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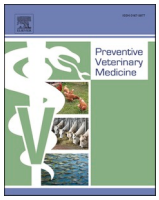

Epidemiology of *Anaplasma* species amongst cattle in Africa from 1970 to 2022: A systematic review and meta-analysis

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ABSTRACT

Tick-borne pathogens of the genus *Anaplasma* cause anaplasmosis in livestock and humans, impacting health and livelihoods, particularly in Africa. A comprehensive review on the epidemiology of *Anaplasma* species is important to guide further research and for implementation of control approaches. We reviewed observational studies concerning *Anaplasma* species amongst cattle in Africa. Peer-reviewed studies published in PubMed, Google Scholar, and Web of Science - from database inception to 2022 - were searched. The quality of individual studies was assessed using the Joanna Briggs Institute Critical Appraisal Tool and the pooled prevalences by diagnostic method were estimated using random-effects models. Heterogeneity across the studies was tested and quantified using the Cochran's Q statistic and the I^2 statistic. Potential sources of heterogeneity were investigated by subgroup analysis. A total of 1117 records were retrieved and at the end of the screening, 149 records (155 studies) were eligible for this meta-analysis. The occurrence of *Anaplasma* species was reported in 31/54 countries in all regions. Seven recognised species (*A. marginale*, *A. centrale*, *A. phagocytophilum*, *A. platys*, *A. capra*, *A. bovis*, *A. ovis*) and nine uncharacterised genotypes (*Anaplasma* sp. Hadesa; *Anaplasma* sp. Saso; *Anaplasma* sp. Dedessa; *Anaplasma* sp. Mymensingh; *Anaplasma* sp. Lambwe-1; *Candidatus* Anaplasma africae; *Anaplasma* sp.; *Candidatus* Anaplasma boleense) were reported in African cattle. *Anaplasma marginale* was the most frequently reported (n=144/155 studies) and the most prevalent species (serology methods 56.1%, 45.9–66.1; direct detection methods 19.9%, 15.4–24.7), followed by *A. centrale* (n=26 studies) with a prevalence of 8.0% (95% CI: 4.8–11.9) and *A. platys* (n=19 studies) with prevalence of 9.7% (95% CI: 5.4–15.2). *Anaplasma marginale, A. centrale* and *A. platys* were reported in all Africa's regions, while *A. ovis* and *A. capra* were reported only in the northern and central regions. The uncharacterised *Anaplasma* taxa were mostly detected in the eastern and southern regions. Subgroup analysis showed that significant determinants for *A. marginale* exposure (serology) were geographical region (p=0.0219), and longitude (p=0.0336), while the technique employed influenced (p<0.0001) prevalence in direct detection approaches. Temperature was the only significant variable (p=0.0269) for *A. centrale*. These findings show that various *Anaplasma* species, including those that are zoonotic, circulate in African cattle. There is need for more genetic and genome data, especially for unrecognised species, to facilitate effective identification, improve livestock and minimise the health risk in human populations. Additional epidemiological data including pathogen occurrence, tick vectors and host range, as well as pathogenicity are essential.

1. Introduction

Anaplasmosis is a tick-borne disease caused by a Gram-negative obligate haemoparasitic proteobacteria of the genus *Anaplasma*, with notable impact on human and animal health in both temperate and tropical regions (Goodger et al., 1979; Alderink and Dietrich, 1983; Railey and Marsh, 2021). The genus was discovered by Sir Arnold Theiler in 1910, and in 2001, Dumler and colleagues re-organised the order Rickettsiales to include *Anaplasma* in the family *Anaplasmataceae* based on the 16 S rRNA and *groESL* sequences (Theiler, 1910; Dumler et al., 2001). The classification included seven species, namely *Anaplasma marginale*, *A. centrale*, *A. bovis*, *A. phagocytophilum*, *A. ovis*, *A.*

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platys, *A. caudatum* (Dumler et al., 2001). Since then, about 25 presumed species have been identified (Kolo et al., 2020; Caudill and Brayton, 2022; Makgabo et al., 2023), while *A. capra* (Li et al., 2015) and *A. odocoilei* sp. Nov. (Tate et al., 2013) have been published, but not formally recognised. Although humans and various domestic and wild ruminants are affected by *Anaplasma* species, clinical disease and economic losses are most remarkable in cattle (Kocan et al., 2003). Losses arising from anaplasmosis include mortalities, reduced weight and milk production, and costs related to diagnosis, treatment, vaccination, tick control and restriction of cattle movements (Uilenberg, 1995; De Waal, 2000; Makala et al., 2003; Jonsson et al., 2008). Studies in the USA showed that the disease can cause 30% increase in culling rate in cattle herds and 20–30% loss in body weight in individual animals (Goodger et al., 1979). The average minimal and expected costs were USD$ 285 and 660, respectively, per head of cattle (Alderink and Dietrich, 1983). In another study, the total cost per cow in terms of diagnostic testing, preventive vaccination, preventative feed additive and post-infection antibiotic treatment was $USD 67.7 (Railey and Marsh, 2021). Transmission of *Anaplasma* species is intrastadially, transovarially, or transstadially by ticks of various genera such as *Rhipicephalus*, *Ixodes*, *Amblyomma*, *Dermacentor* and *Hyalomma*. The pathogens have been detected in over 17 tick species in Africa (Cossu et al., 2023), meaning several of these could be involved in the epidemiology of anaplasmosis. Infection in cattle is mainly by *A. marginale, A. centrale*, *A. bovis*, *A. phagocytophilum* and perhaps *Anaplasma* sp. Omatjenne (Kocan et al., 2010).

Anaplasma marginale is an intra-erythrocytic parasite and is the most prevalent and pathogenic agent of bovine anaplasmosis (Kuttler, 1984). It has worldwide distribution, especially in tropical and sub-tropical areas, and affects both domestic and wild ruminants (Aubry and Geale, 2011). The pathogen is biologically transmitted by about 20 species of ticks (Kocan et al., 2010) and mechanically by bloodsucking arthropods (Potgieter et al., 1981; Scoles et al., 2005). Transplacental transmission of *A. marginale* has also been reported (Costa et al., 2016). *Anaplasma centrale* causes mild signs in cattle and is used as a live vaccine against *A. marginale* infections (Kocan et al., 2003). The hosts for *A. centrale* include various species of domestic and wild ruminants (Wu et al., 2015; Khumalo et al., 2016). *Anaplasma bovis* is a parasite of monocytes and is distributed in Asia, Africa, South and North America and southern Europe (Uilenberg, 1993; Goethert and Telford III, 2003; Ceci et al., 2014; García-Pérez et al., 2016). The main hosts are cattle and buffalo. *Anaplasma phagocytophilum* is an intra-granulocytic parasite distributed across Asia and Middle East, Europe, Americas, and Africa and causes tick-borne fever in a wide range of domestic and wild animals and granulocytic anaplasmosis in humans (Stuen et al., 2013). *Anaplasma* sp. Omatjenne was detected for the first time by Allsopp et al. (1997) in healthy Boer goats in South Africa. Although its role in causing clinical disease is still obscure, infections have been detected in wild and domestic animals in Africa and the Mediterranean (Teshale et al., 2018; Kolo, 2023).

In Africa, cattle are central to the livelihoods of people, as a source of nutrition and food, draft power, income, manure and for socio-cultural purposes (Dessie and Mwai, 2019). A diversity of indigenous and exotic cattle are assets for about 800 million people across the continent (Dessie and Mwai, 2019). Several studies have investigated the occurrence of *Anaplasma* species and associated risk factors amongst cattle in Africa, showing that prevalences vary amongst countries (Verhulst et al., 1983; Solomon et al., 1998; Hamou et al., 2012; Byaruhanga et al., 2018; Hove et al., 2018; Abanda et al., 2019a; Fernandes et al., 2019).

Although these studies may provide useful information, there is need for a systematic review and meta-analysis to obtain data summaries and provide a more extensive overview of the epidemiological situation at regional and continental levels. Change in distribution and increase in incidence of anaplasmosis are expected in part due to climate change, which may influence the spread of the tick vectors (Jonsson and Reid, 2000). Other factors such as changes in livestock populations, breed composition and sharing of grazing areas between cattle and free-ranging wildlife are also concerns about increasing transmission and severity of anaplasmosis. Moreover, transboundary movement of carrier cattle for trade and grazing is expected to result in introduction and spread of competent tick vectors (Nyangiwe et al., 2018; Silatsa et al., 2019; Kanduma et al., 2020; Muhanguzi et al., 2020) and in biological and mechanical transmission of tick-borne pathogens to susceptible cattle from those that are persistently infected (Sutherst, 2001).

Identification of temporal and spatial patterns in the prevalence of anaplasmosis as well as associated risk factors can be highly beneficial in the prevention and control of the disease as well as to guide future research. There are key knowledge gaps regarding how the diverse climatic and geographical factors in Africa may influence distribution and impact of anaplasmosis. In a previous study, Paramanandham et al. (2019) analysed *Anaplasma* species, but only in dairy cattle and in a few countries for the period of 1978–2017. The study did not differentiate between *Anaplasma* species and there was no analysis of risk factors. More recently, two reviews related to tick-borne pathogens (including *Anaplasma*) were conducted. Tawana et al. (2022) reviewed the occurrence of tick-borne pathogens in cattle and ticks in the Southern African Development Community, a regional block that comprises 16 States, and Cossu et al. (2023) and Mucheka et al. (2023) highlighted the distribution and prevalence of various tick-borne pathogens in African ticks. A comprehensive review on bovine anaplasmosis epidemiology in cattle populations in Africa is still lacking.

The objectives of this study were therefore to establish the distribution and pooled prevalence of *Anaplasma* species in cattle populations in Africa and to identify determinants of infection or exposure using subgroup analysis.

2. Methods

2.1. Study design

This meta-analysis was conducted in accordance with the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) guidelines (Shamseer et al., 2015; Page et al., 2021) (Table S2). A protocol for this study is registered in the International Prospective Register of Systematic Reviews database (PROSPERO: CRD42022345974). The literature review on the prevalence of *Anaplasma* species amongst cattle in Africa was performed on three international bibliographic databases: PubMed (1996), Web of Science ('all databases' option, which includes MEDLINE, Zoological Records and CAB Abstracts-1900) and Google Scholar (2004), from July through October 2022. The search was for publications from database inception to June 2022. Africa was defined as the area encompassing 54 sovereign countries and four semi-autonomous or autonomous territories. The continent covers a total land area of 29,648,481 km^2 and is home to over 1.44 billion people, as of June 23, 2023, representing 16.7% of the total world's population (https://www.worldometers.info/world-population/africa-population/).

2.2. Search strategy

The literature search strategy was developed by the two authors (CB, CJA), who have experience in systematic reviews and meta-analyses. The search terms were grouped into three topics: 1) animal species, 2) *Anaplasma* species, and 3) study area. The Boolean operators "AND" and "OR" were used to connect the search topics and search terms within a topic, respectively, as follows: ((Cattle OR Bovine OR *Bos grunniens* OR *Bos indicus* OR *Bos taurus* OR Cow OR taurine OR Yak) AND (anaplasmosis OR *Anaplasma* OR *Anaplasma phagocytophilum* OR *Anaplasma marginale* OR *Anaplasma centrale* OR *Anaplasma bovis* OR *Anaplasma* sp. Omatjenne) AND (Africa OR Algeria OR Angola OR Benin OR Botswana OR Burkina Faso OR Burundi OR Cameroon OR Cabo Verde OR Cape Verde or Republic of Cabo Verde OR Central African Republic OR Chad

OR Comoros OR Congo OR Republic of the Congo OR Congo-Brazzaville OR Congo Republic OR DR Congo OR Democratic Republic of Congo OR Zaire OR Côte d'Ivoire OR Ivory Coast OR Djibouti OR Equatorial Guinea OR Egypt OR Eritrea OR Ethiopia OR Gabon OR Gambia OR Ghana OR Guinea OR Guinea-Bissau OR Kenya OR Lesotho OR Liberia OR Libya OR Madagascar OR Malawi OR Mali OR Mauritania OR Mauritius OR Morocco OR Mozambique OR Namibia OR Niger OR Nigeria OR Rwanda OR Sao Tome and Principe OR Sâo Tomé and Príncipe OR Senegal OR Seychelles OR Sierra Leone OR Somalia OR Somaliland OR Puntland OR South Africa OR South Sudan OR Sudan OR Swaziland OR Eswatini OR Tanzania OR United Republic of Tanzania OR Zanzibar OR Togo OR Tunisia OR Uganda OR Western Sahara OR Zambia OR Zimbabwe)). Synonyms that refer to the same country were included in the list, for example, the search terms for Democratic Republic of Congo were "DR Congo", "Democratic Republic of Congo" and "Zaire". For Tanzania, we included the semi-autonomous island of Zanzibar, while for Somalia, we added the autonomous states of Somaliland and Puntland. We also added the Western Sahara, a non-self-governing territory claimed by Morocco.

