Parasitology

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Global prevalence of *Cryptosporidium* spp. in pigs: a systematic review and meta-analysis

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Research Article

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Cite this article: Chen Y, Qin H, Wu Y, Xu H, Huang J, Li J, Zhang L (2023). Global prevalence of *Cryptosporidium* spp. in pigs: a systematic review and meta-analysis. *Parasitology* **150**, 531–544. https://doi.org/10.1017/S0031182023000276

Received: 9 November 2022
Revised: 18 February 2023
Accepted: 4 March 2023
First published online: 20 March 2023

Key words:
Cryptosporidium; meta-analysis; pig; prevalence

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Abstract

Cryptosporidium spp. are significant opportunistic pathogens causing diarrhoea in humans and animals. Pigs are one of the most important potential hosts for *Cryptosporidium*. We evaluated the prevalence of *Cryptosporidium* in pigs globally using published information and a random-effects model. In total, 131 datasets from 36 countries were included in the final quantitative analysis. The global prevalence of *Cryptosporidium* in pigs was 16.3% (8560/64 809; 95% confidence interval [CI] 15.0–17.6%). The highest prevalence of *Cryptosporidium* in pigs was 40.8% (478/1271) in Africa. Post-weaned pigs had a significantly higher prevalence (25.8%; 2739/11 824) than pre-weaned, fattening and adult pigs. The prevalence of *Cryptosporidium* was higher in pigs with no diarrhoea (12.2%; 371/3501) than in pigs that had diarrhoea (8.0%; 348/4874). Seven *Cryptosporidium* species (*Cryptosporidium scrofarum*, *Cryptosporidium suis*, *Cryptosporidium parvum*, *Cryptosporidium muris*, *Cryptosporidium tyzzeri*, *Cryptosporidium andersoni* and *Cryptosporidium struthioni*) were detected in pigs globally. The proportion of *C. scrofarum* was 34.3% (1491/4351); the proportion of *C. suis* was 31.8% (1385/4351) and the proportion of *C. parvum* was 2.3% (98/4351). The influence of different geographic factors (latitude, longitude, mean yearly temperature, mean yearly relative humidity and mean yearly precipitation) on the infection rate of *Cryptosporidium* in pigs was also analysed. The results indicate that *C. suis* is the dominant species in pre-weaned pigs, while *C. scrofarum* is the dominant species in fattening and adult pigs. The findings highlight the role of pigs as possible potential hosts of zoonotic cryptosporidiosis and the need for additional studies on the prevalence, transmission and control of *Cryptosporidium* in pigs.

Introduction

Cryptosporidium is an opportunistic zoonotic parasite found worldwide that infects many vertebrate hosts and typically causes self-limiting diarrhoea in humans and livestock (Kotloff, 2017; Hatam-Nahavandi *et al.*, 2019). *Cryptosporidium* is commonly found in the intestines of humans and animals and is transmitted by the fecal–oral route (Bouzid *et al.*, 2013). Children, immunodeficient individuals and newborn animals are among the groups that are susceptible to *Cryptosporidium* infection (Checkley *et al.*, 2015). Among animals susceptible to *Cryptosporidium*, pigs are considered as one of the main reservoir hosts (Qi *et al.*, 2020). There are no effective vaccines that can prevent cryptosporidiosis in humans or livestock (Dumaine *et al.*, 2020).

Globally, the first report of 3 pig cases of cryptosporidiosis was in 1977 (Kennedy *et al.*, 1977). Pigs with cryptosporidiosis are characterized by diarrhoea, vomiting, dehydration, reduced daily gain and a lower feed conversion rate (Vítovec and Koudela, 1992; Quílez *et al.*, 1996; Enemark *et al.*, 2003), and the parasites mainly live in the intestinal tract and gallbladder (Fleta *et al.*, 1995). There is considerable genetic variation in the genus *Cryptosporidium*; there are 44 known species, and more than 120 genotypes of *Cryptosporidium* have been identified (Ryan *et al.*, 2021). Thirteen different *Cryptosporidium* species/genotypes have been isolated in pigs, namely *Cryptosporidium scrofarum* (previously *Cryptosporidium* pig genotype II), *Cryptosporidium suis* (previously *Cryptosporidium* pig genotype I), *Cryptosporidium muris*, *Cryptosporidium parvum*, *Cryptosporidium tyzzeri* (previously *Cryptosporidium* mouse genotype I), *Cryptosporidium hominis*, *Cryptosporidium meleagridis*, *Cryptosporidium felis*, *Cryptosporidium andersoni*, *Cryptosporidium struthioni*, *Cryptosporidium* rat genotype, *Cryptosporidium* sp. Eire w65.5 and unknown *Cryptosporidium* genotype from pig slurry (Němejc *et al.*, 2013*b*; Wang *et al.*, 2021, 2022). *Cryptosporidium scrofarum* and *C. suis* infections account for more than 90% of cryptosporidiosis in pigs (Feng *et al.*, 2018). Cryptosporidiosis in pigs does not always cause clinical symptoms, and cases of human infection with *C. scrofarum* and *C. suis* suggest that these 2 *Cryptosporidium* species may be zoonotic (Kvác *et al.*, 2009*c*; Moore *et al.*, 2016; Sannella *et al.*, 2019). However, their pathogenicity and infectivity to humans are not well understood; so, they remain a potential threat to human health.

The global pig population was estimated at 952.6 million in 2020 (https://www.fao.org/). In animal husbandry, cryptosporidiosis causes huge economic losses due to weight loss in young animals, stunted growth and reduced production in adult animals (Pumipuntu and Piratae, 2018). Pigs are also animals that humans often contact directly or indirectly. Therefore, we performed a systematic review and meta-analysis to assess the global prevalence of *Cryptosporidium* in pigs. The potential risk factors including region, age and geographical and climatic factors were also analysed. The results describe the distribution characteristics of *Cryptosporidium* species in different age groups of pigs, and provide a basis for the prevention and control of *Cryptosporidium* infections.

Materials and methods

Search strategy and selection criteria

We used 5 literature databases (PubMed, Web of Science, the China National Knowledge Infrastructure, VIP Chinese Journals Database and Wanfang Data) to search for studies on the global prevalence of *Cryptosporidium* in pigs. All published studies on *Cryptosporidium* in pigs from 31 September 2022 onwards were included. We searched the 2 English databases with the term '*Cryptosporidium*', 'Cryptosporidiosis' cross-referenced with 'pig', 'swine', 'hog', 'wart', 'warthog', 'Phacochoerus', 'Suidae', 'boar' or 'piglet'. In the 3 Chinese databases, '*Cryptosporidium*' (Chinese) and 'pig' (Chinese) were used as keywords. We conducted analyses in accordance with the preferred reporting items for systematic reviews and meta-analyses (PRISMA) statement and the PRISMA 2009 checklist (Table S1). The articles for which full text was not available, the first author was not contacted for more research information and/or statistics.

The following clauses were used as the criteria for article exclusion:

1) the purpose of the study was not the prevalence of *Cryptosporidium* in pigs;
2) the total number of pigs tested and the number of pigs that tested positive were not provided;
3) the testing method was not clearly described;
4) the sample was a mixture of specimens from multiple pig feces;
5) the study sample size was less than 20;
6) the study was a review or a case report.

Quality assessment

We used established methods to evaluate the quality of the studies (Guyatt *et al.*, 2008). Studies with scores of 0 or 1 point were classified as low quality, studies with scores of 2 or 3 points were classified as medium quality, and studies with scores of 4 or 5 points were classified as high quality. A study scored 1 point if it included one of the following items:

1) a clear research goal;
2) a clearly defined research period;
3) a sample size of greater than 200;
4) a clear detection method;
5) analysis involving 3 or more influencing factors.

Data extraction

Two authors (Y. C. and H. Q.) separately screened all titles, abstracts and full texts and independently extracted the data. Disagreements were resolved by discussion with Y. W. Y. C. and H. Q. extracted information, including the first author, publication date, country, sampling time, detection method, total samples, positive samples, prevalence, study quality and *Cryptosporidium* species (Table S2).

Statistical analysis

All data were analysed using Stata version 14.0 (https://www.stata.com). Due to high heterogeneity ($I^2 > 50\%$, $P < 0.1$) of the data, the random-effects model was used for the meta-analysis. To investigate the potential sources of heterogeneity, sensitivity analysis, subgroup analysis and meta-regression analysis were performed on the extracted data. If a study involved multiple detection methods for *Cryptosporidium*, the molecular results in the analysis were the first choice. We used sensitivity analysis to test the stability of the data, and the overall study was evaluated using forest plots. We evaluated the effect of selected studies on the pooled prevalence by excluding single studies sequentially (Wang *et al.*, 2018*b*). Publication bias of the study was evaluated using a funnel plot and Egger's tests (Egger *et al.*, 1997). The following potential sources of heterogeneity were examined: region (Asia compared to other regions), age (post-weaned compared to the other age groups), presence or absence of diarrhoea (diarrhoea compared to non-diarrhoea) and *Cryptosporidium* species (*C. scrofarum* compared to the other species).

The global longitude and latitude span was large, and there were significant geographical differences. The data related to geographic factors were obtained from the National Oceanic and Atmospheric Administration (NOAA, https://gis.ncdc.noaa.gov/maps/ncei/cdo/monthly). We also used subgroup analysis and meta-regression analysis to evaluate the impact of geographical risk factors, including latitude (30°–60° *vs* others), longitude (<−60° *vs* others), mean yearly temperature (5–10 °C *vs* others), mean yearly relative humidity (<60% *vs* others), mean yearly precipitation (0–400 mm *vs* others).

Results

Characteristics of studies

A total of 833 publications were initially identified. After screening of the title and abstract, 162 potentially relevant articles were selected for full text search. Of these, 6 were review studies, 9 had incomplete information or only provided prevalence, 6 had sample sizes less than 20, 4 were case reports and 9 lacked full text. In total, 128 publications (including 131 datasets) were of sufficient quality and were considered suitable for meta-analysis (Fig. 1).

The selected studies came from 36 countries (Fig. 2, Table 1). A total of 71 datasets originated from Asia [China ($n = 54$), India ($n = 2$), Indonesia ($n = 1$), Japan ($n = 6$), Korea ($n = 3$), Thailand ($n = 1$), Turkey ($n = 1$), Vietnam ($n = 3$)]. A total of 30 datasets were from countries in Europe [Austria ($n = 1$), Czech Republic ($n = 6$), Denmark ($n = 2$), Germany ($n = 2$), Ireland ($n = 1$), Norway ($n = 1$), Poland ($n = 2$), Serbia ($n = 1$), Slovak Republic ($n = 2$), Spain ($n = 8$), Sweden ($n = 1$), Switzerland ($n = 1$) and the UK ($n = 1$)]. Eight datasets were from countries in Africa [Ghana ($n = 1$), Madagascar ($n = 1$), Malawi ($n = 1$), Nigeria ($n = 3$), South Africa ($n = 1$), Zambia ($n = 1$)]. A total of 10 datasets were from countries in North America [Canada ($n = 4$), Trinidad ($n = 1$), the USA ($n = 4$), Cuba ($n = 1$)]. Eight datasets were from South America [Argentina ($n = 1$), Brazil ($n = 4$), Colombia ($n = 2$), Ecuador ($n = 1$)]. Four datasets were from countries in Oceania [Australia ($n = 4$)] (Tables 1 and 2). Pre-weaned pigs were described in 48 datasets, post-weaned pigs were described in 63 datasets, fattening pigs were described in 48 datasets and adult pigs were described in 53 datasets. Most datasets lacked information on pig health status. Diarrhoea in pigs was reported in 14 datasets, and no diarrhoea in pigs was reported in 10 datasets (Table 2).

