars, Sweden	<i>Y. enterocolitica</i> in total n = 36/354 (10.2%) <i>Y. enterocolitica</i> in tonsils n = 19/136 (14.0%) <i>Y. enterocolitica</i> in submandibular lymph node n = 3/25 (12%) <i>Y. enterocolitica</i> in other tissue from the throat region n = 4/14 (28.6%) <i>Y. enterocolitica</i> in mesenteric lymph node n = 6/90 (6.7%) <i>Y. enterocolitica</i> in faeces n = 4/90 (4.4%) <i>Y. enterocolitica</i> in animals n = 28/90 (31.1%) <i>Y. pseudotuberculosis</i> in total n = 26/354 (7.3%) <i>Y. pseudotuberculosis</i> in tonsils n = 20/136 (14.7%) <i>Y. pseudotuberculosis</i> in mesenteric lymph node n = 4/90 (4.4%) <i>Y. pseudotuberculosis</i> in faeces n = 2/90 (2.2%) <i>Y. pseudotuberculosis</i> in animals n = 20/90 (22.2%)	(97)
2020	2017-2019	Mesenteric lymph nodes (MLNs) and faeces samples from 305 wild boars, northern Italy	<i>Y. enterocolitica</i> 1A in animals n = 25/305 (8.2%) <i>Y. enterocolitica</i> 1A in MLNs n = 10/305 (3.3%) <i>Y. enterocolitica</i> in faeces n = 19/305 (6.2%) <i>Y. enterocolitica</i> in adults n = 16/140 (11.4%) <i>Y. enterocolitica</i> in subadults n = 6/85 (7.1%) <i>Y. enterocolitica</i> in young animals n = 3/80 (3.8%) <i>Y. bercovieri</i> in animals n = 108/305 (35.4%) <i>Y. bercovieri</i> in MLNs n = 63/305 (20.7%) <i>Y. bercovieri</i> in faeces n = 64/305 (21.0%) <i>Y. bercovieri</i> in adults n = 41/140 (29.3%) <i>Y. bercovieri</i> in subadults n = 28/85 (32.9%) <i>Y. bercovieri</i> in young animals n = 39/80 (48.8%)	(15)
2020	2014-2016	Fecal samples from 54 wild boars, Japan	<i>Yersinia</i> spp. in animals n = 40/54 (74.1%) <i>Yersinia</i> spp. in total n = 69 <i>Y. enterocolitica</i> 1A n = 38/69 (55.1%) <i>Y. enterocolitica</i> 3 n = 1/69 (1.4%) <i>Y. kristensenii</i> n = 14/69 (20.3%) <i>Y. mollaretii</i> n = 7/69 (10.1%) <i>Y. bercovieri</i> n = 3/69 (4.3%) <i>Y. aldovae</i> n = 2/69 (3.0%) <i>Y. pseudotuberculosis</i> n = 2/69 (3.0%) <i>Y. frederiksenii</i> n = 1/69 (1.4%) <i>Y. intermedia</i> n = 1/69 (1.4%)	(111)