2.3. Eligibility criteria

Records were included in this meta-analysis when they met the following criteria (i) concerning occurrence of *Anaplasma* species in cattle within African countries; (ii) written in English; (iii) published from database inception up to and including June 2022; (iv) conducted in cattle populations; (v) study design**:** observational studies with sample size of at least 30; (vi) diagnosis was performed on blood samples using at least one of the methods: morphological, molecular and serological; and (vii) peer-reviewed journal article, conference proceeding and dissertation or thesis. Furthermore, only studies that reported the sample size and number or proportion of positive animals were included. Records that did not meet the above-outlined criteria were excluded, in addition to duplicated data, review papers and articles reporting outcomes based on case studies, clinical trials or pharmacological studies. We did not search non-peer-reviewed reports and other grey literature. The thresholds for test-positivity were those in the detection methods as defined by the author(s) of individual studies.

2.4. Selection of studies

The titles and abstracts were exported to EndNote™ 20 (Philadelphia, PA, United States of America) by JCA. Duplicate records were removed after compilation of search results from the three databases, and further checked manually during subsequent stages. The two authors jointly screened the titles and abstracts of the first 500 records, and then JCA screened the rest of the records. The second reviewer (CB) verified the records excluded by JCA to ensure effectiveness of screening. The full texts of the eligible studies were retrieved and independently evaluated by CB and JCA based on the same criteria as outlined above (Section 2.3). Any discrepancies in opinion of the reviewers were resolved through discussions to reach a consensus.

2.5. Data extraction

We jointly developed a standardised data extraction form in Microsoft Excel® version 15.0 (Microsoft Corporation, Redmond, WA, United States). Relevant data from the full text of eligible studies were extracted by JCA, who double checked for accuracy. Subsequently, CB reviewed the extracted data to ensure clarity and completeness. Any disagreements were resolved through discussions to reach a consensus.

Extracted data included author(s), title, year of publication, journal, study design, sampling method, sample size, study location (country, region), sampling season or year, diagnostic method, sample size and number of cattle with a positive *Anaplasma* result. Additionally, we extracted data on potential risk factors investigated: animal signalment (age, sex, breed) and management system (e.g., zero grazing, extensive, intensive). For each subgroup, we extracted discrete data on the number of cattle sampled and the number of animals that tested positive for *Anaplasma* spp. When investigators of a study did not specify the required study characteristics, for example age (as young, adult), we assumed generally accepted classification (e.g., at least 2 years for adult). Africa is a vast continent, and due to production and climatic differences, countries were clustered by region according to the United Nations geoscheme

(https://en.wikipedia.org/wiki/United_Nations_geoscheme_for_Africa): northern Africa, western Africa, eastern Africa, central Africa, and southern Africa. Furthermore, significant variations occur within regions, and therefore we extracted data on geographical/climatic factors, namely average annual precipitation, average annual temperature, and average annual humidity for the period and area of study from CLIMATE-DATA.ORG (https://en.climate-data.org/africa). In addition, the geographical coordinates (altitude, longitude, latitude) of the involved location were searched for on the Latitude and Longitude Finder (https://www.latlong.net/ or https://gps-coordinates.org/).

The current competitive enzyme-linked immunosorbent assay (cELISA) cannot differentiate between *Anaplasma* species, and therefore in studies that used only cELISA for detection, the reported prevalence was recorded for *A. marginale*, which is usually the dominant species. When a study reported multiple prevalences from more than one method on the same group of animals, we chose the outcome from the more sensitive method, in the order nucleic acid-based> serology>microscopy, for inclusion in the analyses. We pooled data in these categories: serological tests (ELISA, fluorescent antibody test [FAT], capillary tube-agglutination test [CAT], western blot [WB]); nested and conventional polymerase chain reaction [PCR] (most data were from the later); reverse line blot [RLB] hybridisation and liquid-crystal display [LCD] (only one study utilised LCD). In subgroup analyses, we further categorised the diagnostics into groups: serology and direct detection methods. In records that reported prevalence from more than one country, or study period, we replicated and recorded each condition as a separate study. South Sudan became an independent state in 2011, and therefore all studies published from Sudan before that year were categorised under the later.

2.6. Quality assessment

The two authors independently assessed selection bias and quality of reporting of selected studies by employing the Joanna Briggs Institute (JBI) Critical Appraisal Tool for prevalence studies (Munn et al., 2014). The JBI tool has 'yes', 'no', 'Unclear' or 'Not applicable' question types and scores were assigned as 1 for 'yes' and 0 for 'no'. The number of 'yes' scores for each study were added and the percentage computed by dividing by the total number of questions. Studies were assessed based on 8 of the 9 JBI questions, which were relevant to this review. The studies were rated as low quality (less than 50% total score), moderate quality (50–70%), and high quality (>70%). The score reflected confidence or certainty that the study outcomes are representative of the true prevalence. Any inconsistencies in the scoring were discussed and resolved. All studies irrespective of the obtained score were included.

2.7. Statistical analyses

We analysed the data using the packages 'meta' (Schwarzer, 2007), 'metafor' (Viechtbauer, 2010) and 'ggResidpanel' (Goode and Rey, 2022) in the R statistical software version 4.3.2 (R Core Team, 2023) at 0.05 level of significance.

Pooled prevalence and 95% confidence intervals for each species or taxa and diagnostic category were estimated based on the random-effects model, due to expected high heterogeneity and the fact that this model considers both between-study and within-study variances (Wang et al., 2020). The random-effects model was estimated using the

restricted maximum likelihood method (REML) (Raudenbush and Bryk, 1985), and data were transformed to conform to normal distribution using the double-arcsine transformation (PFT) method (Miller, 1978). Variation across the studies was tested and quantified using the Cochran's Q statistic (Cochran, 1954) and the inconsistency index I^2 (Higgins et al., 2003). Heterogeneity was considered significant if p-value was less than 0.05 in the Cochran Q test, and I^2 was greater than 50%, following the commonly used benchmarks for I^2 heterogeneity levels as 25%, 50% and 75%, for low, moderate, and high, respectively (Higgins and Thompson, 2002). The true between-study variance, τ^2, and standard deviation, τ, were also determined using the tau statistic to estimate the amount of heterogeneity (Borenstein et al., 2017).

A forest plot was produced for each *Anaplasma* species or taxa (those with at least two studies) to visualise heterogeneity regarding prevalence and 95% confidence interval. Publication bias and small-study effects for individual *Anaplasma* species and taxa were analysed using funnel plots and the unweighted Egger's regression test (Egger et al., 1997; Rücker et al., 2011). The Egger's regression test has good power to support presence of symmetry when the number of included studies is greater than 10. Bias was considered based on the visual plots and if the statistical analysis was significant ($p<0.1$). *Anaplasma marginale* and *A. centrale* appeared in more than 20 studies; therefore, potential sources of heterogeneity for these infections were evaluated by subgroup analyses, separately for serology and direct detection methods. Factors considered were geographical region (central, eastern, northern, southern, western), animal signalment (age, breed, sex), detection method and sampling year (2007 or before, 2008–2014, after 2014). Others were climate (annual average humidity, average temperature, average precipitation), study quality (low, moderate, high), management system (semi--intensive/intensive, extensive) and geographical factors (latitude, longitude, altitude). Sampling season was not assessed because few studies (< 10) reported this variable. Mixed-effects models were employed in the subgroup analyses, in which the random-effects model was used to pool study prevalences within each subgroup, and the fixed-effects model was used to test whether the prevalences across the subgroups varied significantly from each other (Cuijpers, 2016; Cuijpers et al., 2021). We then assessed the distribution of residuals in multivariable meta-regressions, which included variables with heterogeneity p-values <0.1 and/or amount of heterogeneity accounted (R^2) >0 from subgroup analyses. This was done to determine adequacy of the models or if there might be further information in our data that is not expressed in the variables considered. Analyses for normality of residuals was achieved by generating Q-Q plots and by the Shapiro-Wilk's normality test. Separate analyses were conducted for direct detection methods and serology. The meta-analysis results were also visualised in form of summary tables and maps generated using QGIS desktop version 3.28.1.

3. Results

3.1. Search results

A total of 1117 records were obtained from three databases (Web of Science, PubMed, and Google Scholar) (Fig. 1). After removal of duplicate records (n=275) and removal of others (n=121) based on the

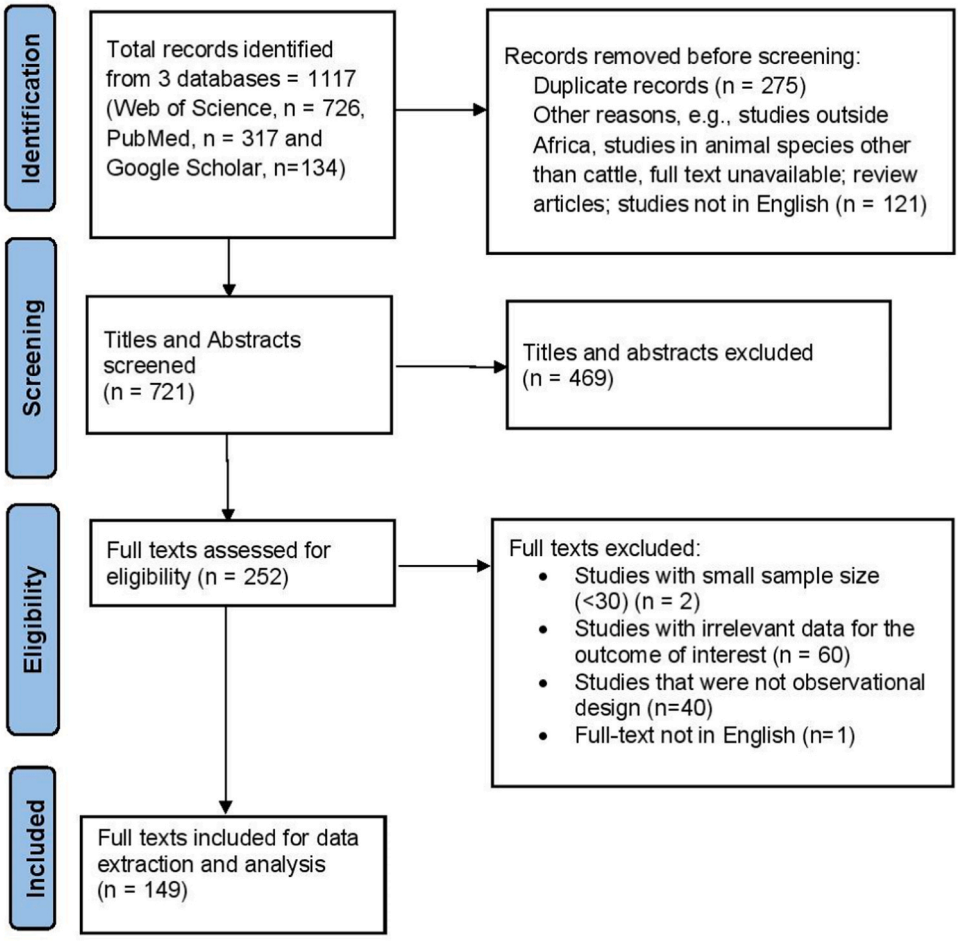

Fig. 1. Flow chart of literature search and selection regarding prevalence of *Anaplasma* species amongst cattle in Africa. The studies were limited to English, and the review excluded review papers, clinical trials, or pharmacological studies. The search steps were in accordance with the Preferred Reporting Items for Systematic reviews and Meta-Analyses guidelines.

exclusion criteria, 721 records were screened based on title and/or abstract. During title/abstract screening, 469 records were excluded. Therefore, 252 full-text articles fulfilled the eligibility criteria for assessment, but of these, two had a small sample size of less than 30 (Fig. 1). During evaluation of the remaining 250 records, 101 were excluded due to unclear data on outcome of interest, full texts not in English or of different scope (case studies, clinical trials, or pharmacological studies). Thus, 149 records comprising 155 studies from 31 countries were included in this meta-analysis.

