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REVIEW

Carbapenem Resistance in Animal-Environment-Food from Africa: A Systematic Review, Recommendations and Perspectives

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Background: The World Health Organization (WHO) has classified carbapenem-resistant *Enterobacteriaceae, Pseudomonas aeruginosa* (*P. aeruginosa*), and *Acinetobacter baumannii* (*A. baumannii*) as high-priority pathogens, and carbapenem-resistant bacteria (CRB) have been reported to spread between humans, animals, and the environment.

Objective: This study aimed to conduct a systematic review of carbapenem resistance in animals, foods, and the environment on the African continent and to provide recommendations and perspectives for better prevention and control of carbapenem resistance in Africa.

Results: A total of 137 research articles collected from 2009 to 2023 were selected for this review, including articles reporting carbapenem-resistant bacteria in animals (81/137; 59.1%), the environment (66/137; 48.2%), and foods (26/137; 19%). Carbapenem-resistant bacterial species belonged to 31 genera and 17 families, including mainly *Escherichia* spp. (68/127; 53.5%); *Klebsiella* spp. (45/127; 35.4%); *Pseudomonas* spp. (20/127; 15.7%), *Enterobacter* spp. (19/127; 15%) and *Acinetobacter* spp. (15/127; 11.8%). The prevalence of CRBs by country ranged from 1.1% to 48.5%, and the pooled prevalence of CRBs isolated from animal-environment-food in Africa was 19.1% (2804/14,684; Standard Deviation = 15). Twenty carbapenemase families belonging to A, B, C, and D Ambler classes were reported, including mainly carbapenemase genes from bla_{OXA} (44/84; 52.4%), bla_{NDM} (34/84; 40.5%), bla_{SHV} (23/84; 27.4%), bla_{KPC} (22/84; 26.2%), bla_{VIM} (19/84; 22.6%), and bla_{IMP} (12/84; 14.3%) families. The reported mobile genetic elements (MGE) carrying carbapenemase-encoding genes included plasmids (16/19; 84.2%), integrons (3/19; 15.8%), transposons (3/19; 15.8%), and insertion sequences (2/19; 10.5%). $bla_{\text{OXA-48}}$ was often carried by (60kb-65kb) IncL/M-type pOXA-48 plasmids, while $bla_{\text{NDM-5}}$ was often carried by (45–50kb) IncX-type plasmids. Moreover, 25 articles investigated and reported virulent and hypervirulent CRBs that carried multiple virulence factors.

Conclusion: Animal-environment-food ecosystems would constitute reservoirs of CRBs involved in human infections. The One Health approach and constant collaboration between governments are necessary to drastically reduce the mortality rates linked to antimicrobial resistance.

Keywords: carbapenem resistance, animal-environment-food, Africa, mobile genetic element, carbapenemase gene

Introduction

Carbapenems constitute a class of antibiotics of last resort against severe infections caused by multidrug- (MDR) and extensively drug-resistant (XDR) bacteria.[1–3] Unfortunately, carbapenem-resistant bacteria (CRB) are increasingly being reported worldwide, with several cases of CRB epidemics reported in all continents.[4–8] In addition, many cases of hypervirulent CRBs have been reported worldwide, making CRBs a real threat to public health.[9–11] Furthermore, the World Health Organization (WHO) classified carbapenem-resistant *Enterobacteriaceae, Pseudomonas aeruginosa* (*P.*

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aeruginosa), and *Acinetobacter baumannii* (*A. baumannii*) as high-priority pathogens.[12] In Africa, clinical CRB prevalence of up to 21% has been reported in certain countries.[13,14]

Carbapenemase production is the main mechanism causing carbapenem-resistance.[15,16] Carbapenemases are molecules that break the beta-lactam ring, preventing the action of carbapenems.[16,17] Carbapenemases are encoded by genes located mostly on mobile genetic elements (MGE) such as plasmids, integrons, and transposons.[18–20] In addition to carbapenemase genes, these MGEs often carry resistance genes for quinolones, aminoglycosides, and CTX-M extended spectrum beta-lactamase (ESBL) genes.[21–23]

In addition to humans, CRBs have also been reported in animals (wild animals, companion animals, farmed animals, seafood, fish), foods (fruits, cooked foods, retail foods), and the environment (wastewaters, hospital environment, rivers, oceans).[24,25] Animal and environmental ecosystems are powerful reservoirs that catalyze the occurrence of human CRB-associated infections.[24,26–28] Therefore, the reservoirs and vectors of CRBs must be carefully considered.

Global surveys have shown that in 2019, antimicrobial resistance killed more people than HIV/AIDS or malaria.[29,30] Therefore, improving surveillance, investigation, and in particular prevention of MDR- and XDR-associated infections must be a priority of public health authorities.

Thus, this study aimed to conduct a systematic review of carbapenem resistance in the animal-food-environment in Africa, and to provide recommendations and perspectives for better prevention and control of carbapenem resistance in Africa.

Materials and Methods

Literature Review

Keywords (carbapenem resistance, carbapenemase, food, animal, seafood, bird, fish, environment, Africa, country name) were used to perform a comprehensive literature search of databases (Google Scholar, African Journals Online, ResearchGate, PubMed, Embase, and Scopus). Articles published in both English and French were included to ensure comprehensive and relevant data. Animals, seafood, birds, and fish are grouped in "animal".

Study Selection Criteria

Peer-reviewed research articles reporting carbapenem-resistant or carbapenemase-producing bacteria (CPB) collected in African countries were pre-selected for this study. After this stage, studies reporting CRBs or CPBs isolated from humans were excluded. Review articles reporting CRBs or CPBs collected in Africa were also excluded. Ocean water samples collected from the territorial oceans of African countries were also included in this study.

Data Extraction and Synthesis

The following data were extracted from every research article: country where the samples were collected, year of sample collection, isolated bacteria, prevalence of CRB or CPB, carbapenemase-encoding genes, virulence genes (if reported), mobile genetic supports carrying the carbapenemase –encoding genes, and references.

Statistical Analysis

Microsoft Excel 2016 was used for statistical analysis and graphical representation. p-values were obtained from the chi-square proportion comparison test at 5%, and the level of significance for all statistical tests was set at $p < 0.05$.