Year of publication	Year of study	Source of isolation / type of samples / country	Occurrence	References
2020	2016	Serum and visceral organ samples from 366 wild boars, Finland	<i>Yersinia</i> spp. antibodies in animals n = 102/181 (56%) ail-positive <i>Yersinia</i> spp. N = 22/130 (17%)	(34)
2021	2018-2020	Rectal swabs from 287 hunted wild boars during two hunting seasons, central Italy	<i>Yersinia</i> spp. in animals n = 71/287 (24.7%) <i>Y. enterocolitica</i> in total n = 54/71 (76.1%) <i>Y. enterocolitica</i> 1 n = 26/54 (48.1%) <i>Y. enterocolitica</i> 2 n = 9/54 (16.7%) <i>Y. enterocolitica</i> 3 n = 17/54 (31.5%) <i>Y. enterocolitica</i> 4 n = 1/54 (1.9%) <i>Y. enterocolitica</i> 5 n = 1/54 (1.9%) <i>Y. frederiksenii</i> or <i>Y. intermedia</i> n = 17/71 (23.9%)	(19)
2021	2013-2018	4890 liver samples collected from wild boars hunted in Liguria during five hunting seasons, north-western Italy	<i>Y. enterocolitica</i> in total n = 126/4890 (2.6%) <i>Y. enterocolitica</i> 1A n = 117/126 (92.9%) <i>Y. enterocolitica</i> 1A/O:8 n = 46/117 (39.3%) <i>Y. enterocolitica</i> 1A/O:5 n = 12/117 (10.3%) <i>Y. enterocolitica</i> 1A/O:9 n = 11/117 (9.4%) <i>Y. enterocolitica</i> 1A/O:3 n = 8/117 (6.8%) <i>Y. enterocolitica</i> 1A/O1, 2 n = 3/117 (2.6%) <i>Y. enterocolitica</i> 1A NT n = 37/117 (31.6%) <i>Y. enterocolitica</i> 1B n = 8/126 (6.3%) <i>Y. enterocolitica</i> 1B/O:8 n = 2/8 (25%) <i>Y. enterocolitica</i> 1B/O:5 n = 1/8 (12.5%) <i>Y. enterocolitica</i> 1B/O:1, 2 n = 1/8 (12.5%) <i>Y. enterocolitica</i> 1B NT n = 4/8 (50%) <i>Y. enterocolitica</i> 2 NT n = 1/126 (0.8%)	(60)
2023	2020-2022	181 samples (66 colon content, 66 mesenteric lymph node and 49 carcass surface) from 66 wild boars from northern and central Sardinia, Italy	<i>Y. enterocolitica</i> in animals n = 20/66 (30.3%) <i>Y. enterocolitica</i> in colon content n = 18/66 (27.3%) <i>Y. enterocolitica</i> in MLNs n = 3/66 (4.5%) <i>Y. enterocolitica</i> on carcass surface n = 3/49 (6.1%) <i>Y. enterocolitica</i> in total n = 24/181 (13.2%)	(104)
2023	No data	12 wild boar minced-meat samples obtained from six approved wild-game-handling establishments and 20 samples obtained from private hunters, Sweden	<i>Y. enterocolitica</i> in total n = 10/32 (31.3%) <i>Y. enterocolitica</i> in samples from wild-game-handling establishments n = 6/12 (50.0%) <i>Y. enterocolitica</i> in samples from private hunters n = 4/20 (20.0%)	(98)

Spain (6) and Bulgaria (79), Italy (15, 19, 60, 104) and Finland (34). Table 2 presents data published during the years 2011-2025 on the occurrence of *Yersinia* among wild boars. In Sweden 20.5% (n = 18/88) of wild boars were *Y. enterocolitica*-positive and 19.3% (n = 17/88) were *Y. pseudotuberculosis*-positive (96). In 2018 Sannö et al. has published data on prevalence of *Y. enterocolitica* in Swedish wild boar tonsils and faeces. They demonstrated that that 31% (n = 28/90) of wild boars were positive for *Y. enterocolitica* indicating a high prevalence of enteropathogenic *Yersinia* spp. (97). In a study conducted between October 2007 and March 2008 in Switzerland, it was found that 44% (n = 68/153) of wild boars tested positive for enteropathogenic *Y. enterocolitica* and *Y. pseudotuberculosis* (36). Fredriksson-Ahomaa et al. in 2011 compared the same strains to fattening pig isolates indicating differences in genotype profiles and antimicrobial resistance patterns (35). In northern Spain there were 33.3% (n = 24/72) positive samples for *Y. enterocolitica* indicating a high prevalence among wild boars in the Basque country (6). Von Altrock et al. (4) confirmed that 17.1% (n = 19/111) of the wild boar tonsils were positive for *Y. enterocolitica* in Lower Saxony in Germany, during the hunting season, between November 2012 and January 2013. Another