Majority of the studies (n=61) presented data from eastern Africa, while others included data from northern Africa (n=38 studies), western Africa (n=29 studies), southern Africa (n=17 studies) or central Africa (n=10 studies) (Table S1). The highest number of studies from a single country was 21 from Nigeria, followed by 16 from Uganda, 15 from Kenya, 14 from South Africa and 12 from Egypt (Table S1). Two records each covered more than one country; one record covered five countries - Ethiopia, Ivory Coast, Morocco, Rwanda, and Zambia (Teshale et al., 2018) and another one covered three countries - Morocco, Cameroon, and Democratic Republic of Congo (Verhulst et al., 1983) (Table S1). Twelve countries (Burkina Faso, Burundi, Comoros, Democratic Republic of Congo, Ivory Coast, Libya, Zimbabwe, Madagascar, Malawi, Rwanda, Senegal, and The Gambia) had single studies (Table S1). No published records were available on the prevalence of *Anaplasma* spp. from 23 (42.6%) of the 54 African sovereign states and four territories: Cabo Verde, Central African Republic, Chad, Djibouti, Equatorial Guinea, Eritrea, Eswatini, Gabon, Gambia, Guinea-Bissau, Lesotho, Liberia, Mali, Mauritania, Mauritius, Namibia, Niger, Republic of the Congo (Congo-Brazzaville), Seychelles, São Tomé and Príncipe, Somalia, Sierra Leone, Togo, Western Sahara, Zanzibar, Somaliland, and Puntland. All countries or territories in which data on occurrence of *Anaplasma* spp. were available are indicated in Fig. 2.

The sample size of individual studies ranged from 31 to 5290 cattle and a total of 73238 blood samples were included in the analysis. Samples were tested using PCR/nested PCR (n=52 studies), microscopy (n=36 studies), ELISA (n=34 studies), RLB hybridisation (n=13 studies), CAT (n=8 studies), quantitative real-time PCR [qPCR] (n=6 studies), indirect FAT (n=4 studies), LCD (n=1 study), and WB (n=1 study) (Table 1). All serology studies (n=47 studies) were performed to determine exposure to *A. marginale*, while the microscopic method was applied for the detection of both *A. marginale* and *A. centrale* (Table 1). Nucleic acid-based methods were employed for all species/taxa (Table 1).

About a third of the eligible studies (53/155, 34.2%) were conducted in the last eight years (2014–2021) (Fig. 3), and of these, 40 applied nucleic acid-based methods (PCR, nPCR, RLB, qPCR), highlighting the significant increase in research in *Anaplasma* species and a shift in diagnostics. We did not come across records published before 1970. Apart from studies on *A. marginale*, which were published as early as 1975, studies on other species and genotypes were published only after 2010 (Table S1; Figure A-I S1).

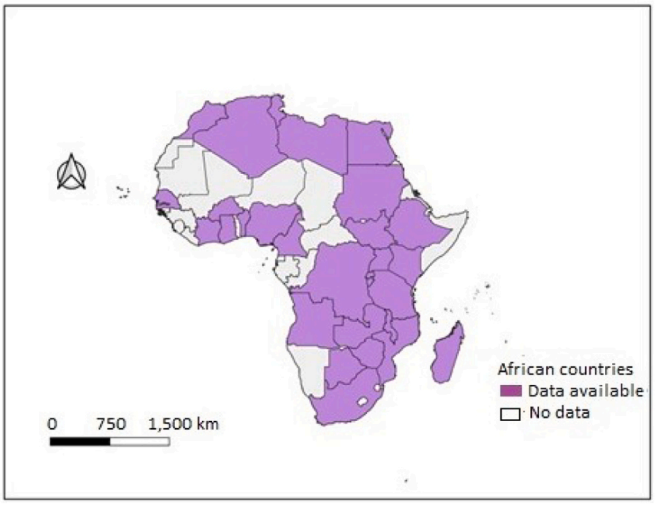

Fig. 2. African countries with published records on the occurrence of *Anaplasma* species or taxa amongst cattle (1970–2022).

3.2. Quality of studies

According to the JBI assessment, the overall minimum, maximum, median, and average quality scores were 0, 100, 75 and 68.1%, respectively. The quality scores for individual *Anaplasma* species or taxa are shown in Table 2. Low and medium qualities were due to some studies not justifying the sample size and/or selection criteria for the study subjects. There were 84 (58.3%) high-quality studies, 32 (22.2%) medium-quality studies and 28 (19.4%) low-quality studies for *A. marginale* (Table 2). The quality for prevalence estimates of *A. centrale* was mostly high (53.8%, 14/26 studies), while equal number of studies (n=6) were of low and moderate quality (Table 2).

3.3. Publication bias

Funnel plots for individual *Anaplasma* species or taxa are shown in Figs. 4 and 5. Fourteen of the 16 taxa funnel plots were symmetrical. The Egger's mixed-effects meta-regression test was not significant for *A. marginale* (z=0.7636, p=0.4451), *A. centrale* (z=1.4639, p=0.1432), *A. platys* (z=0.2016, p=0.8402), *Anaplasma* sp. Omatjenne (z=-1.1157, p=0.2645), *A. bovis* (z=-0.7737, p=0.4391), *Anaplasma* sp. Hadesa (z=1.2055, p=0.228) and *Anaplasma* sp. (z=1.1488, p=0.2507), but was significant for *A. phagocytophilum* (z=2.3256, p=0.02) and *A. ovis* (z=1.7293, p=0.0838). Analysis was inconclusive for *A. capra*, *Anaplasma* sp. Saso, *Anaplasma* sp. Dedessa, *Anaplasma* sp. Mymensingh, *Anaplasma* sp. Lambwe-1, *Candidatus* Anaplasma africae and *Candidatus* Anaplasma boleense due to few studies (<3 for each taxon). Unsignificant Egger's test for most species suggests no publication bias and no small-study effects in the analysed data, and no further assessment was therefore performed to correct the bias.

3.4. Spatial distribution of studied Anaplasma species or genotypes

A total of seven recognised *Anaplasma* species and nine uncharacterised genotypes (including *Anaplasma* sp. Omatjenne) were reported in African cattle (Tables 1, 2 and 3). We observed spatial differences in the distribution of the studied *Anaplasma* species or taxa. *Anaplasma marginale* and *A. centrale*, the most important species that affect cattle, were reported in 29 and 15 countries, respectively, and in all Africa's regions (central, eastern, northern, southern, western), while *A. phagocytophilum* and *A. bovis* were reported in 10 and 11 countries, respectively, in all but the western part of the continent (Table S1; Table 3; Fig. 6). *Anaplasma platys* was identified in 12 countries in all regions, while *Anaplasma ovis* and *A. capra* were predominantly distributed in the northern region, except for one report each from Angola in central Africa (Table S1; Table 3; Fig. 6). *Anaplasma marginale* was the most frequently reported species (n=144/155 studies) followed by *A. centrale* (n=26) and *A. platys* (n=19) (Table S1; Table 3). Most reports (n=12/18) about uncharacterised *Anaplasma* taxa were from the eastern and southern regions (each region = 6 studies), while two studies were published from each of the central, western, and northern regions (Table S1; Fig. 7; Table 3).

3.5. Pooled prevalence and heterogeneity of Anaplasma species or taxa

Anaplasma marginale was the most prevalent species (serology methods 56.1%, 45.9–66.1; direct detection methods 19.9%, 15.4–24.7), followed by *Anaplasma* sp. Omatjenne (12.3%; 95% CI: 6.4–19.7%) and *A. platys* (9.7%; 95% CI: 5.4–15.2) (Table 3). Prevalence

Table 1
Prevalence of different *Anaplasma* species or taxa, grouped by detection method.

Species/taxon	Detection method	Number of studies	Number of countries	Regions and number of studies	Prevalence (95% CI)
Anaplasma marginale	Serology (ELISA, IFAT, CAT, WB)	47	19	Central=2, eastern=22, northern=8, southern=10, western=5	56.1(45.9, 66.1)
	Microscopy	34	12	Central=2, eastern=11, northern=8, western=13	13.0(8.1, 18.8)
	PCR/nPCR	44	20	Central=3, eastern=14, northern=18, southern=4, western=5	20.5(14.6, 27.2)
	qPCR	6	5	Eastern=2, northern=1, southern=2, western=1	65.7(34.8, 90.6)
	RLB/LCD array[c]	13	10	Central=3, eastern=6, southern=1, western=3	18.7(9.5, 30.1)
Anaplasma centrale	Microscopy	4	3	Eastern=2, Western=2	2.4(1.0, 4.4)
	PCR	12	10	Central=2, eastern=3, northern=6, western=1	56.7(46.3, 66.8)
	qPCR	3	2	Eastern=1, southern=2	10.3(3.4, 20.1)
	RLB/LCD array[a]	7	6	Central=3, eastern=3, western=1	8.5(2.7, 17.0)
Anaplasma phagocytophilum	PCR	7	6	Central=1, eastern=1, northern=4	7.2(0.9, 18.1)
	qPCR	2	2	Eastern=1, southern=1	2.1(0.7, 4.1)
	RLB	2	2	Eastern=2	1.3(0.0, 4.3)
Anaplasma platys	PCR	17	12	Central=2, eastern=5, northern=7, southern=1, western=2	8.3(4.3, 13.3)
	RLB/LCD array[a]	2	2	Central=2	28.3(8.5, 53.8)
Anaplasma bovis	PCR	9	6	Eastern=3, northern=6	3.7(1.4, 6.9)
	RLB	6	6	Central=1, eastern=3, southern=2	5.2(0.1, 15.7)
Anaplasma ovis	PCR	5	4	Central=1, northern=4	3.5(0.0, 12.3)
Anaplasma capra	PCR	2	2	Central=1, northern=1	2.0(0.0, 10.9)
Anaplasma sp. Omatjenne	PCR	6	6	Eastern=3, northern=1, southern=1, western=1	6.8(2.9, 12.1)
	RLB	8	8	Central=2, Eastern=4, southern=1, western=1	16.4(7.0, 28.8)
Anaplasma sp. Hadesa	PCR	2	2	Central=1, southern=1	4.1(0.05, 12.7)
	RLB	2	2	Central=1, Eastern=1	24.6(2.7, 57.6)
Anaplasma sp. Saso	qPCR	1	1	southern=1	1.0(0.0, 4.2)
	RLB	1	1	Eastern=1	14.3(11.0, 18.0)
Anaplasma sp. Dedessa	PCR	1	1	Southern=1	1.0(0.0, 4.2)
	RLB	1	1	Eastern=1	5.6(3.5, 8.1)
Anaplasma sp. Mymensingh	PCR	1	1	Southern Africa=1	2.0(0.03, 5.9)
Anaplasma sp. Lambwe-1	PCR	1	1	Eastern=1	14.3(11.7, 17.0)
Candidatus Anaplasma africae	PCR	1	1	Western=1	8.1(2.4, 16.4)
Anaplasma sp.	PCR/nPCR	5	4	Eastern=2, northern=2, western=1	7.3(2.4, 14.4)
	qPCR	1	1	Southern=1	11.0(5.5, 18.0)
Candidatus Anaplasma boleense	PCR	1	1	Southern=1	1.0(0.0, 4.2)

CI, confidence interval
ELISA, enzyme-linked immunosorbent assay; CAT, capillary tube-agglutination test; IFAT, indirect fluorescent antibody test; LCD, liquid-crystal display; nPCR, nested polymerase chain reaction; RLB, reverse line blot; qPCR, quantitative real-time PCR; WB, western blot
[a] One study was conducted using LCD-array

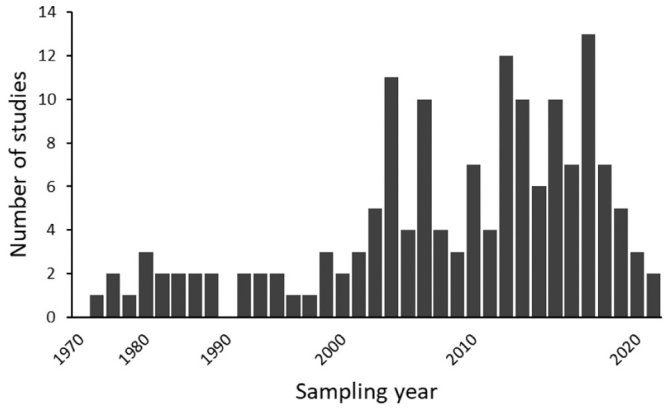

Fig. 3. Number of studies on the detection of *Anaplasma* species in cattle in Africa, published from data base inception up to and including June 2022. The 155 eligible studies were retrieved from three databases: PubMed (1996), Google Scholar (2004), Web of Science (all databases option) (1900).

of *A. centrale* (all studies based on direct detection methods) was 8.0% (95% CI: 4.8, 11.9). Within-species heterogeneity (I^2) was greater than 78% ($p<0.0001$ to $p=0.032$). The prediction intervals covered a wider range than the 95% confidence interval, an indication of high variability of probable prevalence estimates in future studies and that future prevalence will not exceed the upper prediction limits (Tabe 3). High heterogeneity is also observed in the forest plots (Figure A-I S1). Heterogeneity across studies was further confirmed by small amount of true between-study variance, τ^2 (Table 3). The nine uncharacterised genotypes were each reported in 1–14 studies, with *Candidatus* Anaplasma boleense having the lowest prevalence 1.0%; 95% CI: 0.0–4.2) from a South African study and *Anaplasma* sp. Lambwe-1 having the highest prevalence (14.3%; 95% CI: 11.7–17.0) from a Kenyan study (Table 3; Fig. 7). We conducted subgroup analyses for the most frequently reported species (*A. marginale* and *A. centrale*), to establish factors that could contribute to heterogeneity in these studies.