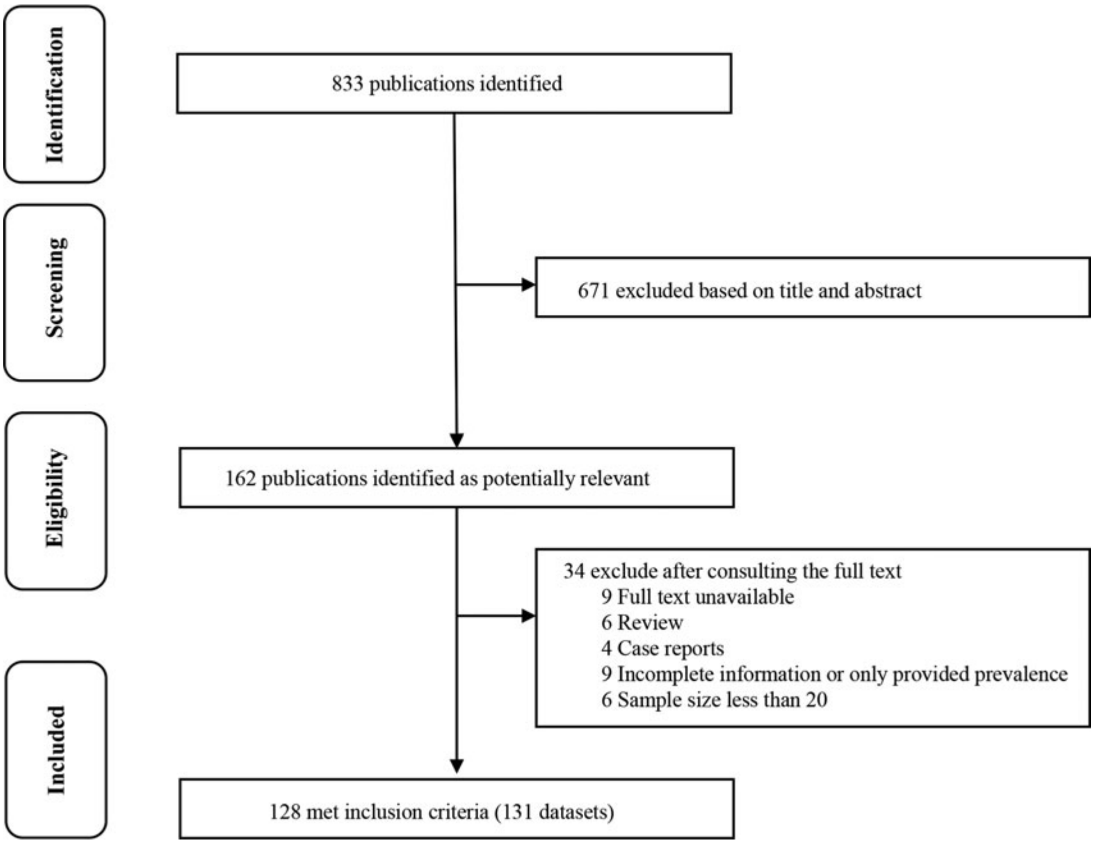


Fig. 1. Flow diagram of the selection of eligible studies.

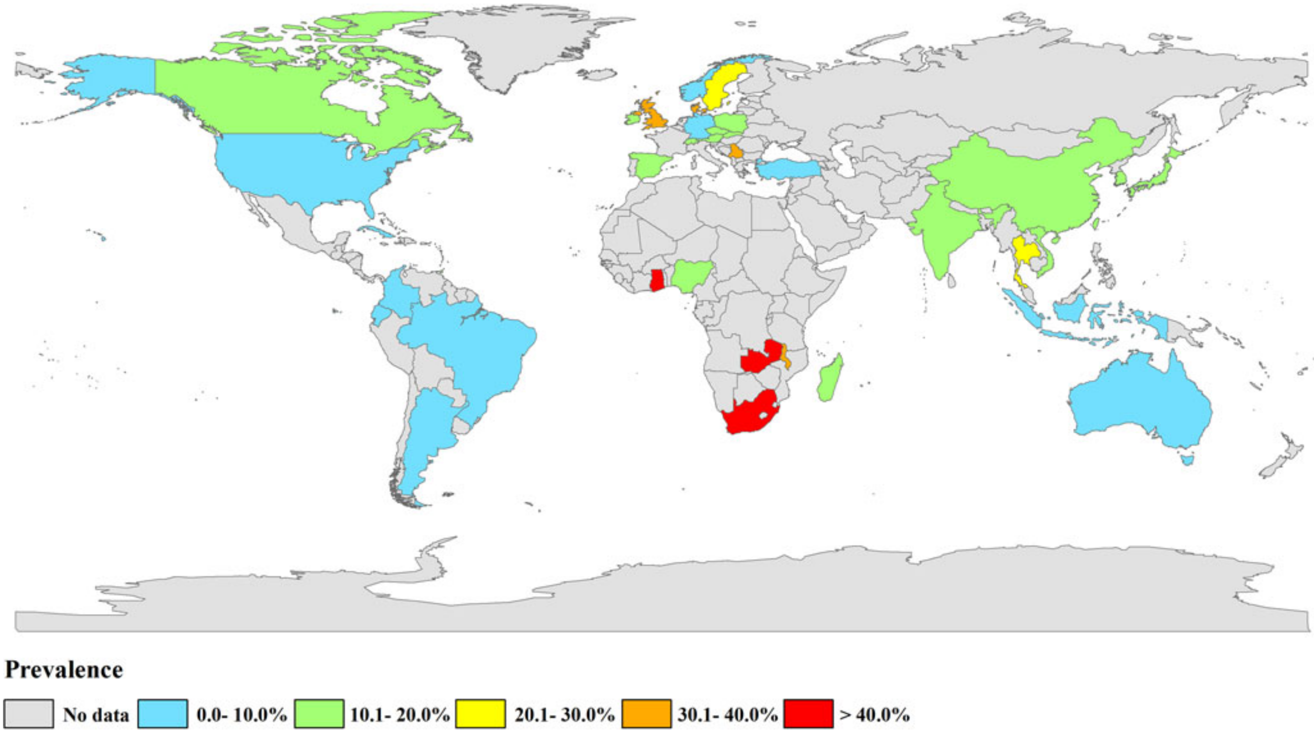


Fig. 2. Map of *Cryptosporidium* infection in pigs across the world. Prevalence ranges are shown in different colours. [The figure was designed using Arcgis 10.2, and the original vector diagram imported in Arcgis was adapted from Natural Earth (http://www.naturalearthdata.com).]

Cryptosporidium *infection in pigs by region*

The estimated *Cryptosporidium* prevalence in pigs ranged from 7.1% [95% confidence interval (CI) 3.6–10.5%] to 40.8% (95% CI 20.6–61.0%), with substantial heterogeneity ($I^2 = 98.8\%$, $P <$ 0.001). On a global scale, pooled estimated prevalence of *Cryptosporidium* infection in pigs was 16.3% (95% CI 15.0–17.6%, 8560/64 809) (Table 2). On 6 continents (Table 2, Figs 3–8), the infection rates of *Cryptosporidium* in pigs were 14.8% in

Table 1. Estimated pooled prevalence of *Cryptosporidium* infection by country/region

Country/regions	No. of studies	Region	No. tested	No. positive	% Prevalence	% (95% CI)
China	54	Asia	34650	4066	11.7	11.4–12.1
India	2	Asia	1195	131	11.0	9.2–12.7
Indonesia	1	Asia	205	13	6.3	3.0–9.7
Japan	6	Asia	2039	283	13.9	12.4–15.4
Korea	3	Asia	1582	212	13.4	11.7–15.1
Thailand	1	Asia	245	51	20.8	15.7–25.9
Turkey	1	Asia	238	21	8.8	5.2–12.5
Vietnam	3	Asia	961	164	17.1	14.7–19.4
Austria	1	Europe	44	8	18.2	6.3–30.0
Czech Republic	6	Europe	6939	943	13.6	12.8–14.4
Denmark	2	Europe	2093	745	35.6	33.5–37.6
Germany	2	Europe	1714	6	0.4	0.1–0.6
Ireland	1	Europe	342	39	11.4	8.0–14.8
Norway	1	Europe	684	57	8.3	6.3–10.4
Poland	2	Europe	295	57	19.3	14.8–23.9
Serbia	1	Europe	260	89	34.2	28.4–40.0
Slovak Republic	2	Europe	156	19	12.2	7.0–17.4
Spain	8	Europe	2378	325	13.7	12.3–15.0
Sweden	1	Europe	222	56	25.2	19.5–31.0
Switzerland	1	Europe	125	18	14.4	8.2–20.6
UK	1	Europe	308	119	38.6	33.2–44.1
UK/Ireland	1	Europe	56	25	44.6	31.2–58.1
Ghana	1	Africa	200	154	77.0	71.1–82.9
Madagascar	1	Africa	40	8	20.0	7.0–33.0
Malawi	1	Africa	92	30	32.6	22.8–42.4
Nigeria	3	Africa	632	118	18.7	15.6–21.7
South Africa	1	Africa	90	72	80.0	71.6–88.4
Zambia	1	Africa	217	96	44.2	37.6–50.9
Canada	4	North America	2593	302	11.6	10.4–12.9
Trinidad	1	North America	275	54	19.6	14.9–24.4
USA	4	North America	922	42	4.6	3.2–5.9
Cuba	1	North America	90	9	10.0	3.7–16.3
Argentina	1	South America	520	47	9.0	6.6–11.5
Brazil	4	South America	499	15	3.0	1.5–4.5
Colombia	2	South America	628	57	9.1	6.8–11.3
Ecuador	1	South America	26	2	7.7	0.0–18.7
Australia	4	Oceania	1254	107	8.5	7.0–10.1

Asia, 18.3% in Europe, 40.8% in Africa, 13.6% in North America, 7.1% in South America and 9.3% in Oceania. The highest number of studies on *Cryptosporidium* infections in pigs originated from Asia ($n = 71$). The highest prevalence rate was reported in South Africa [80.0% (95% CI 71.6–88.4%)], and the lowest prevalence rate was in Germany [0.4% (95% CI 0.1–0.6%)] (Table 1).

Prevalence related to age, presence or absence of diarrhoea and Cryptosporidium *species*

The *Cryptosporidium* infection rate in post-weaned pigs was 25.8% (95% CI 21.8–29.8%, 2739/11 824). This was significantly higher than that in pre-weaned pigs [12.0%, 95% CI 9.9–14.0%, 1061/11 370, odds ratio (OR) 2.93, $P < 0.05$], fattening pigs (17.4%, 95% CI 14.8–20.0%, 1186/8815, OR 1.94, $P < 0.05$) and adult pigs (12.7%, 95% CI 10.4–15.1%, 980/9658, OR 2.67, $P < 0.05$) (Table 2). The infection rate for pigs with diarrhoea was 8.0% (95% CI 5.6–10.3%, 348/4874), while the infection rate for pigs without diarrhoea was 12.2% (95% CI 8.4–15.9%, 371/3501) (Table 2). Seven *Cryptosporidium* species (*C. scrofarum*, *C. suis*, *C. parvum*, *C. muris*, *C. tyzzeri*, *C. andersoni*, *C. struthioni*) were detected in pigs globally (Table 3). The prevalence rate of *C. scrofarum* was 7.9% (95% CI 6.9–8.8%, 1491/23 168) and that of *C. suis* was 4.7% (95% CI 3.8–5.6%, 1385/25 036) (Table 2).