study from Germany confirmed 6.36% (n = 32/503) of wild boars positive for *Y. pseudotuberculosis* (93). Bulgarian findings (79) showed that wild animals such as rabbit (*Lepus europeus*), boar (*Sus scrofa scrofa*), asiatic jackal (*Canis aureus*), red fox (*Vulpes vulpes*), mouflon (*Ovis musimon*), european river otter (*Lutra lutra*), beech marten (*Martes foina*), polecat (*Mustela putorius*) and wild cat (*Felis silvestris*) could act as reservoirs for pathogenic *Yersinia* spp. Their results showed that 40.5% (n = 15/37) of *Y. enterocolitica* O:3, 5.4% (n = 2/37) of *Y. enterocolitica* O:5 and 5.4% (n = 2/37) of *Y. enterocolitica* O:8 were isolated from 37 wild animals. 5.4% (n = 2/37) of *Y. pseudotuberculosis* O:1, 24.3% (n = 9/37) of *Y. pseudotuberculosis* O:2, 27% (n = 10/37) of *Y. pseudotuberculosis* O:3, and 10.8% (n = 4/37) of *Y. pseudotuberculosis* O:5 were also isolated from wild animals living in Bulgaria (79).

Y. enterocolitica occurrence in wild boars in Poland has been confirmed by several studies. Morka K. et al. reported 4.6% positive cases (n = 6/130) in western Poland in 2018 (63). Syczyło K. et al. detected the bacteria in 25.3% of wild boars (n = 110/434) during hunting seasons between 2011 and 2014, based on samples collected in North-Eastern Poland and across 12 out of 16 voivodeships (97, 98). In North-East Poland, Bancerz-Kisiel A. et al. Reported a prevalence

of 55% during the 2013 hunting season ($n = 11/20$) (10) while in another study covering northern, central and southern Poland, the prevalence was 26.5% ($n = 40/151$) (9).

Yersiniosis in humans in Europe

The primary transmission route of *Y. enterocolitica* is the consumption of contaminated food. Strains of this species have been detected in a wide variety of food products; in addition to pork and wild boar meat, they have also been found in milk and dairy products, processed meat, seafood, fruits, and vegetables. Contaminated, untreated water can also serve as a potential source of infection (40, 95, 107). Additionally, domestic animals such as dogs and cats can act as asymptomatic carriers of the pathogen. Close contact with these animals, especially without proper hygiene, may increase the risk of transmission (29, 33, 46, 122). A possible, though rarely described, route of *Y. enterocolitica* transmission is human-to-human infection. Several such cases have been documented in the literature (44, 62, 92). One of the earliest pieces of evidence for this route of transmission is Gutman's 1973 study, in which the spread of infection between families likely occurred via the fecal-oral route (44). Additionally, a nosocomial outbreak of *Y. enterocolitica* has been reported, where the transmission mechanism involved direct person-to-person contact and contaminated hands of healthcare personnel (92). In addition to other documented transmission routes, *Y. enterocolitica* has been reported to spread through blood transfusions (42). According to the same review (42), in most reported cases, donors were asymptomatic carriers, and blood was collected during episodes of bacteremia. Bacteremia developed after intestinal yersiniosis, which had a self-limiting course. The bacteria proliferated in the stored blood, as low temperatures and the presence of nutrients favored their growth. The fatality rate was 54.5%, primarily due to septic shock induced by bacterial endotoxins. Among the transmission mechanisms of *Y. enterocolitica*, direct transmission is also noteworthy. Although this is a very rare mode of transmission, such cases have been reported in the literature (18, 51, 59). Reports describe cases of axillary abscesses in a construction worker following a finger injury (59), a butcher exposed to raw pork (51), and pyomyositis of the calf in a diabetic patient (18). In these cases, direct inoculation of the bacteria through damaged

skin or contact with contaminated material seems to be a likely route of infection, leading to soft tissue infections, such as abscesses and pyomyositis, not associated with typical foodborne transmission routes.