3.6. Predictors for A. marginale and A. centrale infections

Outputs of subgroup analyses for *A. marginale* and *A. centrale* are shown Tables 4 and 5, respectively. Only variables with heterogeneity *p*-value<0.1 are shown. Significant determinants for *A. marginale* (serology methods) were geographical region ($QM=11.45$, $p=0.0219$) and longitude ($QM=8.69$, $p=0.0336$), while in direct detection methods, the technique used was the only significant variable ($QM=24.88$, $p<0.0001$) (Table 4). Other variables, namely sampling year, latitude, altitude, rainfall, temperature, humidity, age, breed, sex, study quality and management system showed no statistical significance ($p>0.05$). Although most studies that employed serological methods were from eastern Africa (n=22 studies), the highest seroprevalence for *A. marginale* (74.8%) was reported in southern Africa (n=10 studies) followed

Table 2
Quality of studies on the prevalence of *Anaplasma* spp. amongst cattle in Africa (1970–2022).

Pathogen	Number and percentage of studies by quality category		
	Low	Moderate	High
Anaplasma marginale **(n=144 studies)**	**28(19.4)**	**32(22.2)**	**84(58.3)**
Anaplasma centrale **(n=26)**	**6(23.1)**	**6(23.1)**	**14(53.8)**
Anaplasma phagocytophilum **(n=11)**	**5(45.5)**	**3(27.3)**	**3(27.3)**
Anaplasma platys **(n=19)**	**8(42.1)**	**3(15.8)**	**8(42.1)**
Anaplasma bovis **(n=15)**	**3(20.0)**	**3(20.0)**	**9(60.0)**
Anaplasma ovis **(n=5)**	**4(80.0)**	**0(0)**	**1(20.0)**
Anaplasma capra **(n=2)**	**1(50.0)**	**0(0)**	**1(50.0)**
Anaplasma **sp. Omatjenne (n=14)**	**1(7.1)**	**8(57.1)**	**5(35.7)**
Anaplasma **sp. Hadesa (n=4)**	**2(50.0)**	**0(0)**	**2(50.0)**
Anaplasma **sp. Saso (n=2)**	**1(50.0)**	**0(0)**	**1(50.0)**
Anaplasma **sp. Dedessa (n=2)**	**1(50.0)**	**0(0)**	**1(50.0)**
Anaplasma **sp. Mymensingh (n=1)**	**1(100)**	**0(0)**	**0(0)**
Anaplasma **sp. Lambwe-1 (n=1)**	**0(0)**	**0(0)**	**1(100)**
Candidatus **Anaplasma africae (n=1)**	**1(100)**	**0(0)**	**0(0)**
Anaplasma **sp. (n=6)**	**3(50.0)**	**0(0)**	**3(50.0)**
Candidatus **Anaplasma boleense (n=1)**	**1(100)**	**0(0)**	**0(0)**

Low quality, <50% total score; moderate quality, 50–70% score; high quality, >70% score.
Low, meaning the true effects are significantly different from the estimated effects; moderate, the true effects might have been significantly different from the estimated effects; high, there is high confidence that the true prevalence values are close to the estimated prevalence.
Quality assessment was performed using the Joanna Briggs Institute (JBI) critical appraisal tool.

by the former (61.7%), while central (20.9%, only 2 studies) and northern (32.7%, n=8 studies) regions showed relatively low exposure levels (Table 4). According to geographical coordinates, locations across longitudes >32° and 24–32 showed higher seroprevalence (Table 4). Amongst direct detection methods, highest detection level for *A. marginale* was by qPCR (65.8%), and the lowest was by microscopic examination (13.1%; Table 4). Temperature was the only statistically significant factor (QM=9.2, p=0.0269) for *A. centrale,* while other variables were not statistically involved (Table 5).

The amounts of heterogeneity accounted (R^2) were 28.9% (*A. marginale*; serology methods), 44.5% (*A. marginale*; direct methods) and 32.4% (*A. centrale*). We analysed the distribution of multivariable meta-regression residuals by graphical and statistical methods. The scatterplot smoother in the residual vs fitted plots were generally flat, although with little detectable non-linear trends (non-constant variance) and with a few residuals outside the confidence interval (Figs. 8, 9, 10). The Shapiro-Wilk's tests showed significant concordance of our data to normal distribution: W=0.97412, p=0.3768 (*A. marginale* serology); W=0.97603, p=0.07279 (*A. marginale* direct detection) and W=0.9623, p=0.4387 (*A. centrale*). Taken together, these findings point to only small deviance from normal distribution and therefore only few further variables (probably those that are herd-specific) that are not covered in the individual studies could have affected infection with *Anaplasma* spp.

4. Discussion

Pathogens in the genus *Anaplasma* cause anaplasmosis in various domestic and wild animal species and humans. Various epidemiological studies have assessed the prevalence, distribution and risk factors for *Anaplasma* infections in individual African countries (Byaruhanga et al., 2018; AL-Hosary et al., 2020; Makgabo et al., 2023; Mwale et al., 2023), while others have reviewed *Anaplasma* species in African ticks (Cossu et al., 2023; Mucheka et al., 2023) or in domestic ruminants at regional level, such as southern Africa (Tawana et al., 2022) and North Africa (Ben Said et al., 2018). In the present study, we reviewed epidemiological data on *Anaplasma* species amongst cattle populations from the entire continent.

A total of seven previously described *Anaplasma* species and nine uncharacterised genotypes were detected in African cattle. In a previous study, Tawana et al. (2022) noted the detection of the seven species and uncharacterised *Anaplasma* sp. in blood and tick samples from cattle in the Southern African Development Community (SADC) countries, and similar species except for *A. capra* were reported in ticks from the African continent (Cossu et al., 2023). One possible explanation for high diversity of *Anaplasma* species in cattle in Africa is the increasing social and economic interactions between human and domestic or wild animals, especially in rangeland and pastoral systems (Byaruhanga et al., 2015b; Jori et al., 2021; Makgabo et al., 2023), which facilitate transmission and maintenance of tick-borne pathogens as well as emergence of novel species. Wild animals are regarded as reservoirs of *Anaplasma* species (Kuttler, 1984; Khumalo et al., 2016; Sisson et al., 2023). A recent 16 S microbiome study in South Africa highlighted the presence of four previously described species (*A. marginale*, *A. centrale*, *A. bovis*, *Anaplasma* ST SA dog) and nine novel *Anaplasma* genotypes in nine wildlife species (kudu, African buffalo, hyena, lion, warthog, impala, zebra, leopard and elephant) in different locations that are surrounded by human settlements and grazing areas, signifying potential transmission to domestic animals and humans (Makgabo et al., 2023). In another study, Ledwaba et al. (2022) demonstrated that 63 wild animal species mostly from the *Canidae*, *Felidae*, *Bovidae* and *Muridae* families harboured pathogens of the genera *Anaplasma*, *Babesia*, *Hepatozoon* and *Theileria* and were infested with a total of 49 tick species from nine genera, some with vectorial capacity for pathogens of veterinary and human importance. Climate change and variable ecological plasticity of ticks are also important factors, contributing to the establishment of new species in an area and therefore changing geographical distribution, diversity and abundance of ticks and tick-borne pathogens (Marques et al., 2020). Most parts of Africa have had a temperature increase of more than 1°C since 1901 (United Nations Climate Change, 2020). The spread of *Rhipicephalus microplus* and its displacement of *R. decoloratus* in many African areas is for example apparently associated with rapid adaptation of the tick species to climatic conditions or change in climate that resulted in retreat of *R. decoloratus* (Estrada-Peña and Salman, 2013). Uncontrolled animal movement is another factor; when animals migrate or come into contact with transhumant herds, there is spread of ticks including those that are resistant to acaricides, as well transmission of tick-borne pathogens. In West Africa for example, millions of livestock migrate southwards from the Sahelian regions in search of better pastures and for marketing purposes (Kamuanga et al., 2008; Corniaux et al., 2016).

No records on *Anaplasma* species or taxa were available from 23 countries, which can be attributed inadequate resources (financial, equipment and personnel) for research in some countries brought about by low income, less prioritisation for research, and factors such conflicts and civil strife or inappropriate governance. An elaboration on the spatial distribution of each studied *Anaplasma* pathogens, including information or questions on the respective tick vectors, is provided below under the respective paragraphs.

The relatively higher frequency (144/155 studies) and prevalence of *A. marginale* (19.9% by direct detection; 56.1% by serology) compared with other *Anaplasma* species agrees with findings of Cossu et al. (2023), who reported that highest number of studies (27.0%) and prevalence estimates (12.8%) were for the pathogen. The wider geographical distribution of the *A. marginale* corresponds with the overall distribution of the known tick vectors. In Africa, the pathogen is mainly transmitted by *R. decoloratus*, *R. microplus*, *R. evertsi evertsi* (the three ticks distributed in all regions except northern) and *R. annulatus* (all regions except southern) (Walker et al., 2013; Kanduma et al., 2020; Okely and Al-Khalaf, 2022). Other vectors are *Hyalomma rufipes* (all regions) and *R. simus* (southern region) (Walker et al., 2013). Moreover, numerous tick species could potentially be involved in the epidemiology of the pathogen amongst cattle populations. For example, the pathogen was detected in 17 species of African ticks of the genera *Amblyomma*, *Rhipicephalus* and

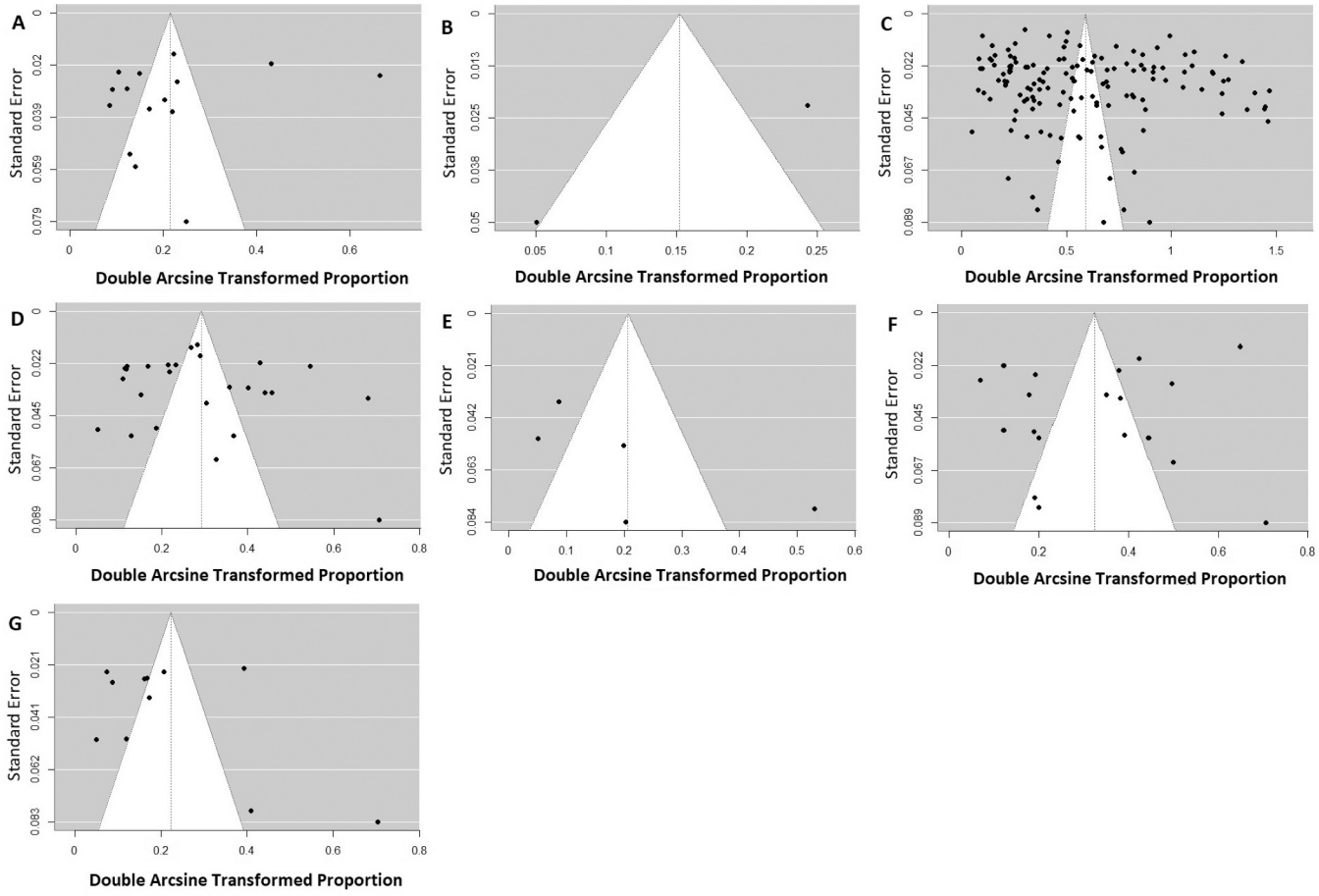

Fig. 4. Funnel plots for the assessment of publication bias for studies regarding the prevalence of *Anaplasma* species amongst cattle in Africa (1970–2022). The x-axis is a measure of prevalence estimates (double arcsine transformed). The y-axis is the precision of the study size (standard error) of corresponding study. The vertical line is situated at the transformed value of the summarised prevalence on the funnel plot, while the two limit lines depict the 95% confidence interval. Circles that represent smaller studies are broadly spread towards the bottom (less precision; higher standard error) and further from the centre of the funnel plot (less like the summarised prevalence), whereas circles from larger studies are narrowly distributed towards the upper part of the graph, and symmetrically clustered around the vertical line. Some circles lie beyond the two limit lines, indicating high heterogeneity. Note: funnel plot as a measure of publication bias needs to be interpreted with caution because sometimes studies with undesirable results are not published due to other factors. (A) *A. bovis*; (B) *A. capra*; (C) *A. marginale*; (D) *A. centrale*; (E) *A. ovis*; (F) *A. platys*; (G) *A. phagocytophilum*.