Table 2. Pooled prevalence of *Cryptosporidium* infection in pigs across the world

					Heterogeneity			Univariate meta-regression		Correlation analysis
	Number of datasets	Total samples	Positive samples	Prevalence % (95% CI)	χ^2	*P* value	I^2	*P* value	Coefficient (95% CI)	Adj R^2
Region								0.381	−0.183 (−0.593 to 0.228)	−0.18%
Asia	71	41 115	4941	14.8 (13.0–16.5)	4585.09	<0.001	98.5%			
Europe	30	15 616	2506	18.3 (14.4–22.2)	3167.63	<0.001	99.1%			
Africa	8	1271	478	40.8 (20.6–61.0)	528.56	<0.001	98.7%			
North America	10	3880	407	13.6 (8.6–18.7)	373.54	<0.001	97.6%			
South America	8	1673	121	7.1 (3.6–10.5)	47.05	<0.001	87.2%			
Oceania	4	1254	107	9.3 (2.2–16.4)	110.28	<0.001	97.3%			
Age								<0.001	0.606 (0.270–0.942)	5.77%
Pre-weaned	48	11 370	1061	12.0 (9.9–14.0)	964.35	<0.001	95.6%			
Post-weaned	63	11 824	2739	25.8 (21.8–29.8)	3198.35	<0.001	98.1%			
Fattening	48	8815	1186	17.4 (14.8–20.0)	1189.03	<0.001	96.3%			
Adult	53	9658	980	12.7 (10.4–15.1)	1224.19	<0.001	96.7%			
Diarrhoea								0.367	−0.323 (−1.051 to 0.405)	−0.66%
Yes	14	4874	348	8.0 (5.6–10.3)	113.84	<0.001	88.6%			
No	10	3501	371	12.2 (8.4–15.9)	94.20	<0.001	90.4%			
Species								0.002	0.775 (0.302–1.248)	7.91%
C. scrofarum	50	23 168	1491	7.9 (6.9–8.8)	1505.18	<0.001	96.7%			
C. suis	43	25 036	1385	4.7 (3.8–5.6)	1060.81	<0.001	96.0%			
Other[a]	19	6701	155	1.8 (1.2–2.5)	147.42	<0.001	87.8%			
Total	131	64 809	8560	16.3 (15.0–17.6)	10 445.02	<0.001	98.8%			

[a] Including *C. parvum*, *C. muris*, *C. tyzzeri*, *C. andersoni*, *C. struthioni*, *Cryptosporidium* spp.

Table 3. Extracted data from included studies for molecular methods of *Cryptosporidium* species

Country/region	Author (year of publication)	No. of positive samples	Species (no.)
Argentina	De Felice *et al.* (2020)	47	*C. scrofarum* (12), *C. suis* (7)
Australia	Johnson *et al.* (2008)	64	*C. scrofarum* (32), *C. suis* (13)
Australia	Ng *et al.* (2011)	3	*C. scrofarum* (3)
Australia	Ryan *et al.* (2003)	39	*C. scrofarum* (14), *C. suis* (14)
Austria	Němejc *et al.* (2013*b*)	8	*C. scrofarum* (6), *C. suis* (5)[a]
Brazil	Fiuza *et al.* (2011)	2	*C. scrofarum* (2)
Canada	Budu-Amoako *et al.* (2012)	163	*C. scrofarum* (69), *C. suis* (42), *C. tyzzeri* (1), *C. parvum* (2)
Canada	Farzan *et al.* (2011)	68	*C. scrofarum* (21), *C. suis* (1), *C. muris* (3), *C. parvum* (31)
China	Chen *et al.* (2011)	800	*C. scrofarum* (12), *C. suis* (63)[a]
China	Feng *et al.* (2020)	15	*C. scrofarum* (15)
China	Han *et al.* (2018)	17	*C. scrofarum* (16), *C. suis* (1)
China	Lam *et al.* (2022)	23	*C. scrofarum* (22), *C. suis* (1)
China	Li *et al.* (2016)	6	*C. scrofarum* (6)
China	Li *et al.* (2017)	3	*C. scrofarum* (3)
China	Li *et al.* (2018*a*)	24	*C. scrofarum* (24)
China	Li *et al.* (2022)	8	*C. scrofarum* (6), *C. suis* (2)
China	Lin *et al.* (2015)	44	*C. scrofarum* (2), *C. suis* (42)
China	Liu *et al.* (2021)	2	*C. parvum* (2)
China	Qi *et al.* (2020)	143	*C. scrofarum* (51), *C. suis* (90), *C. parvum* (2)
China	Wang *et al.* (2010)	111	*C. scrofarum* (14), *C. suis* (94)
China	Wang *et al.* (2018*a*)	28	*C. scrofarum* (10), *C. suis* (18)
China	Wang *et al.* (2019)	41	*C. struthioni* (41)
China	Wang *et al.* (2022)	57	*C. scrofarum* (46), *C. suis* (11)
China	Yang *et al.* (2020)	64	*C. scrofarum* (64)
China	Yao *et al.* (2020)	101	*C. scrofarum* (90), *C. suis* (4), *C. parvum* (7)
China	Yin *et al.* (2011)	16	*C. scrofarum* (16)
China	Yin *et al.* (2013)	79	*C. scrofarum* (65), *C. suis* (14)
China	Zhang *et al.* (2013)	63	*C. scrofarum* (41), *C. suis* (40)[a]
China	Zhang *et al.* (2020)	9	*C. scrofarum* (7), *C. suis* (2)
China	Zheng *et al.* (2019)	23	*C. scrofarum* (11), *C. suis* (12)
China	Zou *et al.* (2017)	70	*C. scrofarum* (70)
Czech Republic	Kvác *et al.* (2009*a*)	38	*C. scrofarum* (36), *C. suis* (15)[a], *C. parvum* (2)
Czech Republic	Kvác *et al.* (2009*b*)	87	*C. scrofarum* (23), *C. suis* (44), *C. muris* (2)
Czech Republic	Němejc *et al.* (2012)	32	*C. scrofarum* (19), *C. suis* (25)[a]
Czech Republic	Němejc *et al.* (2013*a*)	353	*C. scrofarum* (208), *C. suis* (224)[a], *C. parvum* (1), *C. muris* (3)
Czech Republic	Němejc *et al.* (2013*b*)	39	*C. scrofarum* (26), *C. suis* (25)[a]
Czech Republic	Vítovec *et al.* (2006)	394	*C. suis* (394)
Denmark	Langkjaer *et al.* (2007)	395	*C. scrofarum* (133), *C. suis* (50)
Denmark	Petersen *et al.* (2015)	350	*C. scrofarum* (38), *C. suis* (18)
Germany	Wieler *et al.* (2001)	4	*C. parvum* (4)
Indonesia	Resnhaleksmana *et al.* (2021)	13	*C. parvum* (13)
Ireland	Zintl *et al.* (2007)	39	*C. scrofarum* (11), *C. suis* (14), *C. parvum* (2), *C. muris* (1)
Japan	Katsuda *et al.* (2006)	14	C. parvum (14)
Japan	Yui *et al.* (2014*b*)	112	*C. scrofarum* (24), *C. suis* (21)[a]

(*Continued*)

Table 3. *(Continued.)*

Country/region	Author (year of publication)	No. of positive samples	Species (no.)
Poland	Němejc *et al.* (2013*b*)	11	*C. scrofarum* (10), *C. suis* (3)[a]
Poland	Rzeżutka *et al.* (2014)	46	*C. scrofarum* (40), *C. suis* (7), *C. parvum* (1), *Cryptosporidium* spp. (1)
Slovak Republic	Danišová *et al.* (2016)	16	*C. scrofarum* (11), *C. suis* (2), *C. muris* (3)[a], *C. andersoni* (1)
Slovak Republic	Němejc *et al.* (2013*b*)	3	*C. scrofarum* (1), *C. suis* (2)
Spain	García-Presedo *et al.* (2013)	35	*C. scrofarum* (19), *C. suis* (5), *C. parvum* (3)
Spain	Rivero-Juarez *et al.* (2020)	27	*C. scrofarum* (26), *C. suis* (1)
Spain	Suárez-Luengas *et al.* (2007)	32	*C. scrofarum* (16), *C. suis* (10)
Sweden	Pettersson *et al.* (2020)	56	*C. scrofarum* (36), *C. suis* (17), *C. parvum* (2)
Switzerland	Schubnell *et al.* (2016)	18	*C. scrofarum* (8), *C. suis* (4)
Thailand	Thathaisong *et al.* (2020)	51	*C. scrofarum* (42), *C. suis* (9)
UK\Ireland	Xiao *et al.* (2006)	25	*C. scrofarum* (11), *C. suis* (16), *C. muris* (1)
USA	Atwill *et al.* (1997)	12	*C. parvum* (12)
USA	Rodriguez-Rivera *et al.* (2016)	6	*C. scrofarum* (3), *C. suis* (1)
Vietnam	Iwashita *et al.* (2021)	2	*C. suis* (2)
Total		**4351**	***C. scrofarum* (1491), *C. suis* (1385), *C. parvum* (98), *C. struthioni* (41), *C. muris* (13), *C. tyzzeri* (1), *C. andersoni* (1), *Cryptosporidium* spp. (1)**

[a] Mixed infection

In Europe, *C. scrofarum* and *C. suis* infection rates were the highest, at 10.3% (678/6613) and 8.0% (881/10 951), respectively (Table S2).

Prevalence according to geographic and climatic variables

We analysed geographic subgroup factors. The prevalence of *Cryptosporidium* in pigs in regions with a −30° to 0° latitude range (22.9%, 95% CI 8.3–37.5%, 193/872), 0°–60° longitude range (29.3%, 95% CI 17.9–40.7%, 774/5729), 5–10 °C mean yearly temperature (25.4%, 95% CI 16.3–34.6%, 603/4991), <60% mean yearly relative humidity (21.5%, 95% CI 15.0–28.0%, 627/3921), 800–1200 mm mean yearly precipitation (20.7%, 95% CI 15.5–25.9%, 2006/10 586) was higher than that in other regions (Table S3).

Sensitivity analysis and publication bias

Sensitivity analysis indicated that the analysis was reliable (Figs S1–S6). We often used a funnel plot to measure the publication bias in selected articles. Some points fell outside the funnel and the funnel plot showed obvious asymmetry (Fig. 9). The *P* value was less than 0.001 by Egger's test (Table S4), indicating that obvious publication bias was found.