Yersiniosis, caused by *Y. enterocolitica*, was the third most frequently reported zoonosis in the European Union in 2015 (25) and 2016 (26), with the notification rate of 1.9 cases per 100 000 population (23). Between 2015 and 2019, the rate of yersiniosis cases in the EU was stable at 1.7-1.8 per 100,000 people. However, since 2019, there has been a significant increase in the number of cases. In 2023, the highest rate in the last decade was recorded: 2.4 per 100,000 people. The most common cause of infections (97.7% in 2023) is *Y. enterocolitica*, particularly bioserotype 4/O3, which is the most frequently identified bioserotype in Europe. In 2023, a total of 8,738 cases of yersiniosis were reported in 26 EU countries. The highest number of cases was recorded in Germany, France and Spain, which together accounted for 53% of all confirmed cases in the EU (23, 27, 28).

In the years 2010-2019 the number of yersiniosis cases in Poland has remained at constant levels (incidence rate between 0.53-0.67). In the years 2003-2023, the highest number of yersiniosis cases ($n = 350$) was noted in 2023 with an incidence rate of 0.93. Nevertheless, data on the number of cases can be underestimated due to low reportability and lack of bioserotyping as a part of routine diagnostics. The statistics on the incidence of yersiniosis in humans in Poland are presented in Figure 2.

The increasing scientific interest in *Y. enterocolitica* is driven by several factors. First, numerous studies confirm the widespread presence of *Y. enterocolitica*

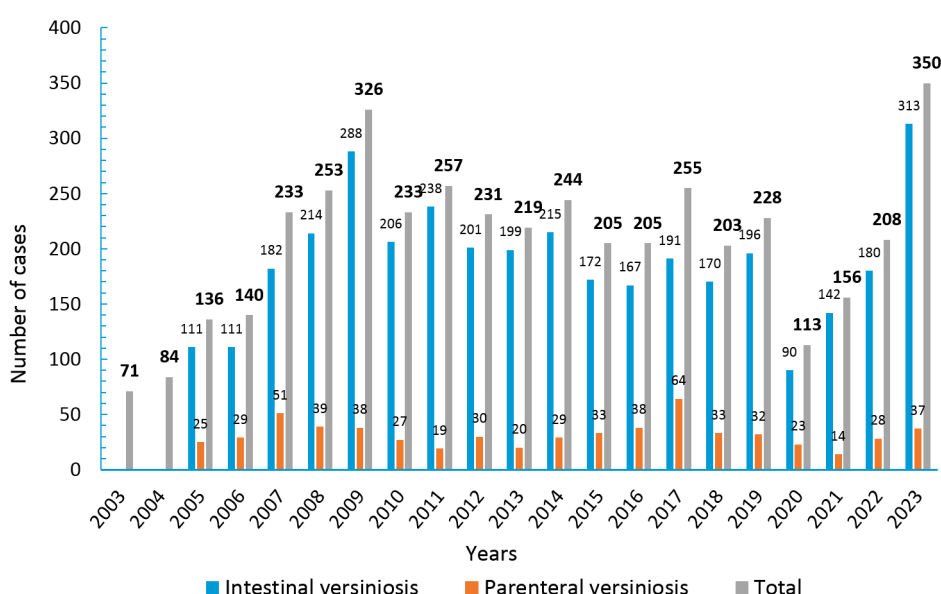


Fig. 2. Yersiniosis in Poland during the years 2003-2023 based on Epidemiological Reviews (14, 37-39, 48-50, 67, 68) and annual newsletters of National Institute of Public Health – National Institute of Hygiene – Department of Epidemiology and Chief Sanitary Inspectorate – Department for Communicable Disease and Infection Prevention and Control (69-74)

in pigs, which are a major source of human infections, primarily through the consumption of contaminated meat products. Additionally, the growing popularity of game meat-based diets and the persistent incidence of human yersiniosis highlight the need for further research on the epidemiology of this pathogen. Another important aspect is the significant wild boar population across many European countries, which highlights the role of these animals as potential carriers of *Y. enterocolitica*. All these factors emphasize the importance of studying the prevalence, microbiological diversity, and transmission mechanisms of this bacterium among different hosts.