Hyalomma, compared to about 12 for other *Anaplasma* species (Cossu et al., 2023). When compared with other continents, our estimated prevalence of *A. marginale* by direct detection methods (19.9%) is lower than that recorded from two regions in Russia (42%, Ferodina et al., 2019) but higher than that in Hainan Province in China (5.7%, Zhou et al., 2023) using similar laboratory methods, suggesting different epidemiological situations, including occurrence of tick vectors, climate, and management practices.

In the present study, the pooled prevalence of *A. marginale* by serology tests was highest in southern Africa followed by eastern Africa, and then western Africa, northern Africa, and central Africa in descending order. This observation could be related to the distribution of tick vectors, cattle breeds kept, management practices and microclimatic conditions. Prevalence and incidence are reportedly higher in regions where *R. microplus* tick is endemic or more prevalent (Futse et al., 2003). Both *R. microplus* and *R. decoloratus* are major vectors of *A. marginale*; however, the former has a higher reproductive potential, higher vectorial capacity and is more affected by acaricide resistance (Futse et al., 2003; Nyangiwe et al., 2018). While *R. decoloratus* is distributed in all African regions, *R. microplus* is more prevalent in southern Africa followed by eastern Africa (Walker et al., 2013). Its only of recent that *R. microplus* has spread to central and western Africa, which is attributed to livestock movements (Gomes and Neves, 2018; Nyangiwe et al., 2018; Silatsa et al., 2019). A climate prediction model on the distribution of ticks in Africa showed that southern Africa and East Africa have higher potential for expansion of the range and distribution of 30 *Rhipicephalus* tick species and therefore associated tick-borne pathogens (Olwoch et al., 2007). Geographical variations in prevalence of *A. marginale* also seem to be related to the host abundance and diversity in the different regions. Conservation efforts and realisation of economic benefits of tourism in southern and eastern Africa countries have led to the protection and/or creation of national parks and conservation areas, with high diversity of animals that could serve as reservoirs for tick species. Incidentally, cattle often graze in vicinity of these areas or share grazing lands, thereby increasing the risk of transmission of tick-borne pathogens (Nicol et al., 2023). In western and northern Africa, and most parts of central Africa, wildlife protection is less satisfactory and national parks have seriously been depleted since independence, with only small parks, if any at all, remaining. Northern Africa, furthermore, is largely occupied by the Sahara Desert, in which the climate is less favourable for tick vector development and livestock keeping, and huge areas are wholly empty (Nicol et al., 2023).

Highest *A. marginale* prevalence was recorded in the longitude range of >32° followed by 24–32°. These ranges correspond to the southern, eastern, and central African regions and are consistent with geographical distribution and spread of *R. microplus*. They in turn follow the local

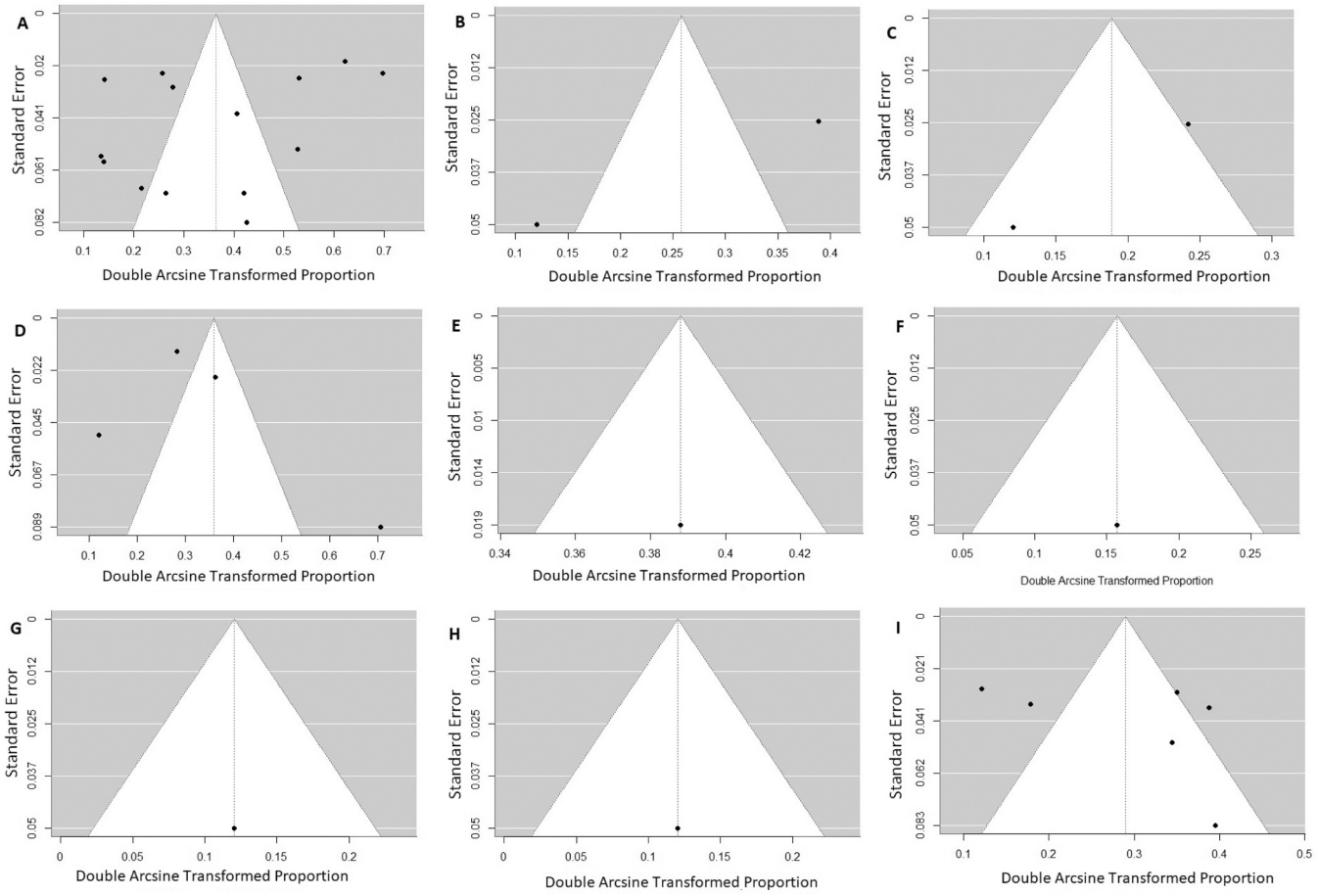

Fig. 5. Funnel plots for the assessment of publication bias for studies regarding the prevalence of uncharacterised *Anaplasma* taxa amongst cattle in Africa (1970–2022). The x-axis is a measure of prevalence estimates (double arcsine transformed). The y-axis is the precision of the study size (standard error) of corresponding study. The vertical line is situated at the transformed value of the summarised prevalence on the funnel plot and the two limit lines depict the summarised prevalence value and 95% confidence interval, respectively. Circles that represent smaller studies are broadly spread towards the bottom (less precision; higher standard error), and further from the centre of the funnel plot (less like the summarised prevalence), whereas circles from larger studies are narrowly distributed towards the upper part of the graph, and symmetrically clustered around the vertical line. Some circles lie beyond the two limit lines, indicating high heterogeneity. Note: funnel plot as a measure of publication bias needs to be interpreted with caution because sometimes studies with undesirable results are not published due to other factors. (A) *Anaplasma* sp. Omatjenne; (B) *Anaplasma* sp. Saso; (C) *Anaplasma* sp. Dedessa; (D) *Anaplasma* sp. Hadesa; (E) *Anaplasma* sp. Lambwe-1; (F) *Anaplasma* sp. Mymensingh; (G) *Candidatus Anaplasma africae*; (H) *Candidatus Anaplasma boleense*; (I) *Anaplasma* sp.

climatic conditions that impact vector adaptation and abundance as well as vector-pathogen interactions (Githaka et al., 2021).

Amongst the direct pathogen detection methods, qPCR-based studies recorded the highest pooled prevalence followed by PCR, while microscopic methods recorded the lowest prevalence. The transient nature of *A. marginale* parasitaemia implies lower sensitivity when applying microscopy with blood smears (Schotthoefer et al., 2013). Furthermore, the sensitivity of microscopic methods is limited in cases of low parasitaemia and by the small number of cells that can be practically examined during routine blood smear analysis (Schotthoefer et al., 2013). In contrast, nucleic acid persists longer in the blood circulation than the infectious pathogen, thereby increasing detection rate by PCR-based methods (Maclachlan et al., 2009). Compared with conventional PCR or RLB techniques, qPCR targets relatively short fragments (<200 bp), which increases the likelihood of amplification and detection of pathogen DNA.

Our analysis highlighted that *A. centrale* was detected in 15 countries in all African regions, with a pooled prevalence of 8.0% (all by direct detection methods) in cattle populations. *Anaplasma centrale* causes subclinical infection, although a clinical case caused by the pathogen was reported in cattle in Italy in 2000 (Carelli et al., 2008). Only adult *R. simus* tick has been implicated in transstadial transmission of the *A. centrale*, in particular the vaccine strain (Potgieter and van Rensburg, 1987). The tick is known to be distributed only in southern Africa countries (Walker et al., 2013), and therefore occurrence of *A. centrale* in other regions possibly means involvement of other tick species in biological transmission or a yet to be confirmed presence of *R. simus*. There have been several purported records of *R. simus* in various African countries, and it has been suggested that these should be treated with caution, due to the extreme difficulties involved in morphological identification of the species (Horak et al., 2018) and possible confusion with other *Rhipicephalus* species (Guglielmone et al., 2023). Therefore, the current geographical distribution of *R. simus* is provisional (Heylen et al., 2021; Guglielmone et al., 2023). A recent review involving African ticks revealed detection of *A. centrale* in four tick species (of *Rhipicephalus* and *Amblyomma* genera) in four countries: Ivory Coast, Ethiopia, Uganda, and South Africa, with very low pooled prevalence (<1%) (Cossu et al., 2023). The significance of wild animals (wildebeest, buffalo, eland, and waterbuck) as reservoirs of *A. centrale* was demonstrated in South Africa, with the observation of diverse strains and frequent co-infections with *A. marginale* (Khumalo et al., 2016; Sisson et al., 2023). There is need for further investigations on the occurrence of *A. centrale* and the role of various tick species in the transmission of the pathogen, especially in areas where cattle share grazing landscape with

Table 3
Pooled prevalence and heterogeneity statistics of *Anaplasma* infections amongst cattle in Africa. Data retrieved from three online databases, from inception through June 2022.