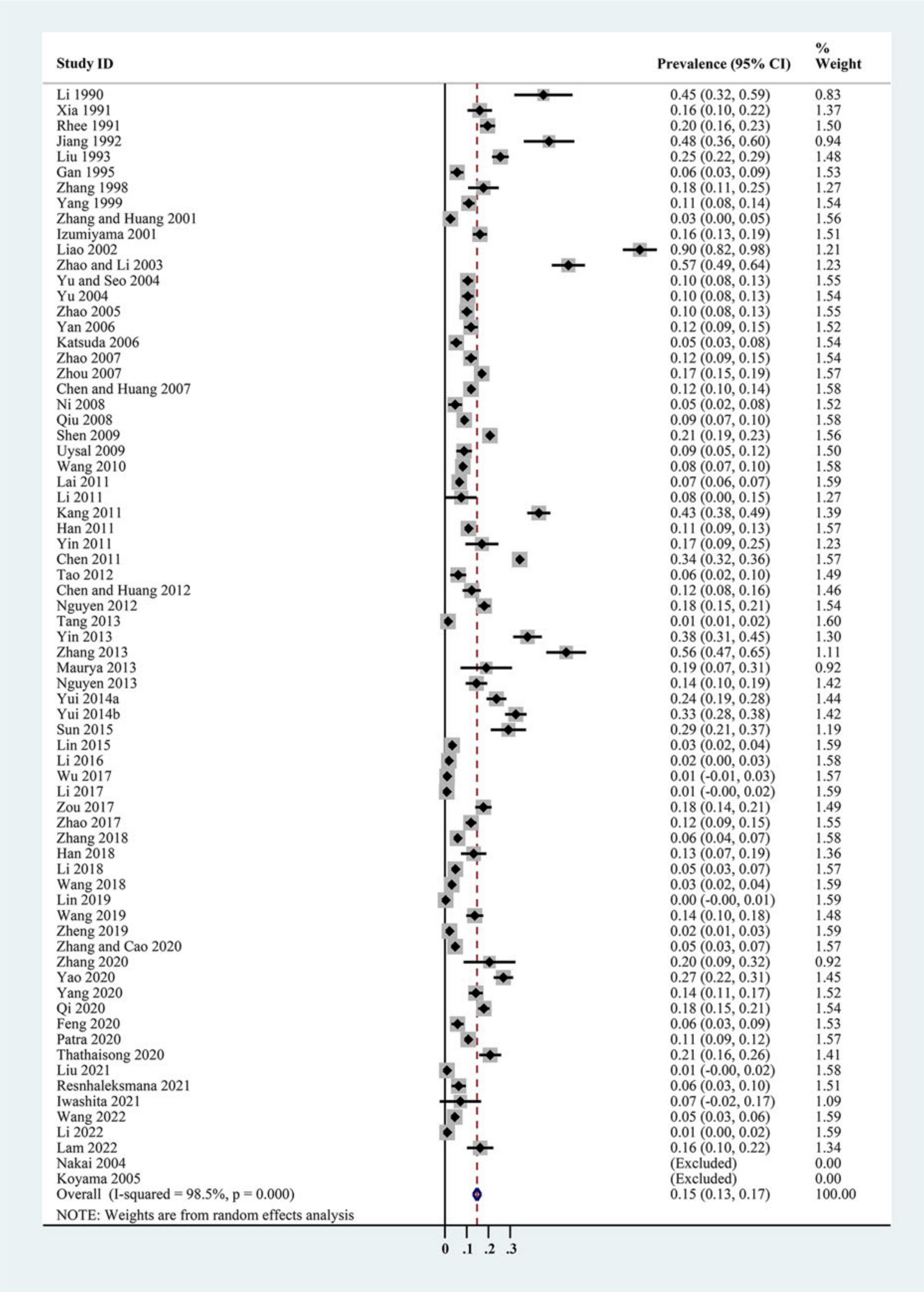
Sources of heterogeneity by meta-regression analysis

Univariate meta-regression analysis was used to determine the sources of heterogeneity. Age ($P < 0.001$), *Cryptosporidium* species ($P = 0.002$) and latitude ($P = 0.028$) were the factors that fostered heterogeneity. Region ($P = 0.381$), presence or absence of diarrhoea ($P = 0.367$), longitude ($P = 0.793$), mean temperature ($P = 0.345$), mean relative humidity ($P = 0.356$) and mean yearly precipitation ($P = 0.548$) were the factors that affected heterogeneity (Tables 2 and S3).

Discussion

A meta-analysis based on selected datasets from 36 countries on 6 continents produced an estimate of *Cryptosporidium* prevalence in pigs. As mentioned in a previous systematic review, *Cryptosporidium* prevalence in pigs was the highest in Asia, Africa and Europe (Hatam-Nahavandi *et al.*, 2019). Compared with previous study, the prevalence of *Cryptosporidium* in pigs was the highest in Africa, Europe and Asia in our study. In Europe, the highest infection rate was in the UK (38.6%, 95% CI 33.2–44.1%) (Featherstone *et al.*, 2010), while the lowest rate was in Germany (0.4%, 95% CI 0.1–0.6%) (Wieler *et al.*, 2001; Epe *et al.*, 2004). *Cryptosporidium* infection in pigs differs between countries and also in different regions of the same country. In China, 1 study reported an infection rate of only 0.9% (2/216) in pigs in Zhejiang (Liu *et al.*, 2021), while another study found a much higher infection rate of 26.9% (101/375) in pigs in Shaanxi (Yao *et al.*, 2020).

Previous studies demonstrated that the rate of *Cryptosporidium* infection in pigs was related to age factors (Maddox-Hyttel *et al.*, 2006; Featherstone *et al.*, 2010). In our analysis, the *Cryptosporidium* infection rate in post-weaned pigs was significantly higher than that in pigs of other age groups. This is consistent with other studies (Wang *et al.*, 2010; Yui *et al.*, 2014*a*, 2014*b*; Petersen *et al.*, 2015; Pettersson *et al.*, 2020; Qi *et al.*, 2020). Post-weaned piglets may be more susceptible to *Cryptosporidium* infection due to reduced immunity resulting from the loss of maternal immunity, or it may be due to weaning stress (Maddox-Hyttel *et al.*, 2006; Li *et al.*, 2018*b*). However, other studies revealed slightly divergent results. In Vietnam, the *Cryptosporidium* infection rate in pre-weaned pigs was higher (24.7%; 67/271) than that in post-weaned pigs (17.2%; 51/296), fattening pigs (7.1%; 7/98) or adult pigs (12.0%; 9/75) (Nguyen *et al.*, 2012). In China, 2 studies showed higher rates of *Cryptosporidium* infection in finishing pigs than in pre-weaned, post-weaned and adult pigs (Chen and Huang, 2007; Wang *et al.*, 2022). In general, *Cryptosporidium* infection



Study ID	Prevalence (95% CI)	% Weight
Li 1990	0.45 (0.32, 0.59)	0.83
Xia 1991	0.16 (0.10, 0.22)	1.37
Rhee 1991	0.20 (0.16, 0.23)	1.50
Jiang 1992	0.48 (0.36, 0.60)	0.94
Liu 1993	0.25 (0.22, 0.29)	1.48
Gan 1995	0.06 (0.03, 0.09)	1.53
Zhang 1998	0.18 (0.11, 0.25)	1.27
Yang 1999	0.11 (0.08, 0.14)	1.54
Zhang and Huang 2001	0.03 (0.00, 0.05)	1.56
Izumiyama 2001	0.16 (0.13, 0.19)	1.51
Liao 2002	0.90 (0.82, 0.98)	1.21
Zhao and Li 2003	0.57 (0.49, 0.64)	1.23
Yu and Seo 2004	0.10 (0.08, 0.13)	1.55
Yu 2004	0.10 (0.08, 0.13)	1.54
Zhao 2005	0.10 (0.08, 0.13)	1.55
Yan 2006	0.12 (0.09, 0.15)	1.52
Katsuda 2006	0.05 (0.03, 0.08)	1.54
Zhao 2007	0.12 (0.09, 0.15)	1.54
Zhou 2007	0.17 (0.15, 0.19)	1.57
Chen and Huang 2007	0.12 (0.10, 0.14)	1.58
Ni 2008	0.05 (0.02, 0.08)	1.52
Qiu 2008	0.09 (0.07, 0.10)	1.58
Shen 2009	0.21 (0.19, 0.23)	1.56
Uysal 2009	0.09 (0.05, 0.12)	1.50
Wang 2010	0.08 (0.07, 0.10)	1.58
Lai 2011	0.07 (0.06, 0.07)	1.59
Li 2011	0.08 (0.00, 0.15)	1.27
Kang 2011	0.43 (0.38, 0.49)	1.39
Han 2011	0.11 (0.09, 0.13)	1.57
Yin 2011	0.17 (0.09, 0.25)	1.23
Chen 2011	0.34 (0.32, 0.36)	1.57
Tao 2012	0.06 (0.02, 0.10)	1.49
Chen and Huang 2012	0.12 (0.08, 0.16)	1.46
Nguyen 2012	0.18 (0.15, 0.21)	1.54
Tang 2013	0.01 (0.01, 0.02)	1.60
Yin 2013	0.38 (0.31, 0.45)	1.30
Zhang 2013	0.56 (0.47, 0.65)	1.11
Maurya 2013	0.19 (0.07, 0.31)	0.92
Nguyen 2013	0.14 (0.10, 0.19)	1.42
Yui 2014a	0.24 (0.19, 0.28)	1.44
Yui 2014b	0.33 (0.28, 0.38)	1.42
Sun 2015	0.29 (0.21, 0.37)	1.19
Lin 2015	0.03 (0.02, 0.04)	1.59
Li 2016	0.02 (0.00, 0.03)	1.58
Wu 2017	0.01 (-0.01, 0.03)	1.57
Li 2017	0.01 (-0.00, 0.02)	1.59
Zou 2017	0.18 (0.14, 0.21)	1.49
Zhao 2017	0.12 (0.09, 0.15)	1.55
Zhang 2018	0.06 (0.04, 0.07)	1.58
Han 2018	0.13 (0.07, 0.19)	1.36
Li 2018	0.05 (0.03, 0.07)	1.57
Wang 2018	0.03 (0.02, 0.04)	1.59
Lin 2019	0.00 (-0.00, 0.01)	1.59
Wang 2019	0.14 (0.10, 0.18)	1.48
Zheng 2019	0.02 (0.01, 0.03)	1.59
Zhang and Cao 2020	0.05 (0.03, 0.07)	1.57
Zhang 2020	0.20 (0.09, 0.32)	0.92
Yao 2020	0.27 (0.22, 0.31)	1.45
Yang 2020	0.14 (0.11, 0.17)	1.52
Qi 2020	0.18 (0.15, 0.21)	1.54
Feng 2020	0.06 (0.03, 0.09)	1.53
Patra 2020	0.11 (0.09, 0.12)	1.57
Thathaisong 2020	0.21 (0.16, 0.26)	1.41
Liu 2021	0.01 (-0.00, 0.02)	1.58
Resnhaleksmana 2021	0.06 (0.03, 0.10)	1.51
Iwashita 2021	0.07 (-0.02, 0.17)	1.09
Wang 2022	0.05 (0.03, 0.06)	1.59
Li 2022	0.01 (0.00, 0.02)	1.59
Lam 2022	0.16 (0.10, 0.22)	1.34
Nakai 2004	(Excluded)	0.00
Koyama 2005	(Excluded)	0.00
Overall (I-squared = 98.5%, p = 0.000)	0.15 (0.13, 0.17)	100.00

NOTE: Weights are from random effects analysis

Fig. 3. Forest plot of the prevalence estimates of *Cryptosporidium* infection in pigs in Asia.

in post-weaned pigs has attracted greater attention. However, high rates of *Cryptosporidium* infection in pigs of other age groups suggest that different management measures among the geographical areas may be involved in infection.