Pathogenesis and immune response in experimental *Y. enterocolitica* infections in pigs

The pathogenesis of *Y. enterocolitica* infection in pigs, as well as the associated host immune responses, remain insufficiently elucidated. Pigs often serve as asymptomatic reservoirs of *Y. enterocolitica*, and the infection typically progresses without clinical signs or visible pathological lesions, making detection at both the farm and slaughterhouse levels particularly challenging. This silent carriage not only facilitates environmental dissemination but also poses a significant risk for zoonotic transmission and food safety, especially in the context of asymptomatically infected animals entering the food chain without detection. Therefore, a comprehensive understanding of the porcine immunological mechanisms involved in *Y. enterocolitica* infection is essential for developing effective control strategies and mitigating public health risks. Numerous studies have investigated experimental infections of pigs with *Y. enterocolitica*, focusing on various factors that influence the course and outcome of infection. Parameters such as the age of the animals, infection dose, and the route of exposure – particularly oral versus nasal inoculation – have been shown to affect the manifestation of clinical signs, the duration and extent of bacterial shedding, the persistence of asymptomatic carriage, and the distribution of the pathogen in internal organs over time (22, 66, 85-88). Esnault et al. confirmed that experimental inoculation of pigs with a pYV-positive *Y. enterocolitica* 4/O:3 strain, whether administered orally or nasally, does not result in clinical symptoms or pathological lesions under tested conditions. The infection progresses through three phases: primary detection, systemic colonization with immune response, and intermittent shedding. Despite bacterial persistence up to 56 days post-inoculation, changes such as *yad A* gene loss and new MLVA profiles indicated in vivo adaptation (22). Najdenski et al. demonstrated that oral infection of piglets with 5×10^{10} CFU of *Y. enterocolitica* 4/O:3 induced purulent meningoencephalitis, necrotic tonsillitis, lymphoid and leucocytic infiltration in the lungs, and catarrhal enteritis (66).

Further evidence is provided by the experimental studies conducted by Platt-Samoraj et al., who investigated the influence of *Y. enterocolitica* infection on the pregnancy course in sows (85-88). Twelve pregnant sows were infected *per os* with 2.7×10^9 CFU/ml of a pathogenic strain isolated from the tonsils of an aborted fetus, on days 33, 54, and 89 of gestation. The most pronounced clinical and pathological changes were observed in the group infected on day 89, where delayed deliveries, purulent vaginal discharge, and the highest number of stillborn piglets (14.6%) were recorded. Bacteriological examination confirmed the presence of *Y. enterocolitica* in the tonsils, mesenteric lymph nodes, and intestinal mucosa of infected sows, as well as in internal organs of stillborn piglets and placentas, particularly in the group infected in late gestation. These findings provide microbiological evidence for systemic and transplacental infection in the developing fetuses (86). Post-mortem examination of fetuses revealed hyperaemia, edema, necrosis, and degeneration of internal organs, suggesting a generalized bacterial infection. Histopathological evaluation revealed lymphoid tissue atrophy, poorly formed follicles, inflammatory infiltrations, and placental lesions (88). In sows, activation of lymphatic structures, eosinophilic and plasmacytic inflammation, and granulomatous changes were identified, particularly in those infected earlier in pregnancy. While no abortions occurred and clinical signs during gestation were absent, slight leukocytosis was observed in all infected groups. Hormonal analysis showed that the infection could influence plasma levels of progesterone and estrone sulphate depending on the pregnancy phase at the time of exposure (87). The combined bacteriological, histological, and endocrine findings suggest that *Y. enterocolitica* is capable of inducing intrauterine infection in pigs and negatively affecting reproductive outcomes, and that the timing of infection plays a decisive role in the severity and nature of the lesions observed (85-88).

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Corresponding author: Katarzyna Morka, PhD, DVM; e-mail: katarzyna.morka@upwr.edu.pl