Pathogen species or taxon	No. of studies	African regions (no. of studies)	No. of countries	Cattle tested			Heterogeneity			
				No. tested	No. positive	Prevalence (95% CI); prediction interval	Q-statistic	*p*-value	I^2 (%)	τ^2, H^2
Anaplasma marginale	144	northern (n=35), eastern (n=54), southern (n=18), western (n=27), central (n=10)	29	70,970	21,132	30.8(25.5, 36.4); 0.0, 92.8	32223.9	<0.0001	99.60	0.1282, 250.74
Anaplasma centrale	26	northern (n=6), eastern (n=9), southern (n=2), western (n=4), central (n=5)	15	9232	797	8.0(4.8, 11.9); 0.0, 33.4	643.8	<0.0001	97.36	0.0266, 37.82
Anaplasma phagocytophilum	11	northern (n=5), eastern (n=4), southern (n=1), central (n=1)	10	2981	144	4.5(1.0, 10.2); 0.0, 30.2	180.6	<0.0001	96.98	0.0308, 33.12
Anaplasma platys	19	northern (n=7), eastern (n=5), southern (n=1), western (n=2), central (n=4)	12	5057	836	9.7(5.4, 15.2); 0.0, 38.8	807.2	<0.0001	96.78	0.0301, 31.02
Anaplasma bovis	15	Northern (n=6), eastern (n=6), southern (n=2), central (n=1)	11	5143	407	4.3(1.6, 8.2); 0.0, 24.8	555.8	<0.0001	96.82	0.0230, 31.42
Anaplasma ovis	5	Northern (n=4), central (n=1)	4	457	15	3.5(0.0, 12.3); 0.0, 29.9	31.8	<0.0001	90.9	0.0300, 10.9
Anaplasma capra	2	Northern (n=1), central (n=1)	2	606	29	2.0(0.0, 10.9); 0.0, 20.3	12.3	0.0005	91.85	0.0171, 12.27
***Anaplasma* sp. Omatjenne**	14	northern (n=1), eastern (n=7), southern (n=2), western (n=2), central (n=2)	11	3274	652	12.3(6.4, 19.7); 0.0, 45.0	530.2	<0.0001	96.70	0.0334, 30.50
***Anaplasma* sp. Hadesa**	4	Eastern (n=1), southern (n=1), central (n=2)	3	1783	161	11.9(1.2, 30.7); 0.0, 57.8	41.4	<0.0001	98.24	0.0522, 56.81
***Anaplasma* sp. Saso**	2	Eastern (n=1), southern (n=1)	2	492	57	6.3(0.0,24.6); 0.0, 42.2	23.1	<0.0001	95.66	0.0345, 23.07
***Anaplasma* sp. Dedessa**	2	Eastern (n=1), southern (n=1)	2	492	23	3.2(0.2, 8.9); 0.0, 13.4	5.7	0.0302	78.72	0.0058, 4.70
***Anaplasma* sp. Mymensingh**	1	Southern (n=1)	1	100	2	2.0(0.03, 5.9); 0.03, 5.9	0.0	-	-	0.0000, 1.00
***Anaplasma* sp. Lambwe-1**	1	Eastern (n=1)	1	680	97	14.3(11.7, 17.0); 11.7, 17.0	0.0	-	-	0.0000, 1.00
***Candidatus* Anaplasma africae**	1	Western (n=1)	1	62	5	8.1(2.4, 16.4); 2.4, 16.4	0.0	-	-	0.0000, 1.00
***Anaplasma* sp.**	6	Northern (n=2), eastern (n=2), southern (n=1), western (n=1)	5	1113	85	7.8(3.3, 13.8); 0.01, 25.1	56.1	<0.0001	89.73	0.0124, 9.74
***Candidatus* Anaplasma boleense**	1	Southern (n=1)	1	100	1	1.0(0.0, 4.2); 0.0, 4.2	0.0	-	-	0.0000, 1.00

95% confidence interval means for 95% of studies, the prevalence will be comprised in the indicated range. The prediction interval as determined using a random effects model is an indicator of the range in which future prevalences may fall.

wildlife. It is also necessary to critically examine the supposedly *R. simus* occurrence in Africa and determine other tick species that could be involved in the transmission of *A. centrale*. The test for moderators showed that increasing temperature was significantly associated with decreased occurrence of *A. centrale*. Warm temperatures are favourable for development and attachment of ticks to their hosts and therefore increasing the risk of transmission of pathogens (Hussein and Mustafa, 1987; Dantas-Torres, 2010), but as it gets hotter, there is increased tick mortality and therefore decreased pathogen transmission and occurrence (Gilbert, 2021).

The prevalence estimate of *A. phagocytophilum* was 4.5% from only 11 studies in 10 countries in four African regions (northern, eastern, southern, central). The pathogen is known to be more common in Southeast Asia, northern Europe, and northeast United States, where it is transmitted by *Ixodes* ticks and through blood transfusions (Matei et al., 2019). However, of the 266 known *Ixodes* species, the highest number are indigenous to the Afrotropical zoogeographic realm, especially sub-Saharan Africa (60 species), where they parasitise a wide range of domestic and wild animals (Apanaskevich et al., 2011; Guglielmone et al., 2023). Moreover, a few *Ixodes* species have been found in northern Africa (Tunisia, Algeria, Morocco), where they parasitise domestic or wild ruminants, dogs, and lizards (Walker et al., 2013). We therefore think that *A. phagocytophilum* is more prevalent and more widely distributed on the continent, but less attention has been paid to *Ixodes*

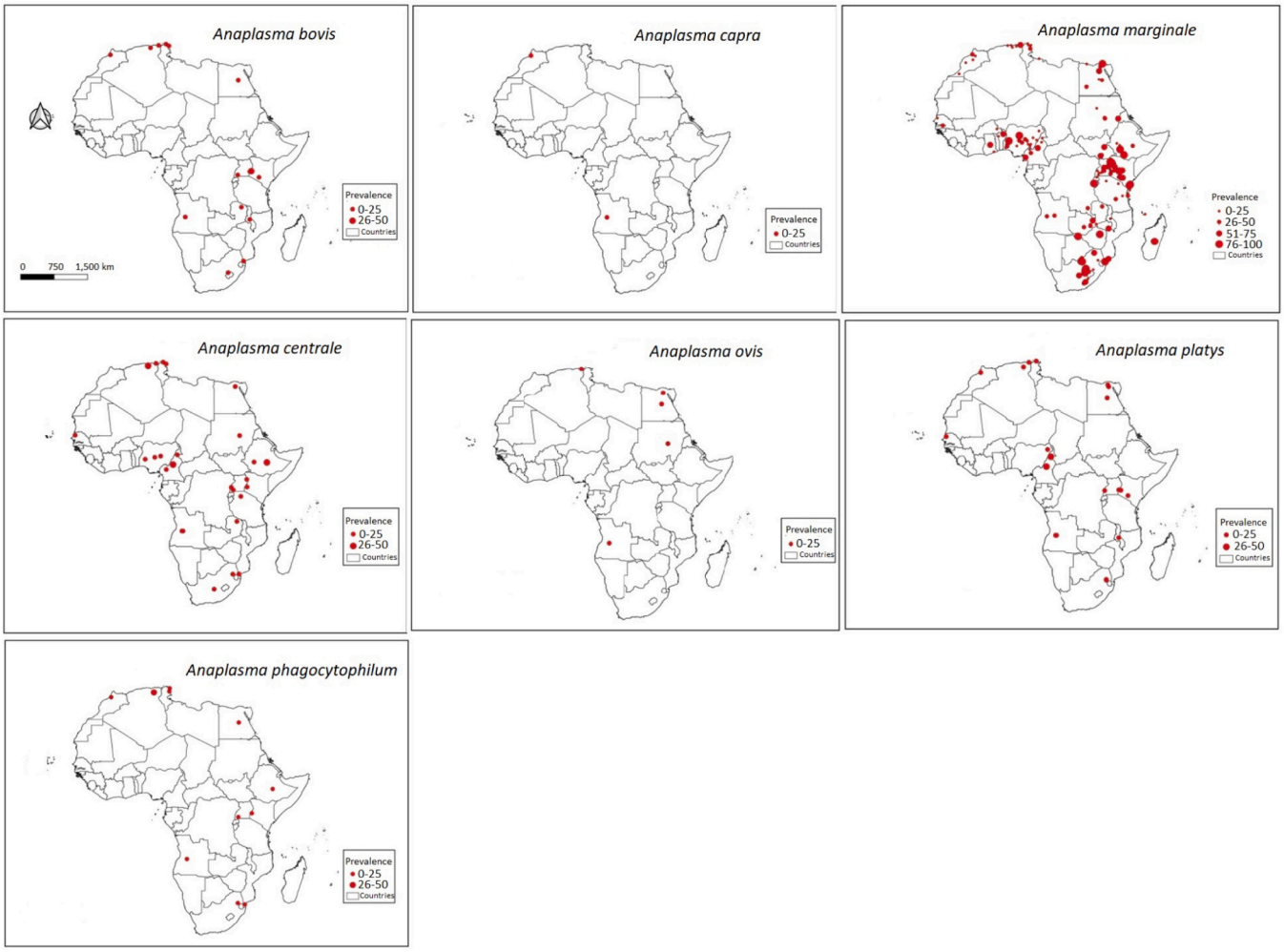

Fig. 6. Country-specific prevalence of *Anaplasma* species detected in cattle in Africa, for studies published up to June 2022. Prevalence categories are denoted by red dots of different sizes on the maps.

ticks and the pathogen itself. Amongst the few studies conducted, the pathogen was detected in non-human primates in Zambia (Nakayima et al., 2014) and captive wild felids in Zimbabwe (Kelly et al., 2014), and was confirmed in rodents, dogs, and humans (acute febrile patients) in South Africa by PacBio circular 16 S rRNA gene sequencing (Kolo et al., 2020). Therefore, despite the previously reported low prevalence (<1%) in 14 African tick species (Cossu et al., 2023), there is possibly a risk of disease in human categories such as herdsmen, hunters, and veterinarians. Given the zoonotic importance of the pathogen, more studies are needed to establish occurrence in humans and peri-domestic animals in Africa and establish the geographical distribution and pathogenicity of genetic groups, especially those of public health importance. There is also a need to establish the vectorial capacity of various tick species, especially *Ixodes* and other genera in which *A. phagocytophilum* has been detected.

Anaplasma bovis was reported in 11 African countries, mostly in the northern (5 countries) and eastern (4 countries) regions, but not in the western region. The known tick vectors of *A. bovis* are distributed throughout Africa: *R. appendiculatus* and *R. zambeziensis* in the southern and eastern regions; and *Amblyomma variegatum* in the western, central, and eastern regions (Walker et al., 2013; Blowey and Weaver, 2011); while *Hyalomma aeqypticus* is implicated in the northern region (Blowey and Weaver, 2011). The skewed distribution of *A. bovis* observed in the present study could therefore be related to limited attention paid to the pathogen, or poor pathogen-vector adaptation, rather than presence of the tick vectors. Our pooled prevalence (4.3%) for *A. bovis* is similar to that reported in China (4.8–8.4%, Yang et al., 2015; Zhou et al., 2019). On the other hand, Cossu et al. (2023) reported a pooled prevalence of about 1% in 10 tick species (mostly *Rhipicephalus*) from only three African countries (South Africa, Tunisia, Kenya). Infection in cattle is usually asymptomatic, although a few clinical monocytic anaplasmosis cases have been reported (Pyriyanka et al., 2017). Apart from cattle, the pathogen has been detected in buffalo, sheep, goats, dogs, cats, and wild deer in South and North America, Asia, and Africa (Sasaki et al., 2012; Atif, 2016; Belkahia et al., 2017a; Fukui and Inokuma, 2019), and was detected in *Haemaphysalis punctata* ticks in Europe (Palomar et al., 2015). More research is required to elucidate the epidemiology (distribution, prevalence, transmission) and pathogenicity of *A. bovis*.