The global prevalence of *Cryptosporidium* infection in pigs without diarrhoea was higher than that in pigs suffering from diarrhoea ($P < 0.05$). Most of the articles did not mention the presence or absence of diarrhoea in pigs. Insufficient data collection may

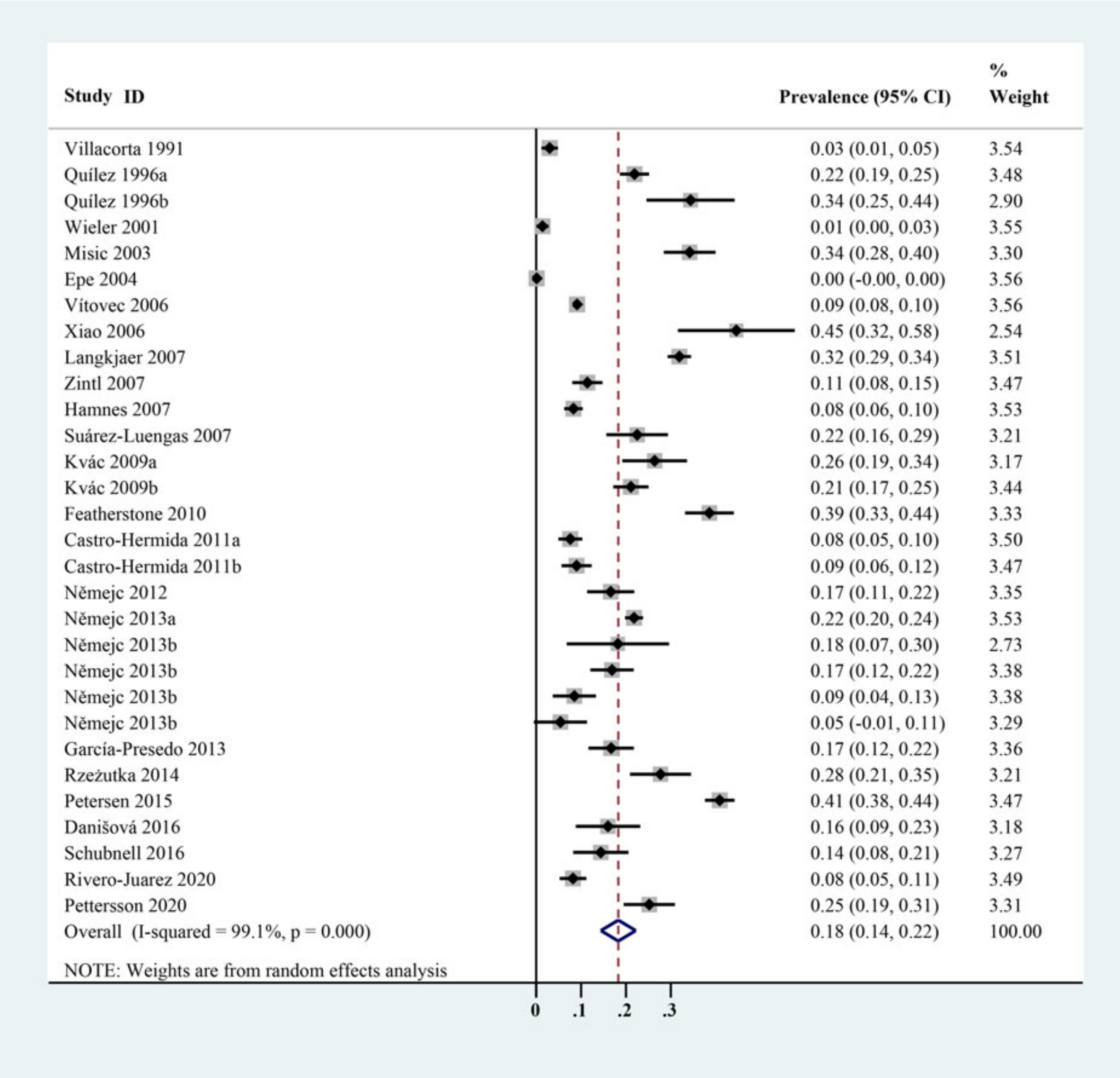


Fig. 4. Forest plot of the prevalence estimates of *Cryptosporidium* infection in pigs in Europe.

also affect the stability of the results. Therefore, the relationship between *Cryptosporidium* infection and diarrhoea in pigs remains unclear. Experimental infection studies showed that pigs shed a high number of *Cryptosporidium* oocysts but had no or mild diarrhoea. When *Cryptosporidium* was co-infected with other enteric pathogens, pigs exhibited significant diarrhoea and had a high mortality rate (Enemark *et al.*, 2003). These results indicated that feces of apparently healthy pigs may also contain *Cryptosporidium* oocysts and that prevention of *Cryptosporidium* transmission in healthy pigs should be considered.

Pre-weaned pigs shed significantly more *Cryptosporidium* oocysts than older pigs, and this was associated with *C. suis* infection (Kvác *et al.*, 2009*b*). Piglets were more susceptible to *C. suis* infection, while older pigs were more susceptible to *C. scrofarum* (Yin *et al.*, 2013). Compared with previous studies, *C. suis* and *C. scrofarum* are still the dominant species in pigs. Other *Cryptosporidium* species (*C. parvum*, *C. muris*, *C. tyzzeri*, *C. andersoni*, *C. struthioni*) have occasionally been reported in pigs. House mice were the main hosts of *C. muris* and *C. tyzzeri* (Feng *et al.*, 2018), and mice on pig farms may be involved in transmitting *Cryptosporidium*. *Cryptosporidium parvum* infection in pigs mainly occurred in Europe (Wieler *et al.*, 2001; Zintl *et al.*, 2007; Kvác *et al.*, 2009*a*; García-Presedo *et al.*, 2013; Němejc *et al.*, 2013*a*; Rzeżutka *et al.*, 2014; Pettersson *et al.*, 2020), Asia (Katsuda *et al.*, 2006; Qi *et al.*, 2020; Yao *et al.*, 2020; Liu *et al.*, 2021; Resnhaleksmana *et al.*, 2021) and North America (Atwill *et al.*, 1997; Farzan *et al.*, 2011; Budu-Amoako *et al.*, 2012). *Cryptosporidium parvum* may play a role in zoonotic transmission on pig farms. Therefore, necessary measures should be taken to reduce contact between breeders and pigs to reduce the transmission of *Cryptosporidium* from pigs to humans.

Oocysts can survive for a long time under many environmental conditions (Rose *et al.*, 2002; Gorospe, 2005; Alum *et al.*, 2014), and a single oocyst is sufficient to infect and cause disease in a susceptible host (Ramirez *et al.*, 2004). The prevalence of *Cryptosporidium* in pigs in regions with −30° to 0° latitude range (22.9%, 193/872) and 0°–60° longitude range (29.3%, 774/5729) was higher than that in pigs in other regions. Jagai *et al.* predicted that climate change would increase the spread of cryptosporidiosis infection, and that this spread would vary by season and location (Jagai *et al.*, 2009). The prevalence of *Cryptosporidium* in pigs was higher in areas with a mean yearly precipitation of 800–1200 mm (20.7%, 2006/10 586), mean yearly temperature of 5–10 °C (25.4%, 603/4991) and mean yearly relative humidity of < 60% (21.5%, 627/3921). These results indicated that cryptosporidiosis was more likely to occur in warm and rainy

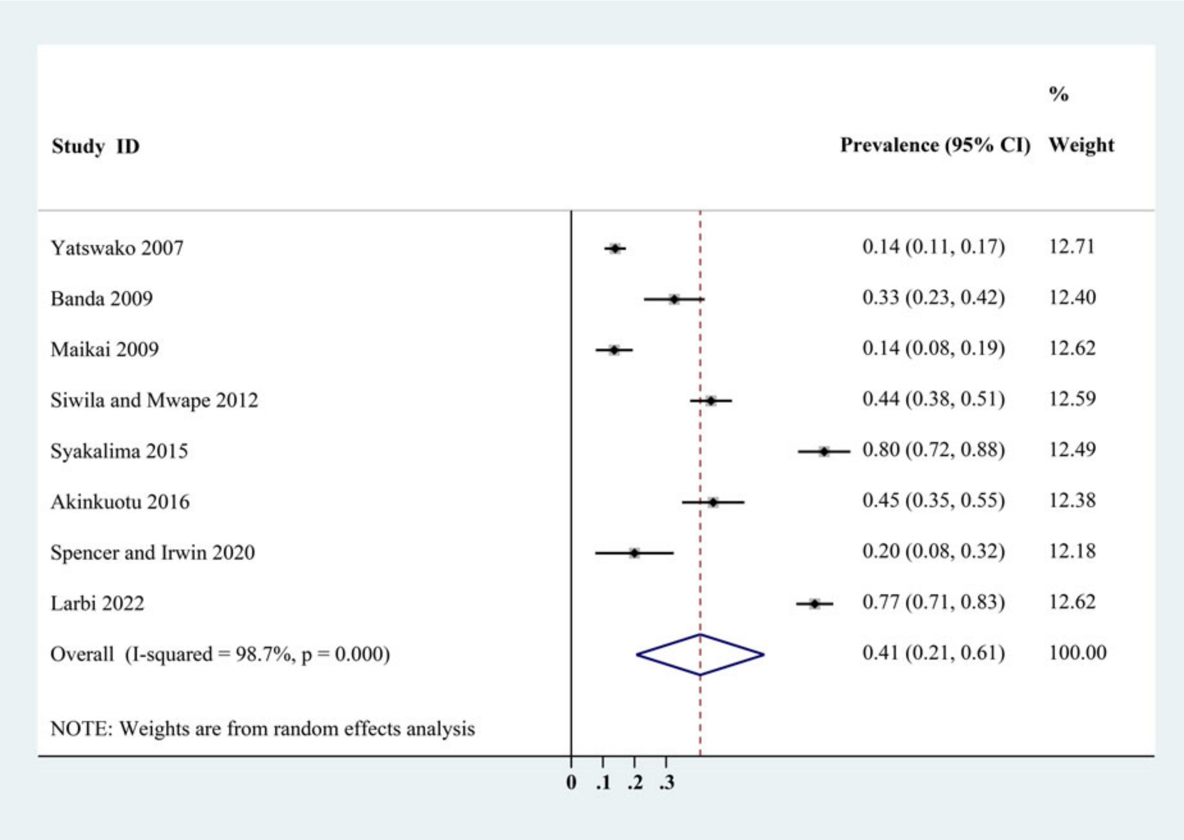


Fig. 5. Forest plot of the prevalence estimates of *Cryptosporidium* infection in pigs in Africa.

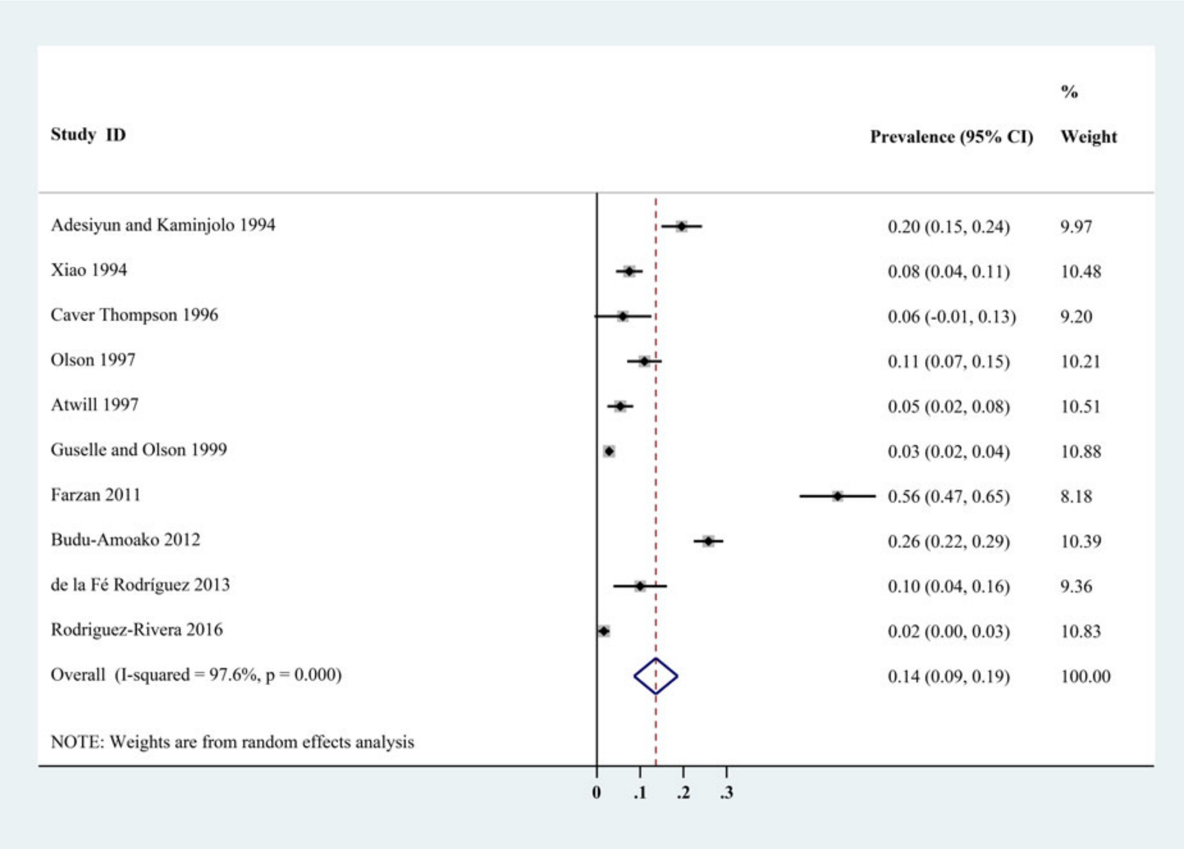


Fig. 6. Forest plot of the prevalence estimates of *Cryptosporidium* infection in pigs in North America.