Results

Literature Search and Eligible Studies

A literature search of databases (Google Scholar, African Journals Online, ResearchGate, PubMed, Embase, and Scopus) generated 2879 research articles. Subsequently, 742, 1605, and 395 research articles were excluded for duplication, data outside Africa, and data collected from humans, respectively. The remaining 137 articles were included in this systematic review (Figure 1). The data collected from 137 research articles are presented in Table 1.

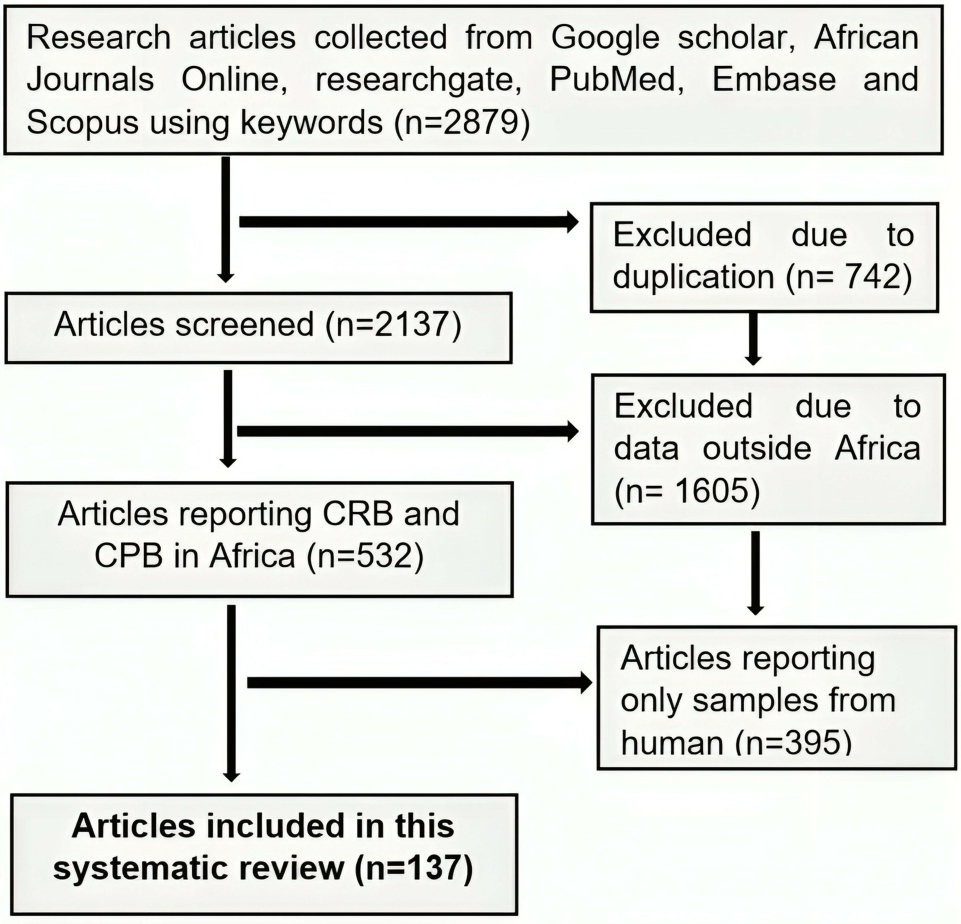

Figure 1 Search flow diagram.

Distribution of Articles

In total, 137 research articles were included in this review, including articles reporting CRBs from animals (81/137; 59.1%), the environment (66/137; 48.2%), and foods (26/137; 19%) (Figure 2). Samples were collected between 2009 and 2023 (14 years). The North African region, with 53 articles, reported significantly more articles than the other regions ($p < 0.0001$). The North African region has mainly reported CRBs of animal origin (40/53; 75.5%), whereas the West African (25/39; 64.1%) and South African (10/13; 76.9%) regions reported mainly CRBs of environmental origin. The distribution of articles according to African regions is displayed in (Figure 2). The number of studies per country ranged from 1 to 22, with an average of 5 articles per country (standard deviation = 6). The distribution of articles by country according to different ecosystems is shown in Figure 3.

Samples Carrying Carbapenem-Resistant Bacteria

According to the articles included in this review, CRBs were isolated from animals (feces, fresh meats, pets, wild animals, farmed animals, cow milk), fish and seafood (tilapia, clams, bivalves, mussels), birds (meat and feces from poultry, migratory birds, urban pigeons), water (wastewater, tap water, fresh water, borehole water, ocean water, irrigation water, river water), soil (sediment, soil, manure), abattoir equipments and environment, foods (household foods, milk and dairy products, ready-to-eat meats, fresh vegetables, lettuce), insects (cockroach, human head lice), and even currency coins. In addition to these samples, 18 of 137 (13.1%) articles reported CRBs isolated from hospital environments (beds, surfaces, doors, taps, sinks, water, wastewater, and hospital devices).

Table 1 Informations Collected from the 137 Research Articles Included in This Review

Country	Year of Isolation / Collection	Origin / source	Bacteria	Prevalence of CRB (%)	Carbapenemase-Encoding Genes (Virulence genes or Factors if Reported)	MGE Carrying Carbapenemase-Encoding Genes	References
Algeria	2012–2013	Fish	ST2 *A. baumannii*	2/300 (0.7)	bla_{OXA-23}, bla_{OXA-51}	Tn*2006*	[31]
	2013	Stool samples of urban pigeons	*A. Baumannii, A. nosocomialis*	4**	bla_{OXA-23}, bla_{OXA-51}-like, bla_{OXA-58}	NA	[32]
	2013	Soil and water samples	*Enterobacteriaceae, Pseudomonadaceae, Xanthomonadaceae, Aeromonadaceae*	49/62 (79)	NA	NA	[33]
	2014–2015	Poultry feces	NA	NA	bla_{OXA-58}, bla_{SHV-11}, bla_{SHV-27}, bla_{SHV-32}, bla_{SHV-99}, bla_{SHV-89}, bla_{SHV-85}	NA	[34]
	2014–2015	Rectal swabs from companion animals (dogs and cats)	*E. coli*	5/200 (2.5)	bla_{NDM-5}, bla_{OXA-48}, bla_{CMY-2} (*fyuA, iutA*)	NA	[35]
	2014–2016	Wild boars	ST635 E. coli, ST13 *K. pneumoniae*	3/168 (1.8)	bla_{OXA-48} (*fimH, mrkD, fyuA, entB, irp-1* for the *K. pneumoniae* strain)	NA	[36]
	2015	Fecal samples of White Stork	*E. coli*	3	bla_{OXA-48}	NA	[37]
	2015	Cow raw milk	ST1284 *E. coli*	4	bla_{NDM-5}	□ 50 kb IncX-3 plasmid	[38]
	2015–2016	Hospital surfaces	*Enterobacter* spp.	6/77 (7.8)	bla_{VIM-2}, bla_{NDM-1}, bla_{IMP}, bla_{OXA-23}	NA	[39]
	2015–2016	Rectal swabs of companion animals (cat, horses, birds, dogs)	*Enterobacter cloacae* *E. coli* *K. pneumoniae*	12**	bla_{OXA-48}	7 kb plasmid	[40]