Our meta-analysis demonstrated a 9.7% pooled prevalence of *A. platys* (all studies based on direct detection methods) in 12 countries in all African regions. Detection was more frequent in the northern (countries bordering the Mediterranean Sea, 7/19 studies in 4 countries) and eastern (5/19 studies in 3 countries) regions. The suspected tick vector is *R. sanguineus sensu lato* (Selim et al., 2021a), which occurs in all climatic regions of Africa due to its association with domestic dogs (Walker et al., 2013). In a study concerning prevalence of *Anaplasmataceae* in African ticks, *A. platys* was detected in 12 *Rhipicephalus* tick species in seven African countries (South Africa, Kenya, Guinea, Ethiopia, DRC, Tunisia, Egypt) (Cossu et al., 2023). It is therefore likely that *A. platys* uniformly occurs in all African regions, but there are variations in research/surveillance efforts towards the pathogen. The pathogen causes cyclic thrombocytopenia in dogs (Abarca et al., 2007)

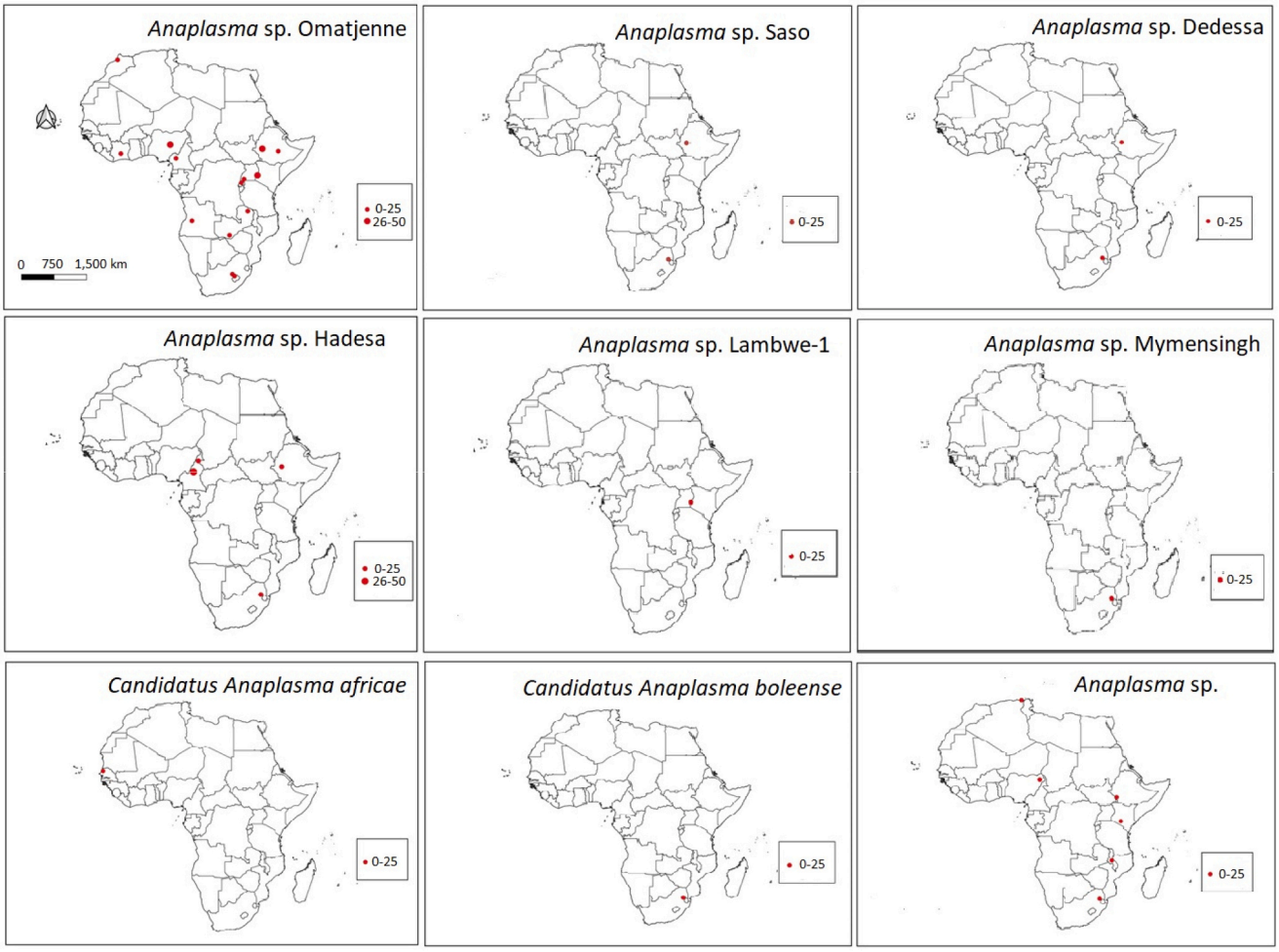

Fig. 7. Country-specific prevalence of uncharacterised *Anaplasma* taxa detected in cattle in Africa, for studies published up to June 2022. Prevalence categories are denoted by red dots of different sizes on the maps.

and because *R. sanguineus sensu lato* parasitises humans (Nava et al., 2017) and various domestic and wild animals (Granick et al., 2021), *A. platys* is an emergent zoonosis (Maggi et al., 2013; Arraga-Alvarado et al., 2014). The close association amongst dogs, cattle, and humans in pastoral areas in Africa, coupled with the ubiquitous occurrence of *R. sanguineus s.l* ticks, is likely to increase the risk of human infections. Further investigation is needed regarding occurrence and ability of *A. platys* to cause disease in various vertebrate hosts, and assessment of the vectorial capacity of different tick species, in particular the competence of the tropical and temperate lineages of *R. sanguineus sensu lato*.

Anaplasma capra was reported only in two studies from the northern and central regions. The pathogen was first identified in a goat (*Capra aegagrus hircus*) and was recently detected in goat erythrocytes (Peng et al., 2021). It has since been shown to infect pet dogs, wild animals (e.g deer), domestic ruminants (goats, sheep, cattle) and humans (Li et al., 2015; Peng et al., 2018; Yang et al., 2018; Jouglin et al., 2019; Shi et al., 2019) in China and France, although is not formally recognised (Li et al., 2015; Yang et al., 2017). It is still unclear about the tick vector(s) of *A. capra*, although studies have revealed detection in *Haemaphysalis*, *Ixodes* and *Rhipicephalus* ticks (Fang et al., 2015; Yang et al., 2016; Seo et al., 2018; Guo et al., 2019), posing an emerging health risk for humans and animals worldwide. Transmission studies are needed to determine the tick vectors involved as well as investigatio on the zoonotic importance, genetics, and pathogenicity of *A. capra*.

Anaplasma ovis was mostly reported in the northern parts of Africa, consistent with the geographical distribution of *R. bursa* and *Ha. sulcata* (Walker et al., 2013; Guglielmone et al., 2023), which are regarded as the biological vectors (Walker et al., 2013), especially in the mediterranean area (Friedhoff, 1997). There is still insufficient epidemiological investigation about the pathogen, especially with regards to occurrence and the tick vectors involved. In one study, the pathogen was identified in *R. turanicus* and *R. bursa* ticks collected from sheep in Algeria (Aouadi et al., 2017), and an association between *A. ovis* infection and the two tick species was reported in Turkey (Aktas and Özübek, 2018). In a review concerning African ticks, the pathogen was reportedly detected in 11 tick species (mostly *Rhipicephalus* genus) in six African countries (Algeria, Tunisia, Ethiopia, Kenya, Mozambique, South Africa) (Cossu et al., 2023). *Anaplasma ovis* causes subclinical anaplasmosis in sheep and goats (Kuttler, 1984) and wild ruminants (Yabsley et al., 2005; de la Fuente et al., 2007), mostly in tropical and subtropical areas. Infection can become more severe in co-infections and in weak or stressed animals (Friedhoff, 1997). Occurrence in cattle can be explained by interaction with small ruminants, especially in communal grazing areas.

The nine uncharacterised *Anaplasma* taxa were mainly reported in eastern and southern Africa, possibly highlighting the differential access and utilisation of sequencing technologies in the identification and discovery of novel pathogens.

The widespread occurrence of *Anaplasma* spp., in particular *A. marginale*, and the alarming spread of the Asian cattle tick *R. microplus* (Adakal et al., 2013), indicates a potentially high burden of anaplasmosis in cattle. Most areas can be considered to be in a state of enzootic instability and given the low infection rates of ticks and therefore little balance in relation between the pathogen, vector, and host (Cossu et al., 2023; Mucheka et al., 2023), there is poor challenge of the immune

Table 4
Subgroup analysis for the relationship between *Anaplasma marginale* occurrence amongst cattle in Africa and predictor variables. For studies published in three databases, from inception up through June 2022. Only variables with $p<0.1$ from subgroup analysis are shown.

Variable	Level	No. of studies	Cattle tested for *A. marginale*[a]			Heterogeneity[b]	Univariate meta-regression (test for moderator association with *A. marginale*)[b]			
			No. tested	No. positive	% (95% CI)	I^2 (%)	*p*-value	τ^2, H^2	Coefficient *QM* (df)	R^2 (%)
Studies based on serology tests										
Geographical region							**0.0219**	**0.1088, 211.69**	**11.45(4)**	**14.03**
	Central Africa	**2**	**359**	**79**	**20.9(0.0, 64.9)**	**99.61**				
	Eastern Africa	**22**	**13,134**	**6189**	**61.7(47.9, 74.5)**	**99.61**				
	Northern Africa	**8**	**3708**	**912**	**32.7(13.6, 55.4)**	**99.56**				
	Southern Africa	**10**	**5364**	**3780**	**74.8(55.3, 90.2)**	**99.57**				
	Western Africa	**5**	**2177**	**957**	**43.8(17.6, 72.1)**	**99.61**				
Longitude (degrees)							**0.0336**	**0.1125, 219.19**	**8.69(3)**	**11.09**
	0–8	**5**	**3293**	**1167**	**42.2 (16.0, 71.1)**	**99.61**				
	9–23	**4**	**1532**	**299**	**16.4(0.6, 46.3)**	**99.57**				
	24–32	**19**	**10,641**	**5203**	**61.0(45.9, 75.1)**	**99.61**				
	>32	**19**	**9276**	**5248**	**63.6 (48.6, 77.4)**	**99.61**				
Studies based on direct pathogen detection methods										
Detection method							**<0.0001**	**0.0663, 121.80**	**24.88**	**19.27**
	Microscopy	**34**	**24,090**	**3453**	**13.1(7.7, 19.6)**	**99.30**				
	PCR	**44**	**16,718**	**3995**	**20.5(14.6, 27.1)**	**99.35**				
	qPCR	**6**	**1638**	**1114**	**65.8(45.2, 83.7)**	**99.21**				
	RLB	**13**	**3782**	**653**	**18.8(9.0, 31.1)**	**99.36**				
Latitude (degrees)							**0.0717**	**0.0787, 137.81**	**7.01(3)**	**4.17**
	0–6	**23**	**14,033**	**2746**	**15.7(8.3, 25.0)**	**99.33**				
	7–12	**28**	**12,902**	**2052**	**17.7(10.4, 26.4)**	**99.35**				
	13–26	**20**	**6662**	**2635**	**32.9(21.8, 45.1)**	**99.30**				
	>26	**26**	**12,631**	**1782**	**17.1(9.6, 26.1)**	**99.33**				
Management system	**Extensive**	**34**	**16,802**	**6190**	**38.0(27.5, 49.2)**	**99.42**	**0.0665**	**0.1100, 172.25**	**3.37(1)**	**4.39**
	Semi-intensive/ intensive	**21**	**5789**	**886**	**22.3(11.6, 35.4)**	**99.42**				

PCR, polymerase chain reaction; RLB, reverse line blot; qPCR, quantitative real-time PCR
Only variables with $p<0.1$ from statistical analysis are shown in the table.
CI: Confidence intervals. 95% CIs were calculated as described by Higgins and Thompson (2002).
I^2 (%): Residual heterogeneity (unaccounted heterogeneity)
R^2: Proportion of between-study variance explained.
QM: Coefficient of test for heterogeneity between subgroups; df=degrees of freedom
τ^2 (tau squared) =between-study variance - estimated variance of the distribution of true prevalence in the population of sub-clinical mastitis studies
H^2=unaccounted variability (sampling variability) – the ratio of the standard deviation of the estimated overall prevalence from the random-effects model compared to the standard deviation from the fixed-effects model.
[c]One study was conducted using LCD-array
[d]Only 8 of the 30 studies were from intensive system
[a] Random-effects model
[b] Mixed-effects model

system and a high likelihood of disease outbreaks. Control of anaplasmosis in cattle will require an integrated approach that considers factors such as animal movements, acaricide resistance, climate change and wildlife-livestock interface. Given the occurrence of zoonotic *Anaplasma* pathogens in cattle populations, it is essential to raise awareness amongst risk groups and consider these in differential diagnosis of acute febrile illness.

5. Strengths and limitations

The strength of this systematic review and meta-analysis is the adherence to the PRISMA guidelines for the design of the protocol and implementation of literature search and data analyses. The study is the first to present comprehensive data on the prevalence, distribution, and risk factors for *Anaplasma* species amongst cattle across the entire African continent, from the 1970 s to 2022. The reported epidemiological evidence is pertinent in the implementation of health and production interventions and to guide further research and surveillance for *Anaplasma* pathogens.

One limitation of this meta-analysis is the small number, or complete lack, of studies from some regions or countries; therefore, the reported prevalence estimates might over- or under-estimate the true value. This may also affect the power of subgroup analysis to establish the true spatial effect. About half of the eligible studies (82/158) were from five countries (Nigeria, Uganda, Kenya, South Africa, Egypt). However, our findings on the spatial and temporal distribution of *Anaplasma* infections can serve as basis for investment in research, surveillance, and control of tick-borne pathogens in those countries that are still lacking data. Fewer studies (less than a third) considered host factors such as age and sex, and only half of the studies considered management factors, which constrains assessment of their impact on infections.

The more sensitive and specific techniques, qPCR and RLB, are more recent innovations and therefore few studies reported on detection using these methods. On the other hand, conventional PCR and microscopy have lower sensitivity, with a likelihood of false negative results in samples with low parasite concentrations. Moreover, some researchers may have inadequate expertise for accurate identification of tick-borne pathogens using microscopic methods. Another limitation is the

Table 5
Subgroup analysis for predictors of *Anaplasma centrale* infection amongst cattle in Africa for studies published up to June 2022. All studies were based on direct pathogen detection methods (microscopy, PCR, qPCR and RLB). Only variables with heterogeneity *p*-value<0.1 from subgroup analysis are shown.