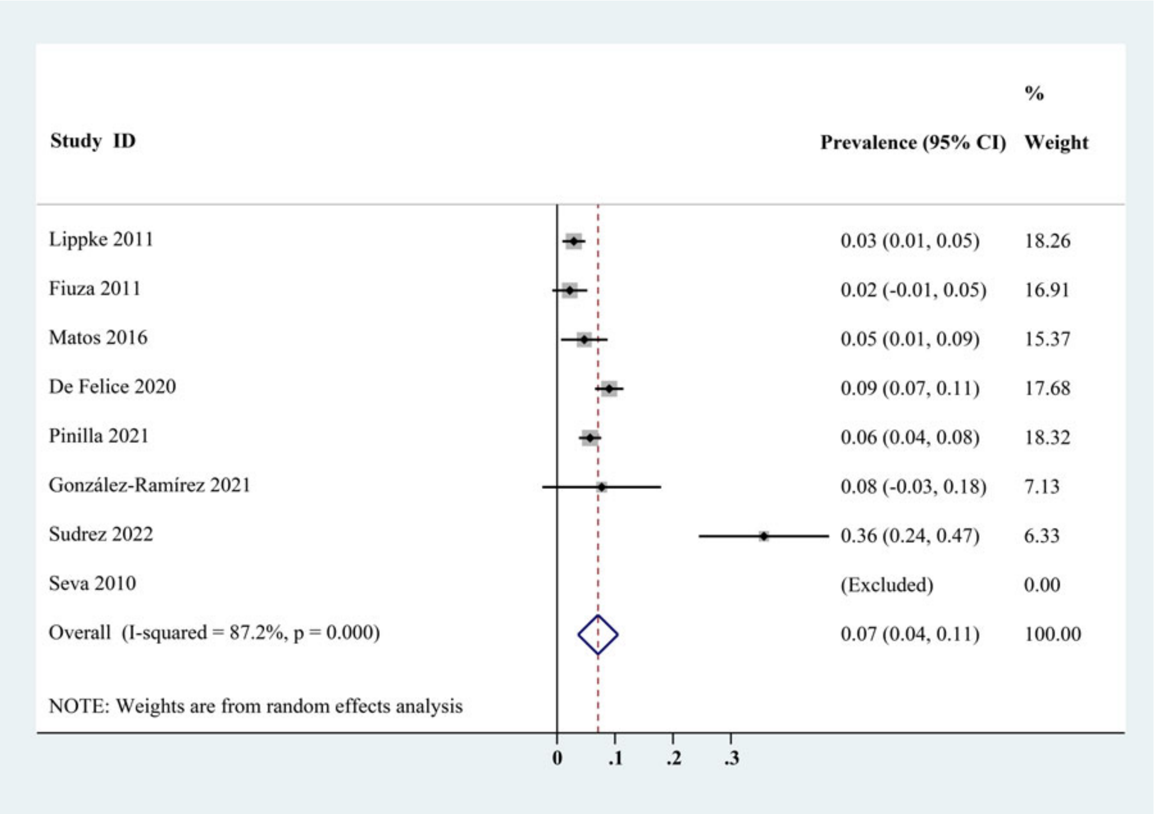


Fig. 7. Forest plot of the prevalence estimates of *Cryptosporidium* infection in pigs in South America.

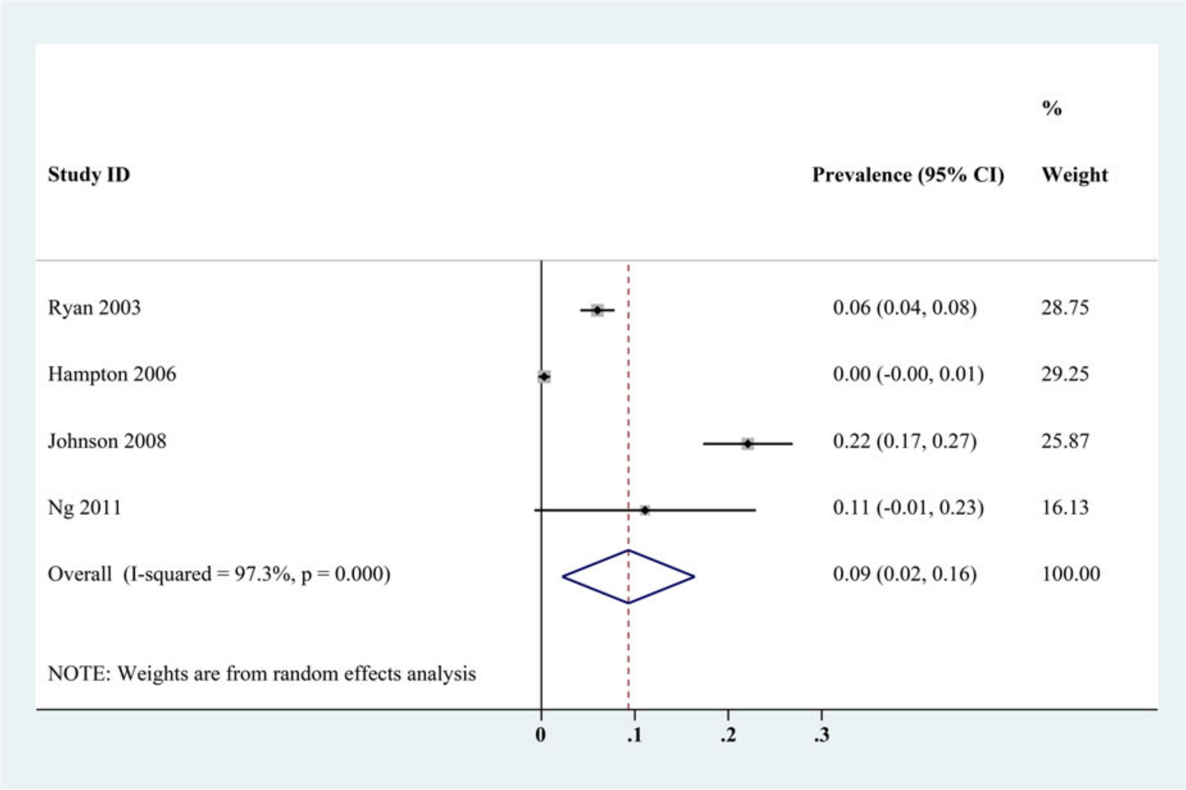


Fig. 8. Forest plot of the prevalence estimates of *Cryptosporidium* infection in pigs in Oceania.

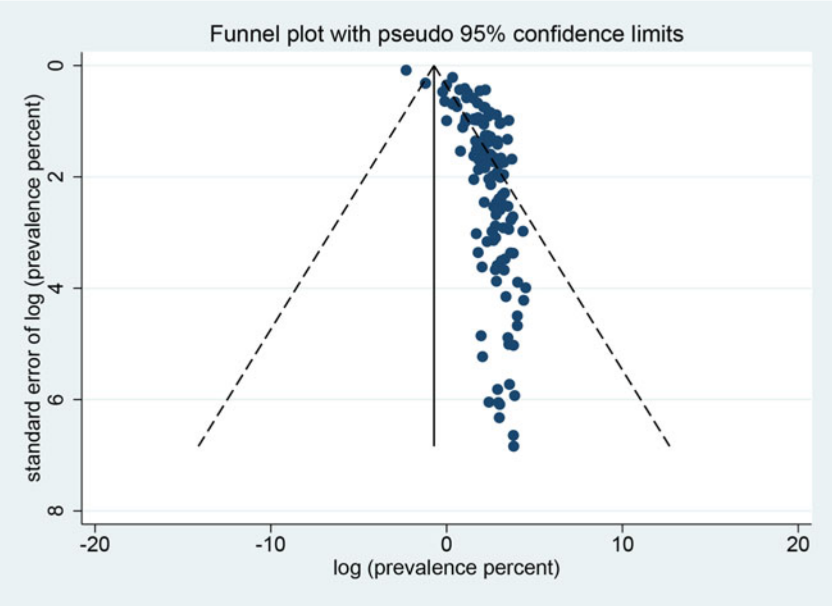


Fig. 9. Funnel plot for examination of publication bias of the prevalence estimates of *Cryptosporidium* infection in pigs across the world.

areas. Factors such as rainfall, temperature and humidity influence the life cycle of *Cryptosporidium* and may influence the timing and intensity of disease outbreaks (Patz *et al.*, 2000).

Limitations

The current study has the following limitations:

1. Some countries had only 1 publication of *Cryptosporidium* infecting pigs in the past 30 years.
2. Unpublished data were not included in the analysis.
3. Data of some conference abstracts were not included in the analysis.
4. Some publications lacked full text, and these articles were excluded.
5. Analysis of the factors involved was limited. Factors such as season, feeding model and pig breed may also be sources of heterogeneity.

Even so, we believe that the results of this study are close to the true global prevalence of *Cryptosporidium* in pigs.

Conclusions

This analysis shows that *Cryptosporidium* infection in pigs is widespread worldwide. *Cryptosporidium* can cause high levels of disease, particularly in Africa where infection rates are as high as 40.8%. *Cryptosporidium suis* is the dominant species in preweaned pigs while *C. scrofarum* is the dominant species in fattening and adult pigs. Pig age is an important risk factor associated with cryptosporidiosis. Age should be considered so that farmers can implement effective management plans based on geographical area and environmental factors and prevent zoonotic transmission. These findings highlight the role of pigs as possible potential hosts of zoonotic cryptosporidiosis and the need for additional studies on the prevalence, transmission and control of *Cryptosporidium* in pigs.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0031182023000276

Data availability. All data generated or used during the study appear in the submitted article.

Acknowledgements. We thank Accdon-LetPub Editor for editing the English text of a draft of this manuscript.

Author's contribution. L. Z. conceived and designed the study; Y. C., H. Q. and J. L. conducted the study; J. H., Y. C., H. X. and Y. W. collected and analysed the data; Y. C. and L. Z. wrote the manuscript. All the authors have read and approved the final version of the manuscript.

Financial support. This research was funded by the NSFC-Henan Joint Fund Key Project (U1904203) and the Leading Talents of the Central Plains Thousand Talents Program (19CZ0122).

Conflict of interest. None.

Ethical standards. Not applicable.