Algeria	2015–2017	Fresh fecal samples from farm animals, wild animals, pets, fresh samples from food products, water environment	*Klebsiella* spp., *R. ornithinolytica, E. cloacae, C. malonaticus, R. planticola, C. werkmanii, P. gergoviae*	74/3159 (2.3)	bla_{OXA-48} (*ureA, fimH, mrkD, ugeF*)	61.9 kb pOXA-48a type plasmid	[41]
	2016–2018	Broiler liver	*E. coli, K. pneumoniae*	0	bla_{SHV-12}	NA	[42]
	2017	Chicken meat	ST48 and ST101 *K. pneumoniae*	29	bla_{NDM-1}, bla_{SHV-11}, bla_{OXA-48} (*fimH, ureA, mrkD, entB, uge, wabG, kfu, ybtS, iutA*)	60kb IncL plasmid type for the bla_{OXA-48} 50kb IncFIIK plasmid type for the bla_{NDM-1}	[43]
	2018–2019	Wastewater, tap water and well water	*Enterobacteriaceae, Acinetobacter* spp., *Pseudomonas* spp.	61/228 (26.8)	bla_{OXA-48}, $bla_{SHV-145}$, bla_{VIM-2}, bla_{VIM-4}, $bla_{OXA-181}$, bla_{OXA-23}, bla_{KPC-2}, bla_{NDM-5}	NA	[44]
	2018–2019	Currency coins	ST108 *E. cloacae*	4/12 (33.3)	bla_{OXA-48}	NA	[45]
	2019	Fresh vegetables	*Enterobacteriaceae, Pseudomonas* spp., *Acinetobacter* spp.	22/67 (32.8)	bla_{OXA-48}, bla_{VIM-4}, $bla_{SHV-168}$, bla_{SHV-11}	NA	[46]
	2019	Fecal samples of pigeon	*E. coli*	14/35 (40)	bla_{OXA-48}	NA	[47]
	NA	Organs and feces / cloacal swabs of broiler chickens	*E. coli*	3/39 (7.7)	(*iss, hlyF, ompT, iroN, fimC, iutA, elt/est, stx, ipaH, eae, aggR*)	NA	[48]
Benin	2013	Market Garden Products and Irrigation Water	*E. coli*	25/65 (38.5)	(*stx-1, stx-2*)	NA	[49]
	2019	Hospital Wastewater	*Bacteroides* spp., *Acinetobacter bereziniae*	NA	$bla_{OXA-129}$, $bla_{OXA-256}$, $bla_{OXA-347}$, $bla_{OXA-229}$, bla_{GES}, bla_{OXA-58}-like	NA	[50]
Benin	2020	Environment and Selected Food Products	*Enterobacteriaceae, Pseudomonas* spp., *Acinetobacter* spp.	39/63 (61.9)	(*fimH*)	NA	[51]
	2023	Hospital effluent	*E. coli*	1/6 (16.7)	NF	NA	[52]
Botswana	NA	Influent, effluent and downstream water	*Staphylococcus* spp.	(9)	NA	NA	[53]
			Pseudomonas spp.	(14)			
			Campylobacter spp.	(6)			
			Listeria spp.	(6)			
			Brucella spp.	(18)			

(*Continued*)

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Table 1 (Continued).

Country	Year of Isolation / Collection	Origin / source	Bacteria	Prevalence of CRB (%)	Carbapenemase-Encoding Genes (Virulence genes or Factors if Reported)	MGE Carrying Carbapenemase-Encoding Genes	References
Burkina-Faso	2015	Wastewater used for urban agriculture	*Comamonadaceae, Chroococcaceae, Streptococcaceae, Enterobacteriaceae, Enterococcaceae, Staphylococcaceae*	NA	$bla_{OXA-226}$, $bla_{OXA-256}$, $bla_{OXA-347}$, bla_{OXA-46}, $bla_{SHV-100}$, bla_{GES-21}, $bla_{OXA-256}$, (multiple virulence genes)	NA	[54]
	2019	Hospital Wastewater	*A. baumannii*	NA	bla_{OXA-58}, bla_{OXA-46}, bla_{CMY-2}, $bla_{OXA-101}$, bla_{OXA-56}, $bla_{OXA-397}$, bla_{OXA-48}, bla_{IMP} bla_{NDM}, bla_{VIM}, bla_{GES}	NA	[50]
	2019–2021	Wastewater from healthcare centers	*E. coli*	35/107 (32.71)	NDM, OXA-48	NA	[55]
			K. pneumoniae	11/60 (18.33)			
Chad	2016–2018	Household meals, fresh milk, fresh meat, fresh fish, fresh vegetables	*E. coli, S. aureus*	6/48 (12.5)	NA	NA	[56]
	NA	Fresh vegetables and fruits	*E. coli, S. aureus*	6/60 (10)	NA	NA	[57]
Cameroon	2015	Raw sewage	*Enterobacteriaceae, Staphylococcaceae, Streptococcaceae, Enterococcaceae*	NA	bla_{IMP-11}, bla_{IMP-12}, $bla_{OXA-232}$, bla_{OXA-9}, $bla_{TEM-126}$, bla_{GES-21}, $bla_{OXA-164}$, $bla_{OXA-212}$, $bla_{OXA-226}$, $bla_{OXA-256}$, $bla_{OXA-347}$, bla_{OXA-46}, bla_{OXA-5}, $bla_{SHV-100}$, bla_{KPC} (multiple virulence genes)	NA	[54]
	2016	Nasal swab from pigs	*K. pneumoniae*	0	$bla_{TEM-116}$, bla_{SHV-28}, bla_{SHV-27}, bla_{SCO-1}	NA	[58]
Cameroon	2017–2018	Water from Boreholes and Hand Dug Wells	*E. coli*	17/17 (100)	NA	NA	[59]
			Burkholderia cepaceae	1/1 (100)			
			Staphylococcus aureus	1/5 (20)			
	2018–2021	Broiler chicken	*Enterobacteriaceae*	16/394 (4.1)	bla_{KPC}	NA	[60]
	2019	Fresh water	*E. coli*	9/79 (11.3)	NA	NA	[61]
	2021–2022	Meat (pork, beef, chicken) and fish products	*E. coli*	(10.5–18.2)	NA	NA	[62]
	NA	Poultry litter	*E. coli*	27/59 (45)	NA	NA	[63]
Democratic Republic of the Congo (DRC)	2012	Sediments, receiving untreated hospital effluents	*Pseudomonas* spp.	12/30 (40)	bla_{VIM-1}, bla_{VIM-2}, bla_{NDM}	NA	[64]