Variable	Level	No. of studies	Cattle tested for *A. centrale*[a]			Heterogeneity[b]	Univariate meta-regression (test for moderator association with *A. centrale*)[b]			
			No. tested	No. positive	% (95% CI)	I^2 (%)	*p*-value	τ^2, H^2	Coefficient *QM* (df)	R^2 (%)
Temperature (°C)							**0.0269**	**0.0206, 27.55**	**9.18(3)**	**22.58**
	14–20	**5**	**2109**	**338**	**20.0(10.8, 31.2)**	**96.17**				
	21–23	**8**	**2107**	**168**	**5.5(1.7, 11.2)**	**97.34**				
	24–28	**9**	**3828**	**244**	**6.7(2.6, 12.5)**	**97.35**				
	>28	**4**	**1188**	**47**	**4.3(0.2, 12.3)**	**97.34**				

Only variables with p<0.1 from statistical analysis are shown in the table.
CI: Confidence intervals. 95% CIs were calculated as described by Higgins and Thompson (2002).
I2 (%): Residual heterogeneity (unaccounted heterogeneity)
R2: Proportion of between-study variance explained.
QM: Coefficient of test for heterogeneity between subgroups; df=degrees of freedom
τ2 (tau squared) =between-study variance - estimated variance of the distribution of true prevalence in the population of sub-clinical mastitis studies
H2=unaccounted variability (sampling variability) – the ratio of the standard deviation of the estimated overall prevalence from the random-effects model compared to the standard deviation from the fixed-effects model.
[c]One study was conducted using LCD-array
[a] Random-effects model
[b] Mixed-effects model.

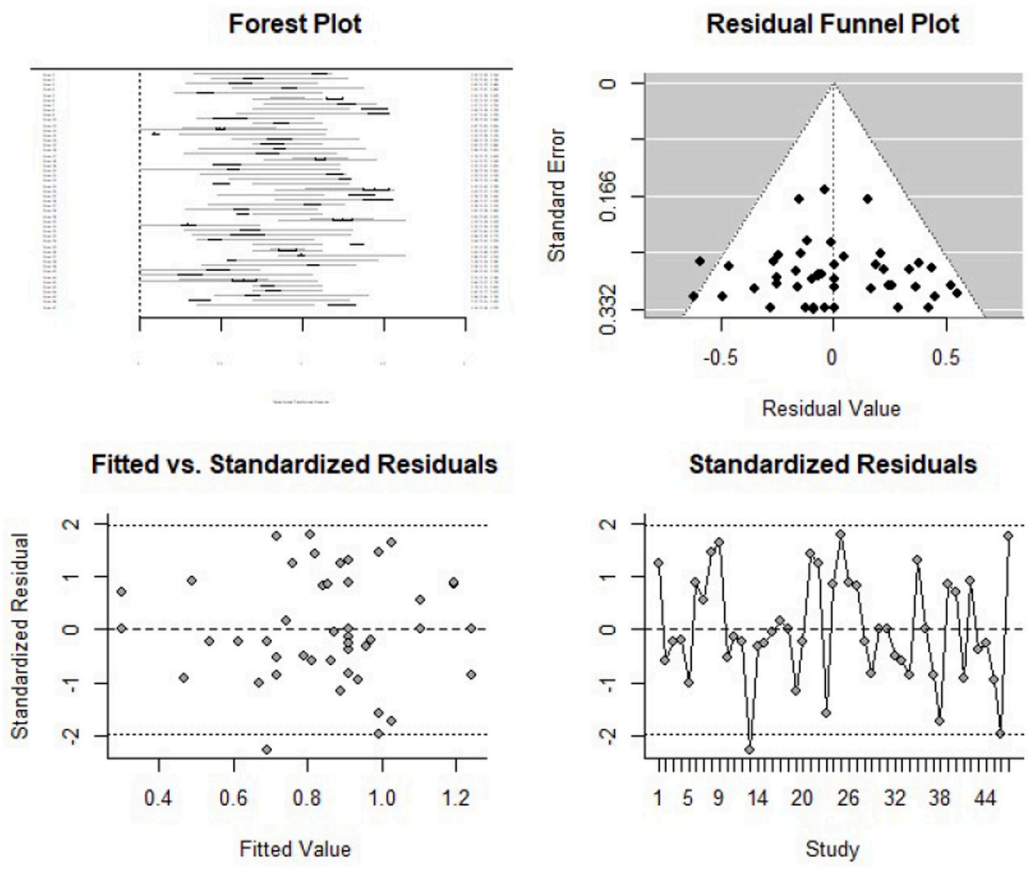

Fig. 8. Q-Q plot of meta-regression residuals for studies on the prevalence of *A. marginale* based on serology methods.

possibility of cross-reactions in conventional PCR methods based on amplification of short sequences of the 16 S rRNA gene, which are highly similar amongst genomically distinct *Anaplasma* species (Caudill and Brayton, 2022). The full length 16 S rRNA gene needs to be amplified and sequenced to increase the specificity of such PCR. Therefore, misclassification of certain *Anaplasma* species may have occurred in some studies, as previously indicated (Kolo et al., 2020). The currently used RLB oligonucleotide probes (Georges et al., 2001; Bekker et al., 2002) can cross-react amongst previously described *Anaplasma* species or uncharacterised genotypes (Makgabo et al., 2023), while the genus-specific cELISA employed in some studies utilises a recombinant major surface protein 5 as an antigen, which is highly conserved amongst *Anaplasma* species (Dreher et al., 2005; Hofmann-Lehmann et al., 2004). The latter therefore cannot differentiate *A. marginale* from other species, which can be a problem in case of co-infections. There is therefore a need to develop and validate more specific assays

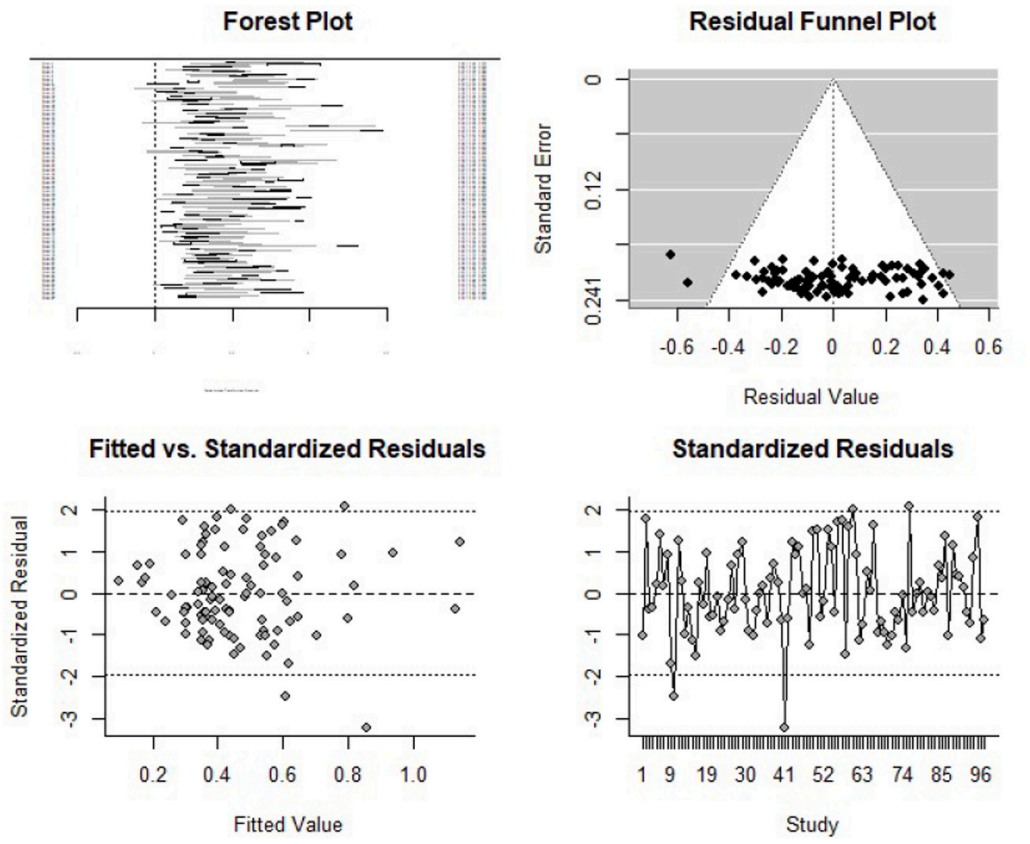

Fig. 9. Q-Q plot of meta-regression residuals for studies on the prevalence of *A. marginale* based on direct detection methods.

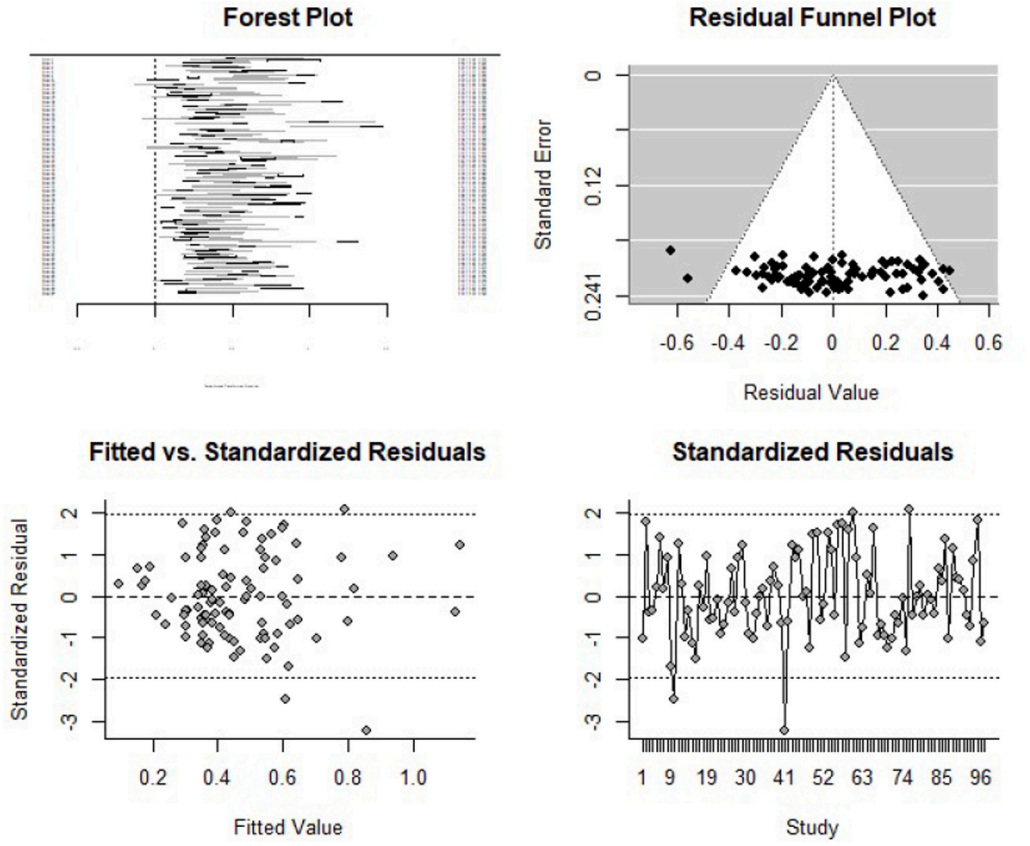

Fig. 10. Q-Q plot of meta-regression residuals for studies on the prevalence of *A. centrale* based on direct detection methods.

for *Anaplasma* pathogens.

6. Conclusions

The most frequently reported *Anaplasma* species in cattle in Africa was *A. marginale* followed by *A. centrale* and *A. platys* (all regions), while *A. ovis* and *A. capra* were reported only in the northern and central regions. Tick vectors, geographical location and temperature were determinants for pathogen occurrence. The high diversity and widespread occurrence of *Anaplasma* pathogens implies that anaplasmosis is an important health problem in Africa. More genetic and genome sequencing data for *Anaplasma* species, especially the unrecognised ones, are required to facilitate accurate identification. Certainly, there is also a need for further epidemiological information (such as tick vectors and pathogen occurrence) and implementation of a One Health approach to achieve optimal health in animals and/or people and/or the environment.

Ethical approval

We did not collect primary data or conduct animal research, and therefore formal ethical approval was not required.

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CRediT authorship contribution statement

Claire Julie Akwongo: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Charles Byaruhanga:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare no conflict of interest.

Data Availability

The data used in this systematic review and meta-analysis are available as a supplementary file to this manuscript. Other data can be availed on request from the corresponding author.

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The authors, and not any institution, made the final decision on publication of the findings.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.prevetmed.2024.106214.

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