References

Alum A, Absar IM, Asaad H, Rubino JR and Ijaz MK (2014) Impact of environmental conditions on the survival of *Cryptosporidium* and *Giardia* on environmental surfaces. *Interdisciplinary Perspectives on Infectious Diseases* **2014**, 210385.

Atwill ER, Sweitzer RA, Pereira MG, Gardner IA, Van Vuren D and Boyce WM (1997) Prevalence of and associated risk factors for shedding *Cryptosporidium parvum* oocysts and *Giardia* cysts within feral pig populations in California. *Applied and Environmental Microbiology* **63**, 3946–3949.

Bouzid M, Hunter PR, Chalmers RM and Tyler KM (2013) *Cryptosporidium* pathogenicity and virulence. *Clinical Microbiology Reviews* **26**, 115–134.

Budu-Amoako E, Greenwood SJ, Dixon BR, Barkema HW, Hurnik D, Estey C and McClure JT (2012) Occurrence of *Giardia* and *Cryptosporidium* in pigs on Prince Edward Island, Canada. *Veterinary Parasitology* **184**, 18–24.

Checkley W, White Jr AC, Jaganath D, Arrowood MJ, Chalmers RM, Chen XM, Fayer R, Griffiths JK, Guerrant RL, Hedstrom L, Huston CD, Kotloff KL, Kang G, Mead JR, Miller M, Petri Jr WA, Priest JW, Roos DS, Striepen B, Thompson RC, Ward HD, Van Voorhis WA, Xiao L, Zhu G and Houpt ER (2015) A review of the global burden, novel diagnostics, therapeutics, and vaccine targets for *Cryptosporidium*. *The Lancet. Infectious Diseases* **15**, 85–94.

Chen F and Huang K (2007) Prevalence and phylogenetic analysis of *Cryptosporidium* in pigs in eastern China. *Zoonoses and Public Health* **54**, 393–400.

Chen Z, Mi R, Yu H, Shi Y, Huang Y, Chen Y and Lin J (2011) Prevalence of *Cryptosporidium* spp. in pigs in Shanghai, China. *Veterinary Parasitology* **181**, 113–119.

Danišová O, Valenčáková A and Petrincová A (2016) Detection and identification of six *Cryptospordium* species in livestock in Slovakia by amplification of SSU and GP60 genes with the use of PCR analysis. *Annals of Agricultural and Environmental Medicine: AAEM* **23**, 254–258.

De Felice LA, Moré G, Cappuccio J, Venturini MC and Unzaga JM (2020) Molecular characterization of *Cryptosporidium* spp. from domestic pigs in Argentina. *Veterinary Parasitology: Regional Studies and Reports* **22**, 100473.

Dumaine JE, Tandel J and Striepen B (2020) *Cryptosporidium parvum. Trends in Parasitology* **36**, 485–486.

Egger M, Davey Smith G, Schneider M and Minder C (1997) Bias in meta-analysis detected by a simple, graphical test. *British Medical Journal* **315**, 629–634.

Enemark HL, Ahrens P, Bille-Hansen V, Heegaard PM, Vigre H, Thamsborg SM and Lind P (2003) *Cryptosporidium parvum*: infectivity and pathogenicity of the 'porcine' genotype. *Parasitology* **126**, 407–416.

Epe C, Coati N and Schnieder T (2004) Results of parasitological examinations of faecal samples from horses, ruminants, pigs, dogs, cats, hedgehogs and rabbits between 1998 and 2002. *DTW. Deutsche Tierarztliche Wochenschrift* **111**, 243–247.

Farzan A, Parrington L, Coklin T, Cook A, Pintar K, Pollari F and Dixon B (2011) Detection and characterization of *Giardia duodenalis* and *Cryptosporidium* spp. on swine farms in Ontario, Canada. *Foodborne Pathogens and Disease* **8**, 1207–1213.

Featherstone CA, Marshall JA, Giles M, Sayers AR and Pritchard GC (2010) *Cryptosporidium* species infection in pigs in East Anglia. *The Veterinary Record*, 9 **166**, 51–52.

Feng Y, Ryan UM and Xiao L (2018) Genetic diversity and population structure of *Cryptosporidium. Trends in Parasitology* **34**, 997–1011.

Feng S, Jia T, Huang J, Fan Y, Chang H, Han S and He H (2020) Identification of *Enterocytozoon bieneusi* and *Cryptosporidium* spp. in farmed wild boars (*Sus scrofa*) in Beijing, China. *Infection Genetics and Evolution* **80**, 104231.

Fiuza VR, Gallo SS, Frazão-Teixeira E, Santín M, Fayer R and Oliveira FC (2011) *Cryptosporidium pig genotype II* diagnosed in pigs from the state of Rio De Janeiro, Brazil. *Journal of Parasitology* **97**, 146–147.

Fleta J, Sánchez-Acedo C, Clavel A and Quílez J (1995) Detection of *Cryptosporidium* oocysts in extra-intestinal tissues of sheep and pigs. *Veterinary Parasitology* **59**, 201–205.

García-Presedo I, Pedraza-Díaz S, González-Warleta M, Mezo M, Gómez-Bautista M, Ortega-Mora LM and Castro-Hermida JA (2013) Presence of *Cryptosporidium scrofarum*, *C. suis* and *C. parvum* subtypes IIaA16G2R1 and IIaA13G1R1 in Eurasian wild boars (*Sus scrofa*). *Veterinary Parasitology* **196**, 497–502.

Gorospe E (2005) Updates on the environmental risks and control of cryptosporidiosis. *International Journal of Infectious Diseases* **5**, 1–5.

Guyatt GH, Oxman AD, Vist GE, Kunz R, Falck-Ytter Y, Alonso-Coello P and Group GW (2008) GRADE: an emerging consensus on rating quality of evidence and strength of recommendations. *British Medical Journal* **336**, 924–926.

Han JQ, Shi LQ, Wu J, Li C, Zhu XQ, Zou FC and Luo ML (2018) Molecular epidemiological investigation and species identification of *Cryptosporidium* on Yunnan pig farm. *Chinese Journal of Veterinary Science* **48**, 311–315 (In Chinese).

Hatam-Nahavandi K, Ahmadpour E, Carmena D, Spotin A, Bangoura B and Xiao L (2019) *Cryptosporidium* infections in terrestrial ungulates with focus on livestock: a systematic review and meta-analysis. *Parasites & Vectors*, 14 **12**, 453.

Iwashita H, Takemura T, Tokizawa A, Sugamoto T, Thiem VD, Nguyen TH and Yamashiro T (2021) Molecular epidemiology of *Cryptosporidium* spp. in an agricultural area of northern Vietnam: a community survey. *Parasitology International* **83**, 102341.

Jagai JS, Castronovo DA, Monchak J and Naumova EN (2009) Seasonality of cryptosporidiosis: a meta-analysis approach. *Environmental Research* **109**, 465–478.

Johnson J, Buddle R, Reid S, Armson A and Ryan UM (2008) Prevalence of *Cryptosporidium* genotypes in pre and post-weaned pigs in Australia. *Experimental Parasitology* **119**, 418–421.

Katsuda K, Kohmoto M, Kawashima K and Tsunemitsu H (2006) Frequency of enteropathogen detection in suckling and weaned pigs with diarrhea in Japan. *Journal of Veterinary Diagnostic Investigation* **18**, 350–354.

Kennedy GA, Kreitner GL and Strafuss AC (1977) Cryptosporidiosis in three pigs. *Journal of the American Veterinary Medical Association*, 1 **170**, 348–350.

Kotloff KL (2017) The burden and etiology of diarrheal illness in developing countries. *Pediatric Clinics of North America* **64**, 799–814.

Kvác M, Sak B, Hanzlíková D, Kotilová J and Kvetonová D (2009a) Molecular characterization of *Cryptosporidium* isolates from pigs at slaughterhouses in South Bohemia, Czech Republic. *Parasitology Research* **104**, 425–428.

Kvác M, Hanzlíková D, Sak B and Kvetonová D (2009b) Prevalence and age-related infection of *Cryptosporidium suis*, *C. muris* and *Cryptosporidium pig genotype II* in pigs on a farm complex in the Czech Republic. *Veterinary Parasitology* **160**, 319–322.

Kvác M, Kvetonová D, Sak B and Ditrich O (2009c) *Cryptosporidium pig genotype II* in immunocompetent man. *Emerging Infectious Diseases* **15**, 982–983.

Lam HYP, Tseng YC, Wu WJ, Yu YH, Cheng PC and Peng SY (2022) Prevalence and genotypes of *Cryptosporidium* in livestock in Hualien Country, Eastern Taiwan. *Parasitology International* **88**, 102553.

Langkjaer RB, Vigre H, Enemark HL and Maddox-Hyttel C (2007) Molecular and phylogenetic characterization of *Cryptosporidium* and *Giardia* from pigs and cattle in Denmark. *Parasitology* **134**, 339–350.

Li W, Yu XM, Zhong ZJ, Wang Q, Liu XH, Yu JQ and Peng GN (2016) Isolation and identification of *Giardia* and *Cryptosporidium* from wild boar source and small fragrant pig source in Sichuan province. *China Veterinary Science* **46**, 1166–1169 (In Chinese).

Li W, Deng L, Wu K, Huang X, Song Y, Su H and Peng G (2017) Presence of zoonotic *Cryptosporidium scrofarum*, *Giardia duodenalis* assemblage A and *Enterocytozoon bieneusi* genotypes in captive Eurasian wild boars (*Sus scrofa*) in China: potential for zoonotic transmission. *Parasites & Vectors* **10**, 10.

Li WC, Yang HH, Kan ZZ, Yang YL, Sun YY, Gu YF and Chen HL (2018a) Investigation on the status of *Cryptosporidium* infection in large-scale pig farms in Jiangbei area, Anhui Province. *Chinese Journal of Schistosomiasis Control* **30**, 420–423, 464. (In Chinese).

Li Y, Guo Y, Wen Z, Jiang X, Ma X and Han X (2018b) Weaning stress perturbs gut microbiome and its metabolic profile in piglets. *Scientific Reports*, 24 **8**, 18068.

Li D, Deng H, Zheng Y, Zhang H, Wang S, He L and Zhao J (2022) First characterization and zoonotic potential of *Cryptosporidium* spp. and *Giardia duodenalis* in pigs in Hubei Province of China. *Frontiers in Cellular and Infection Microbiology* **12**, 949773.

Lin Q, Wang XY, Chen JW, Ding L and Zhao GH (2015) *Cryptosporidium suis* infection in post-weaned and adult pigs in Shaanxi province, northwestern China. *Korean Journal of Parasitology* **53**, 113–117.

Liu H, Ni H, Xu J, Wang R, Li Y, Shen Y and Yin J (2021) Genotyping and zoonotic potential of *Cryptosporidium* and *Enterocytozoon bieneusi* in pigs transported across regions in China. *Microbial Pathogenesis* **154**, 104823.

Maddox-Hyttel C, Langkjaer RB, Enemark HL and Vigre H (2006) *Cryptosporidium* and *Giardia* in different age groups of Danish cattle and pigs – occurrence and management associated risk factors. *Veterinary Parasitology*, 10 **141**, 48–59.

Moore CE, Elwin K, Phot N, Seng C, Mao S, Suy K, Kumar V, Nader J, Bousfield R, Perera S, Bailey JW, Beeching NJ, Day NP, Parry CM and Chalmers RM (2016) Molecular characterization of *Cryptosporidium* species and *Giardia duodenalis* from symptomatic Cambodian children. *PLoS Neglected Tropical Diseases*, 7 **10**, e0004822.