Djibouti	2019–2021	Livestock fecal samples	*E. coli, A. baumannii, K. pneumoniae, P. mirabilis*	16/350 (4.6)	bla_{NDM-1}, bla_{OXA-23}, bla_{OXA-48}, bla_{OXA-66}, bla_{OXA-69}, $bla_{OXA-181}$, bla_{NDM-5}	51.4-kb $bla_{OXA-181}$ ColKP3-IncX3 Plasmid	[65]
		Fish					
		Water samples					
Ethiopia	2016	Leafy vegetable	*A. baumannii*	(94)	bla_{OXA-23}, bla_{OXA-51} (*CsgA, cvaC, kpsMTII, iutA, cnf1*)	ISA*ba1*	[66]
	2019–2020	River water	*Aeromonas* spp.	71/144 (49.3)	NA	NA	[67]
	2020	Sediment and water samples	*Enterobacteriaceae Acinetobacter* spp., *Pseudomonas* spp., *Staphylococcus* spp., *Streptococcus* spp.	NA	bla_{KPC}, $bla_{PER\ 1/2}$, bla_{NDM}, bla_{OXA-23}, bla_{OXA-58}, bla_{IMP-2}, bla_{IMP-5}, bla_{VIM-1}, bla_{SFO}, bla_{GES}, bla_{OXA-24}, bla_{OXA-48}, $bla_{ACT-1/5/7}$, bla_{CcrA}, bla_{OXA-10}	NA	[68]
	2022	Meat, swabs from carcasses, knife, weighing balance and cutting board samples	*E. coli, K. pneumoniae, Serratia spp., Enterobacter spp.*	6/48 (12.5)	NA	NA	[69]
Ethiopia	NA	Leafy Vegetables	*K. pneumoniae*	15/15 (100)	bla_{OXA-48}, bla_{VIM}, bla_{IMP}, bla_{NDM-1} (*uge, wabG, iutA, kpn, fimH*)	NA	[70]
	NA	Milk, yogurt, cheese	*Enterobacteriaceae*	15/19 (78.9)	bla_{KPC} (*hlyA, stx-2, eaeA*)	NA	[71]
Egypt	2013	Retail Chicken meat	*Klebsiella* spp.	12/106 (11.3)**	NA	NA	[72]
	2014	Broiler chickens and their drinking water	*K. pneumoniae*	18/40 (45)	bla_{KPC}, bla_{OXA-48}, bla_{NDM}	NA	[73]
	2014	Rectal swabs and Milk samples from healthy dairy cattle	*E. coli*	6/114 (5.3)**	bla_{OXA-48}, $bla_{OXA-181}$	NA	[74]
	2015–2016	Dogs and their environments (water troughs, feed containers, walls and floors)	*E. coli*	7**	bla_{NDM-5}, $bla_{TEM-217}$, $bla_{OXA-181}$	IncX3-type plasmid for bla_{NDM-5}	[75]
	2016	Cattle and cattle milk	*E. coli*	3/13 (23.1)	bla_{VIM} (*stx1, stx2*)	NA	[76]
	2017	Minced Meat, Beef Burger, kofta	*P. Aeruginosa, E. cloacae complex*	148	bla_{VIM-1}, bla_{VIM-2}, bla_{OXA-10}	Class 1 integron on a > 93 kb A/C and HI2-type plasmid	[77]
	2017	Retail Chicken meat	*K. pneumoniae, E. coli*	155	bla_{NDM-1}, bla_{NDM-5}, ble_{MBL}	ISA*ba125*, 48 kb IncX3-type plasmid for bla_{NDM-5}, 100 kb IncR-type plasmid for bla_{NDM-1}	[78]
	2017	Uncooked beef patty	*Enterobacter hormaechei*	1**	bla_{VIM-1}, bla_{ACT-16}	IncHI2/pMLST1 plasmid, int1 carrying bla_{VIM-1}	[79]

(*Continued*)

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Table 1 (Continued).