Němejc K, Sak B, Květoňová D, Hanzal V, Jeníková M and Kváč M (2012) The first report on *Cryptosporidium suis* and *Cryptosporidium pig genotype II* in Eurasian wild boars (*Sus scrofa*) (Czech Republic). *Veterinary Parasitology* **184**, 122–125.

Němejc K, Sak B, Květoňová D, Kernerová N, Rost M, Cama VA and Kváč M (2013a) Occurrence of *Cryptosporidium suis* and *Cryptosporidium scrofarum* on commercial swine farms in the Czech Republic and its associations with age and husbandry practices. *Parasitology Research* **112**, 1143–1154.

Němejc K, Sak B, Květoňová D, Hanzal V, Janiszewski P, Forejtek P and Kváč M (2013b) *Cryptosporidium suis* and *Cryptosporidium scrofarum* in Eurasian wild boars (*Sus scrofa*) in Central Europe. *Veterinary Parasitology* **197**, 504–508.

Ng J, Yang R, Whiffin V, Cox P and Ryan U (2011) Identification of zoonotic *Cryptosporidium* and *Giardia genotypes* infecting animals in Sydney's water catchments. *Experimental Parasitology* **128**, 138–144.

Nguyen ST, Honma H, Geurden T, Ikarash M, Fukuda Y, Huynh VV, Nguyen DT and Nakai Y (2012) Prevalence and risk factors associated with *Cryptosporidium* oocysts shedding in pigs in Central Vietnam. *Research in Veterinary Science* **93**, 848–852.

Patz JA, Graczyk TK, Geller N and Vittor AY (2000) Effects of environmental change on emerging parasitic diseases. *International Journal for Parasitology* **30**, 1395–1405.

Petersen HH, Jianmin W, Katakam KK, Mejer H, Thamsborg SM, Dalsgaard A and Enemark HL (2015) *Cryptosporidium* and *Giardia* in Danish organic pig farms: seasonal and age-related variation in prevalence, infection intensity and species/genotypes. *Veterinary Parasitology* **214**, 29–39.

Pettersson E, Ahola H, Frössling J, Wallgren P and Troell K (2020) Detection and molecular characterisation of *Cryptosporidium* spp. in Swedish pigs. *Acta Veterinaria Scandinavica* **62**, 40.

Pumipuntu N and Piratae S (2018) Cryptosporidiosis: a zoonotic disease concern. *Veterinary World* **11**, 681–686.

Qi M, Zhang Q, Xu C, Zhang Y, Xing J, Tao D and Zhang L (2020) Prevalence and molecular characterization of *Cryptosporidium* spp. in pigs in Xinjiang, China. *Acta Tropica* **209**, 105551.

Quílez J, Sánchez-Acedo C, Clavel A, del Cacho E and López-Bernad F (1996) Prevalence of *Cryptosporidium* infections in pigs in Aragón (northeastern Spain). *Veterinary Parasitology* **67**, 83–88.

Ramirez NE, Ward LA and Sreevatsan S (2004) A review of the biology and epidemiology of cryptosporidiosis in humans and animals. *Microbes and Infection* **6**, 773–785.

Resnhaleksmana E, Wijayanti MA and Artama WT (2021) A potential zoonotic parasite: *Cryptosporidium parvum* transmission in rats, pigs and humans in West Lombok, Indonesia. *African Journal of Infectious Diseases* **15**, 44–51.

Rivero-Juarez A, Dashti A, López-López P, Muadica AS, Risalde MLA, Köster PC and Carmena D (2020) Protist enteroparasites in wild boar (*Sus scrofa ferus*) and black Iberian pig (*Sus scrofa domesticus*) in southern Spain: a protective effect on hepatitis E acquisition? *Parasites & Vectors* **13**, 281.

Rodriguez-Rivera LD, Cummings KJ, McNeely I, Suchodolski JS, Scorza AV, Lappin MR and Bodenchuk MJ (2016) Prevalence and diversity of *Cryptosporidium* and *Giardia* identified among feral pigs in Texas. *Vector Borne and Zoonotic Diseases* **16**, 765–768.

Rose JB, Huffman DE and Gennaccaro A (2002) Risk and control of waterborne cryptosporidiosis. *FEMS Microbiology Reviews* **26**, 113–123.

Ryan UM, Samarasinghe B, Read C, Buddle JR, Robertson ID and Thompson RC (2003) Identification of a novel *Cryptosporidium* genotype in pigs. *Applied and Environmental Microbiology* **69**, 3970–3974.

Ryan UM, Feng Y, Fayer R and Xiao L (2021) Taxonomy and molecular epidemiology of *Cryptosporidium* and *Giardia* – a 50 year perspective (1971–2021). *International Journal for Parasitology* **51**, 1099–1119.

Rzeżutka A, Kaupke A, Kozyra I and Pejsak Z (2014) Molecular studies on pig cryptosporidiosis in Poland. *Polish Journal of Veterinary Sciences* **17**, 577–582.

Sannella AR, Suputtamongkol Y, Wongsawat E and Cacciò SM (2019) A retrospective molecular study of *Cryptosporidium* species and genotypes in HIV-infected patients from Thailand. *Parasites & Vectors* **12**, 91.

Schubnell F, von Ah S, Graage R, Sydler T, Sidler X, Hadorn D and Basso W (2016) Occurrence, clinical involvement and zoonotic potential of endoparasites infecting Swiss pigs. *Parasitology International* **65**, 618–624.

Suárez-Luengas L, Clavel A, Quílez J, Goñi-Cepero MP, Torres E, Sánchez-Acedo C and del Cacho E (2007) Molecular characterization of *Cryptosporidium* isolates from pigs in Zaragoza (northeastern Spain). *Veterinary Parasitology* **148**, 231–235.

Thathaisong U, Siripattanapipong S, Inpankaew T, Leelayoova S and Mungthin M (2020) High prevalence of *Cryptosporidium* infection caused by *C. scrofarum* and *C. suis* among pigs in Thailand. *Parasitology International* **77**, 102122.

Vítovec J and Koudela B (1992) Pathogenesis of intestinal cryptosporidiosis in conventional and gnotobiotic piglets. *Veterinary Parasitology* **43**, 25–36.

Vítovec J, Hamadejová K, Landová L, Kvác M, Kvetonová D and Sak B (2006) Prevalence and pathogenicity of *Cryptosporidium suis* in pre- and post-weaned pigs. *Journal of Veterinary Medicine. B, Infectious Diseases and Veterinary Public Health* **53**, 239–243.

Wang R, Qiu S, Jian F, Zhang S, Shen Y, Zhang L and Xiao L (2010) Prevalence and molecular identification of *Cryptosporidium* spp. in pigs in Henan, China. *Parasitology Research* **107**, 1489–1494.

Wang H, Zhang Y, Wu Y, Li J, Qi M, Li T and Zhang L (2018a) Occurrence, molecular characterization, and assessment of zoonotic risk of *Cryptosporidium* spp., *Giardia duodenalis*, and *Enterocytozoon bieneusi* in pigs in Henan, Central China. *Journal of Eukaryotic Microbiology* **65**, 893–901.

Wang ZD, Liu Q, Liu HH, Li S, Zhang L, Zhao YK and Zhu XQ (2018b) Prevalence of *Cryptosporidium*, microsporidia and *Isospora* infection in HIV-infected people: a global systematic review and meta-analysis. *Parasites &Vectors* **11**, 28.

Wang FY, Shi WQ, Hou ZF, Zhao ZX, Feng J, Xu JJ, Tao JP and Liu DD (2019) Investigation of *Cryptosporidium* infection in a large-scale pig farm in Yancheng, Jiangsu Province. *Animal Husbandry & Veterinary Medicine* **51**, 78–82 (In Chinese).

Wang W, Gong QL, Zeng A, Li MH, Zhao Q and Ni HB (2021) Prevalence of *Cryptosporidium* in pigs in China: a systematic review and meta-analysis. *Transboundary and Emerging Diseases* **68**, 1400–1413.

Wang P, Li S, Zou Y, Du ZC, Song DP, Wang P and Chen XQ (2022) The infection and molecular characterization of Cryptosporidium spp. in diarrheic pigs in southern China. *Microbial Pathogenesis* **165**, 105459.

Wieler LH, Ilieff A, Herbst W, Bauer C, Vieler E, Bauerfeind R and Zahner H (2001) Prevalence of enteropathogens in suckling and weaned piglets with diarrhoea in southern Germany. *Journal of Veterinary Medicine. B, Infectious Diseases and Veterinary Public Health* **48**, 151–159.

Xiao L, Moore JE, Ukoh U, Gatei W, Lowery CJ, Murphy TM and Rao JR (2006) Prevalence and identity of *Cryptosporidium* spp. in pig slurry. *Applied and Environmental Microbiology* **72**, 4461–4463.

Yang MT, Zhang HJ, Li YH, Lin Q, Song JK and Zhao GH (2020) Study on *Cryptosporidium* infection of Tibetan fragrant pigs in Northwest China. *Progress in Veterinary Medicine* **41**, 130–134 (In Chinese).

Yao Q, Wang JW, Wang SS, Li YH, Zhao SS, Song JK and Zhao GH (2020) Analysis on the infection status of *Cryptosporidium* in piglets from large-scale pig farms in Shaanxi Province. *Chinese Journal of Veterinary Science* **40**, 2348–2352 (In Chinese).

Yin J, Shen Y, Yuan Z, Lu W, Xu Y and Cao J (2011) Prevalence of the *Cryptosporidium pig genotype II* in pigs from the Yangtze River Delta, China. *PLoS ONE* **6**, e20738.

Yin JH, Yuan ZY, Cai HX, Shen YJ, Jiang YY, Zhang J and Cao JP (2013) Age-related infection with *Cryptosporidium* species and genotype in pigs in China. *Biomedical and Environmental Sciences* **26**, 492–495.

Yui T, Shibahara T, Kon M, Yamamoto N, Kameda M and Taniyama H (2014a) Epidemiological studies on intestinal protozoa in pigs in Saitama. *Japanese Jarq-japan Agricultural Research Quarterly* **48**, 87–93.

Yui T, Nakajima T, Yamamoto N, Kon M, Abe N, Matsubayashi M and Shibahara T (2014b) Age-related detection and molecular characterization of *Cryptosporidium suis* and *Cryptosporidium scrofarum* in pre- and post-weaned piglets and adult pigs in Japan. *Parasitology Research* **113**, 359–365.

Zhang W, Yang F, Liu A, Wang R, Zhang L, Shen Y and Ling H (2013) Prevalence and genetic characterizations of *Cryptosporidium* spp. in pre-weaned and post-weaned piglets in Heilongjiang Province, China. *PLoS ONE* **8**, e67564.

Zhang Y, Xu CY, Xing JM, Ao WP, Qi M and Jing B (2020) Detection of *Cryptosporidium* and *Giardia duodenalis* by PCR in a pig farm in Aksu. *Progress in Veterinary Medicine* **41**, 68–71 (In Chinese).

Zheng S, Li D, Zhou C, Zhang S, Wu Y, Chang Y and Zhang L (2019) Molecular identification and epidemiological comparison of *Cryptosporidium* spp. among different pig breeds in Tibet and Henan, China. *BMC Veterinary Research* **15**, 101.

Zintl A, Neville D, Maguire D, Fanning S, Mulcahy G, Smith HV and De Waal T (2007) Prevalence of *Cryptosporidium* species in intensively farmed pigs in Ireland. *Parasitology* **134**, 1575–1582.

Zou Y, Ma JG, Yue DM, Zheng WB, Zhang XX, Zhao Q and Zhu XQ (2017) Prevalence and risk factors of *Cryptosporidium* infection in farmed pigs in Zhejiang, Guangdong, and Yunnan provinces, China. *Tropical Animal Health and Production* **49**, 653–657.