Country	Year of Isolation / Collection	Origin / source	Bacteria	Prevalence of CRB (%)	Carbapenemase-Encoding Genes (Virulence genes or Factors if Reported)	MGE Carrying Carbapenemase-Encoding Genes	References
Egypt	2017–2018	Milk and dairy products	*E. coli*	2/36 (5.6)**	bla_{SHV-12} (*stx1, stx2, eaeA, rfbE*)	NA	[80]
	2017–2018	Chicken giblets, water used to clean chicken carcasses	*Salmonella enterica*	12/15 (80)	bla_{CMY-2}, bla_{KPC} (*invA, stn*)	NA	[81]
	2019	Fresh tomatoes, irrigation surface water	*K. pneumoniae*	2/7 (28.6) **	bla_{NDM}, bla_{OXA-48}	NA	[82]
	2019	Broilers and their environment (water, food, litter)	*K. pneumoniae*	3/19 (15.8)	bla_{VIM}, bla_{NDM-1}, bla_{IMP} (hypervirulent hypermucoviscous Phenotype)	NA	[83]
	2020	Tracheal swab, cloacal swab, liver, heart, lung, gizzard from duks	*P. mirabilis*	3/35 (8.6)	bla_{NDM-1}, bla_{KPC} (*atpD, ureC, rsbA, zapA*)	NA	[84]
	2020	Rectal swabs from pigs	*E coli*	2/47 (4.3)**	$bla_{OXA-244}$	NA	[85]
			K. pneumoniae	2/47 (4.3)**	bla_{NDM-5}	IncX4-type plasmid	
	2020	Retail meat (chicken meat, beef meat, beef carcass swabs)	*Salmonella enterica*	5/34 (14.7)**	bla_{SHV-12}	NA	[86]
				9/34 (26.5)**	bla_{CMY-2}		
	NA	Fishpond water inlets, fresh tilapia fish, tap water	*Enterobacter cloacae complex, K. pneumoniae, E. coli*	86/130 (66.2)	bla_{KPC}, bla_{PER-1}, bla_{OXA-48}, bla_{NDM}	NA	[87]
	NA	Ready to eat Luncheon-meat	*K. pneumoniae*	40/44 (90.9)	bla_{VIM}, bla_{NDM}, bla_{OXA-48}, bla_{KPC}, bla_{IMP}, bla_{ACT-1} (Hypervirulent strains)	NA	[88]
	NA	Sheep, cattle	*P. aeruginosa*	2/24 (8.3)	bla_{KPC}, bla_{NDM-1}, bla_{IMP-1}, bla_{VIM-1} (*toxA, exoS, exoT, exoY*)	NA	[89]
	NA	Fecal sample from buffaloes and cattle, livestock drinking water	*P. aeruginosa*	24/40 (60)	bla_{KPC}, bla_{OXA-48}, bla_{NDM} (*toxA*)	NA	[90]
Gabon	2017	Fecal samples from bats	*E. cloacae, K. pneumoniae, E. coli*	4/11 (36.4)	bla_{SHV-11}	NA	[91]
Gambia	2019	Fecal samples from hooded vultures	*E. coli*	2/52 (3.8)	bla_{SHV-11}	NA	[92]
			K. pneumoniae	2/4 (50)	$bla_{SHV-204}$		

Ghana	2014–2015	Nile tilapia	*S. sonnei, S. typhi, P. mirabilis, K. pneumoniae, E. coli, E. cloacae*	21/26 (80.8)	NA	NA	[93]
	2014–2016	Fecal samples from pigs, catlle	*E. coli*	95/95 (100)	NA	NA	[94]
	2016	Cockroaches	*E. coli, K. pneumoniae*	3/20 (15)	bla_{OXA-48}, bla_{NDM-1}, bla_{SHV-3}, bla_{TEM-24}, bla_{TEM-3}	NA	[95]
	2022	Lettuce	*E. coli*	87/124 (70)	NA	NA	[96]
	NA	Beef, chicken, goat	*Enterobacteriaceae, Pseudomonas* spp., *Acinetobacter* spp., *vibrio* spp.	7/558 (1.3)	NA	NA	[97]
	NA	Poultry litter, environment	*P. aeruginosa*	3/40 (7.5)	NA	NA	[98]
Ivory coast	2012–2013	Environment (hospital effluents and municipal sewage)	*Enterobacteriaceae*	2/74 (2.8)**	bla_{PER}, bla_{GES}	NA	[99]
		Animal (cattle, sheep, pigs)		1/74 (1.4)**	bla_{GES}		
Malawi	NA	River water	NA	NA	bla_{IMP}, bla_{KPC}, bla_{OXA-48}, bla_{VIM}, bla_{NDM}	NA	[100]
Morocco	2016–2017	Effluent from hospital units	*E. coli, P. agglomerans, E. aerogenes, E. cloacae, K. pneumoniae, Aeromonadaceae,* staphylococci	7/15 (46.7)	NA	NA	[101]
	2017–2018	Well waters	*P. aeruginosa*	(73.6)	NA	NA	[102]
	NA	Well waters	*E. coli*	(3.6)	NA	NA	[103]

(*Continued*)

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Table 1 (Continued).

Country	Year of Isolation / Collection	Origin / source	Bacteria	Prevalence of CRB (%)	Carbapenemase-Encoding Genes (Virulence genes or Factors if Reported)	MGE Carrying Carbapenemase-Encoding Genes	References
Nigeria	2009–2014	Chicken feces and meat	*E. coli*	4	NA	NA	[104]
	2011–2012	Wastewater from pharmaceutical industries	*B. cenocepacia, B. cepacia, S. maltophilia, E. brevis, S. paucimobilis*	6/97 (6.2)	bla_{SHV-11}, bla_{SHV-2}, bla_{SHV-12}, bla_{SHV-28}	NA	[105]
	2014–2015	Polluted wetlands	*Pseudomonas putida* group	9**	bla_{VIM-5}	Tn_{402}-like class 1, Tn_{402}-like class 1 integrons	[106]
	2015–2016	Rectal Swabs of Cow, Cloacae Swabs of Poultry Birds, Swabs from slaughter/abattoir benches	*E. coli*	146/168 (86.9)	NA	NA	[107]
			P. aeruginosa	98/147 (66.7)			
			Klebsiella spp.	119/141 (84.4)			
	2015–2017	Shellfish	*Alcaligenes* spp. *Pseudomonas* spp. *Providencia* spp. *Vibrio* spp. *Paenalcaligenes* spp.	119/135 (88.1)	NA	NA	[108]
	2016	Hospital environment (sinks, beddings, equipment, furniture and walls)	*P. aeruginosa*	2/20 (10)	NA	NA	[109]
	2016	Anal swabs of cow	*K. pneumoniae*	46/59 (78)	bla_{IMP-1}	NA	[110]
	2016–2019	Pigs, poultry, hospital environment, cattle, camel, dogs	*E. coli, K. pneumoniae*	77/488 (15.8)	bla_{SHV-11}, bla_{SHV-28}	NA	[111]
	2016–2019	Rectal/cloacae swabs from camels, cattle, dogs, pigs and poultry	*Enterobacteriaceae, Alcaligenes faecalis*	NA	bla_{SHV-11}, bla_{TEM-93}, bla_{TEM-57}	NA	[112]

Nigeria	2017	Water, soil	*Enterobacteriaceae* *A. baumannii, Pseudomonas* spp.	259	bla_{POM-1}, bla_{CGB}-like, bla_{PenA}, $bla_{OXA-181}$, bla_{OXA-23}, bla_{OXA-40}, bla_{NDM-1}, bla_{NDM-5}, bla_{NDM-7}, bla_{VIM-5}	NA	[113]
	2017	Cattle and Poultry Faeces, poultry litter	*E. coli*	17/182 (9.34)**	NA	NA	[114]
	2018	Patients beds, bedside tables, bedside cupboards, antiseptics	*K. pneumoniae*	7/15 (46.7)	NA	NA	[115]
	2018–2019	Fecal Samples of Pig	*E. coli, K. pneumoniae, E. cloacae*	12/300 (4)	NA	NA	[116]
	2019	Water sources use in abattoir	*Enterobacteriaceae*	1/42 (2.38)	NA	NA	[117]
	2019	Knives, tables, butchers hand, floors, water troughs, and carcasses from retail shops and abattoirs	*E. coli*	10/104 (9.6)	NA	NA	[118]
	2019–2020	Well water	*E. coli, Enterobacter* spp., *Klebsiella* spp., *Salmonella* spp., *Citrobacter* spp., *Proteus* spp., *Shigella* spp.	28/148 (19)	NA	NA	[119]
	2021	Cloacal samples from laying hens, broilers, cockerels, ducks, pigeon, local chickens	*E. coli*	29/32 (90.6)	NA	NA	[120]
	NA	Water from wells rivers/streams	*Escherichia* spp. *Klebsiella* spp. *Enterobacter* spp. *Proteus* spp. *Citrobacter* spp. *Morganella* spp. *Salmonella* spp.	45/300 (15)	bla_{NDM-1}	NA	[121]
	NA	Vegetables, borehole and well water	*E. coli*	8/100 (8)	NA	NA	[122]
	NA	Freshwater from river	*Vibrio* spp.	28/315 (8.9)	NA	NA	[123]
	NA	Fish and Fish Storage Water	*Vibrio* spp.	113/128 (88.3)	NA	NA	[124]
	NA	Rectal swab samples of poultry, beef, cattle, poultry and beef vendor table	*E. coli*	78/138 (56.5)	NA	NA	[125]
Reunion island	2016–2017	Pig	*E. coli, K. pneumoniae*	2/181 (1.1)*	NA	NA	[126]

(*Continued*)

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Table 1 (Continued).

Country	Year of Isolation / Collection	Origin / source	Bacteria	Prevalence of CRB (%)	Carbapenemase-Encoding Genes (Virulence genes or Factors if Reported)	MGE Carrying Carbapenemase-Encoding Genes	References
Senegal	2010–2011	Human head lice	*A. baumannii*	3**	*bla*$_{OXA23}$-like	NA	[127]
	2016	Fecal samples of Wild Chimpanzees, Termites	*K. pneumoniae*	23**	*bla*$_{OXA-48}$, bla$_{KPC-2}$, *bla*$_{SHV-28}$, *bla*$_{SHV-11}$, *bla*$_{SHV-106}$, *bla*$_{SHV-145}$, *bla*$_{SHV-110}$, *bla*$_{SHV-168}$	International □ 63Kb IncL/M-OXA-48 plasmid and □ 100 kb plasmid for the pKPC-2	[128]
South Africa	2016–2017	Abattoir equipments, meat and carcasses, aquatic samples	*A. baumannii*	74/100 (74)	*bla*$_{OXA-23}$, *bla*$_{OXA-51}$-like, *bla*$_{OXA-58}$-like	NA	[129]
	2016–2017	Cattle faeces	*E. coli, K. pneumoniae, P. mirabilis, Salmonella* spp.	194/280 (69.3)	*bla*$_{KPC}$, *bla*$_{NDM}$, *bla*$_{GES}$, *bla*$_{OXA-48}$, *bla*$_{VIM}$, *bla*$_{OXA-23}$	NA	[130]
	2018	Fresh pork meat	*E. coli*	34/68 (50)	NA	NA	[131]
	2018	Soil, manure, waterbody	*E. coli*	12/39 (30.8)**	*bla*$_{NDM}$ (*stx1, stx2, flic*$_{H7}$, *rfbE*$_{O157}$ *eaeA*)	NA	[132]
	2018	Domestic water sources	*Vibrio cholerae*	5/61 (8.2)	*bla*$_{IMP}$, *bla*$_{NDM-1}$	NA	[133]
	2018	Surface water, wastewater treatment plants, hospital effluents, irrigation water, soil, vegetables	*Klebsiella* spp.	93/182 (51.1)	*bla*$_{KPC}$, *bla*$_{OXA-48}$-like, *bla*$_{NDM-1}$	NA	[134]
	2018	Benthic sediment, wastewaters, water bodies	*K. pneumoniae*	29	*bla*$_{NDM}$, *bla*$_{OXA-181}$, *bla*$_{OXA-48}$, *bla*$_{KPC-2}$, *bla*$_{OXA-505}$, *bla*$_{OXA-98}$, *bla*$_{SHV-28}$, *bla*$_{SHV-36}$, *bla*$_{SHV-40}$ (Type 3 fimbriae, Type 1 fimbriae, capsules, AcrAB, aerobactin, enterobactin siderophore, salmochelin, RcsAB, T6SS-I, T6SS-II, T6SS-III and LPS rfb locus)	IncL/M-plasmid (pOXA-48)	[135]
	2018–2019	Pig and pig transport systems	*E. coli*	3/1044 (0.3)	NA	NA	[136]
	NA	Hospital wastewater, influent wastewater, river water, riverbed sediment	ST 3559 *K. pneumoniae*	4	*bla*$_{KPC-2}$, *bla*$_{OXA-48}$, *bla*SHV-36 (type 3 fimbriae, type 1 fimbriae, type IV pili, aerobactin, Enterobactin, salmochelin)	NA	[137]
	NA	Fecal samples of baboon and vervet monkey	*Escherichia fergusonii*	8/15 (53,3)	NA	NA	[138]
South Africa	NA	Sewage sludge	*Citrobacter koseri*	33	*bla*$_{MAL-1}$, *bla*$_{OXA-181}$, *bla*$_{OXA-48}$, *bla*$_{KPC-2}$, *bla*$_{SHV-30}$	IncL/M-plasmid (pOXA-48), other plasmids	[139]
	NA	Intensive care unit room sinks	*P. aeruginosa, C. freundii, S. marcescens, K. pneumoniae, P. rettgeri, P. fluorescens*	8	NA	NA	[140]

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Sudan	2017	Raw milk	*E. coli*	(19.9)	NA	NA	[141]
			K. pneumoniae	(49.4)			
	2017–2018	Fecal samples of fennec fox	*E. coli*	0	bla_{ACT-14}	NA	[142]
Tanzania	2015	Fish	*E. cloacae*, *K. pneumoniae*	4**	bla_{ACT-15}, bla_{SHV-11}	NA	[143]
	2021	Community, industrial and hospital effluents water, Soil samples	*E. coli*, *K. pneumoniae*	29/85 (34.1)	NA	NA	[144]
	2021–2022	Hospital and community sewage	*E. coli*, *K. pneumoniae*	136/371 (36.7)	NA	NA	[145]
	NA	Poultry, domestic pig	*E. coli*	24/461 (5.2)	NA	NA	[146]
Tunisia	2011	Fecal samples from chicken	*E. coli*	3**	bla_{CMY-2}, $bla_{TEM-135}$	NA	[147]
	2013	Hospital environment samples (table, door, bedlinen, sink)	*Klebsiella* spp., *E. cloacae*	11/24 (45.8)**	bla_{SHV-28}, bla_{SHV-11}, bla_{SHV-12}	NA	[148]
	2013	Chicken gut	ST2197 *E. coli*	10**	bla_{CMY-2}	97 kb IncI1 plasmid	[149]
	2013–2016	Poultry and bivalve molluscs	*Salmonella* spp.	4/50 (8)	NA (Salmonella intestinal infection A (*siiA*), Salmonella outer protein (*sopB* and *sopE*), putative 4-hydroxybutyrate coenzyme A transferase (*cat2*), Salmonella atypical fimbria C (*safC*), *S. Enteritidis* fimbria B (*sefB*), Salmonella plasmid virulence [*spvC* and *spvB*]), *sopE*	NA	[150]
	2014–2016	Clams	*K. pneumoniae*	2/4 (50)**	bla_{NDM-1}, bla_{OXA-48}	IncF plasmid for the bla_{NDM-1}, IncL plasmid for bla_{OXA-48}	[151]
	2015	Mussel	ST 167 *E. coli*	1/40	bla_{KPC-3}	□ 180 kb IncFII plasmid (F2:A#:B# subtype), (Tn*4401d*)	[152]
Tunisia	2015–2016	Bivalves	*A. baumannii*	2**	bla_{OXA-23}	NA	[153]
	2016	Chicken cloacal swabs	*E. coli*	6**	bla_{CMY-2}, bla_{SHV-12}	NA	[154]
	2017–2018	Rats	*Enterobacteriaceae*	6/55 (10.9)**	$bla_{TEM-128}$, $bla_{TEM-163}$, bla_{TEM-82}	NA	[155]
	2018–2020	Fecal samples from wild boar	*K. pneumoniae*, *E. cloacae*, *Pantoea* spp.	10/102 (9.7)	bla_{IMP}, bla_{VIM}	NA	[156]
	NA	Rabbits	*E. coli*	16/39 (41)	bla_{IMI}, bla_{VIM}	NA	[157]

(*Continued*)

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Table 1 (Continued).

Country	Year of Isolation / Collection	Origin / source	Bacteria	Prevalence of CRB (%)	Carbapenemase-Encoding Genes (Virulence genes or Factors if Reported)	MGE Carrying Carbapenemase-Encoding Genes	References
Uganda	2016–2017	Cattle, pig, layer chicken	*E. coli*	0	bla_{ACT-1}, bla_{ACT-28}, bla_{ACT-12}, bla_{TEM-87}	NA	[158]
	2018–2019	Rectal swabs from cattle	*E. coli, Klebsiella* spp., S. fonticola, *K. ascorbate, Enterobacter* spp.	14/120 (11.7)	NA	NA	[159]
	2018–2020	Stool samples from livestock (sheep, goats, cattle, chicken, swine)	*E. coli*	36/96 (37.5)	bla_{KPC}	NA	[160]
	2022	Cow, pig, goat, dog, duck fecal samples, soil, water for domestic use, swabs from animal feeding equipment, doorknobs	*E. coli*	11/65 (16.9)	NA	NA	[161]
	NA	Hospital sewage	*E. coli*	25	bla_{VIM}, bla_{KPC}, bla_{NDM} (*eae, elt, est, paH, PAI IV536*)	NA	[162]
Zambia	2018	Fecal samples of Impala	*E. coli*	1/48 (2.1)	NA	NA	[163]
	2020–2021	Raw cow milk	*E. coli*	27/214 (12.6)	NA	NA	[164]
Zimbabwe	2021	Wastewater treatment plant and river water	*E. coli*	25/86 (29.1)	bla_{NDM}	NA	[165]

Notes: *Intermediate resistance profil; **Carbapenemase-producing bacteria prevalence.
Abbreviations: CRB, carbapenem resistant bacteria; MGE, mobile genetic element; NA, Not available; NF, not found; □, about.

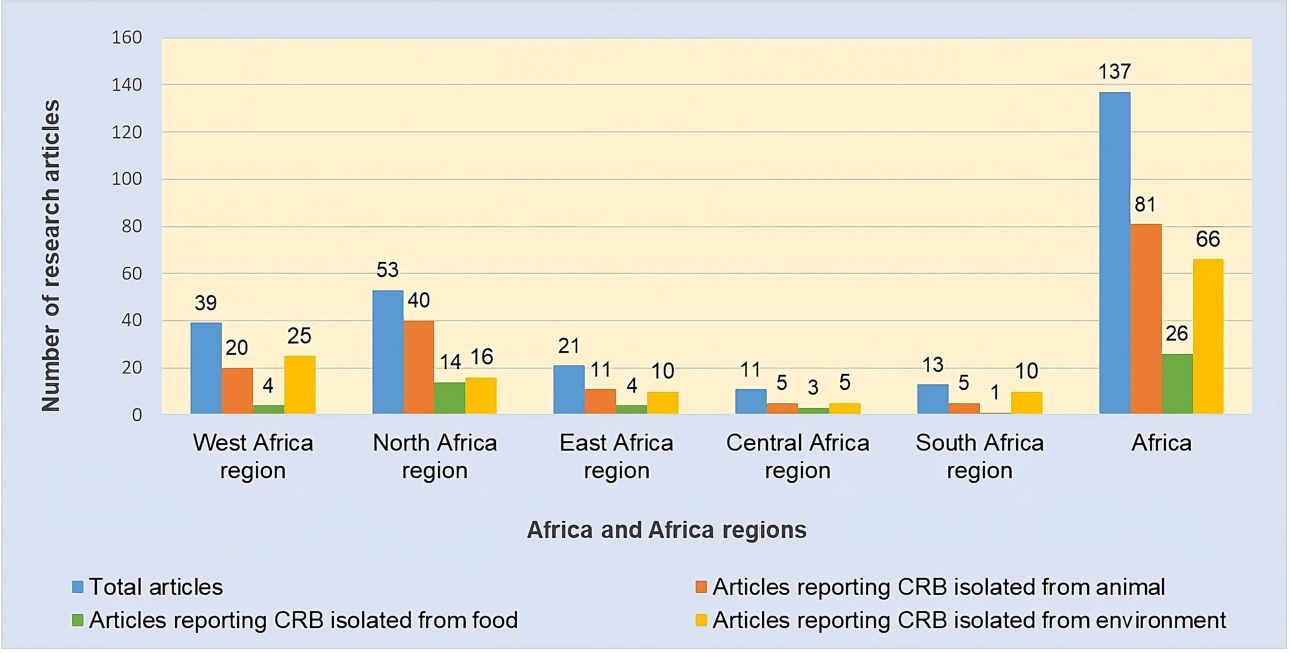

Figure 2 Distribution of articles included in this review according to African regions.

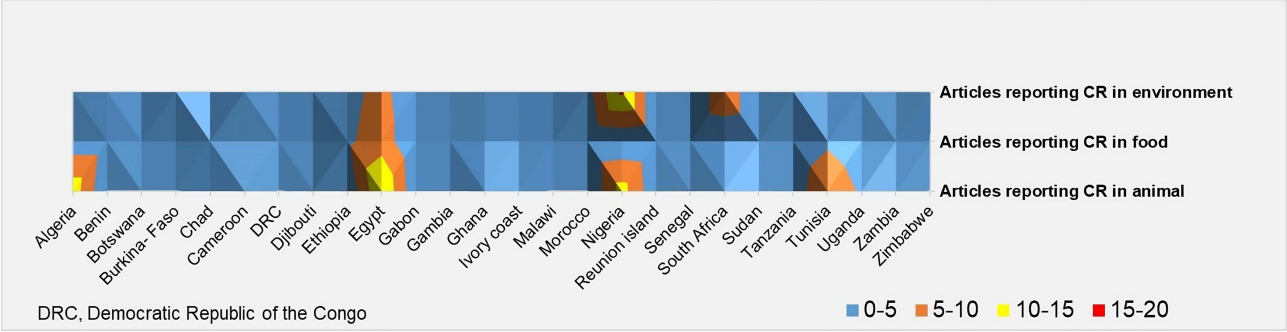

Figure 3 Distribution of articles reporting carbapenem resistance by country.

Distribution of Carbapenem-Resistant Bacteria in Animal-Environment-Food

A total of 127 articles have reported the implicated carbapenem-resistant bacterial species. These carbapenem-resistant bacterial species belonged to 31 genera, including *Escherichia* spp. (68/127; 53.5%); *Klebsiella* spp. (45/127; 35.4%); *Pseudomonas* spp. (20/127; 15.7%), *Enterobacter* spp. (19/127; 15%), *Acinetobacter* spp. (15/127; 11.8%), *Proteus* spp. (6/127; 4.7%), *Salmonella* spp. (6/127; 4.7%), *Staphylococcus* spp. (6/127; 4.7%), *Citrobacter* spp. (5/127; 3.9%), *Vibrio* spp. (5/127; 3.9%), *Burkholderia* spp. (3/127; 2.4%), *Serratia* spp. (3/127; 2.4%), *Pantoea* spp. (2/127; 1.6%), *Providencia* spp. (2/127; 1.6%), *Alcaligenes* spp. (2/127; 1.6%), *Shigella* spp. (2/127; 1.6%), *Raoultella* spp. (1/127; 0.8%), *Cronobacter* spp. (1/127; 0.8%), *Campylobacter* spp. (1/127; 0.8%), *Listeria* spp. (1/127; 0.8%), *Brucella* spp. (1/127; 0.8%), *Paenalcaligenes* spp. (1/127; 0.8%), *Morganella* spp. (1/127; 0.8%), *Stenotrophomonas* spp. (1/127; 0.8%), *Empedobacter* spp. (1/127; 0.8%), *Sphingomonas* spp. (1/127; 0.8%), *Kluyvera* spp. (1/127; 0.8%), *Aeromonas* spp. (1/127; 0.8%), *Pluribacter* spp. (1/127; 0.8%), *Bacteroides* spp. (1/127; 0.8%) and *Streptococcus* spp. (1/127; 0.8%) (Figure 4). Seventeen (17) families were represented, mainly *Enterobacteriaceae, Pseudomonadaceae* and *Moraxellaceae. Xanthomonadaceae, Aeromonadaceae, Comamonadaceae, Chroococcaceae, Streptococcaceae, Enterococcaceae, Staphylococcaceae, Vibrionaceae, Alcaligenaceae, Bacteroidaceae, Sphingomonadaceae,*

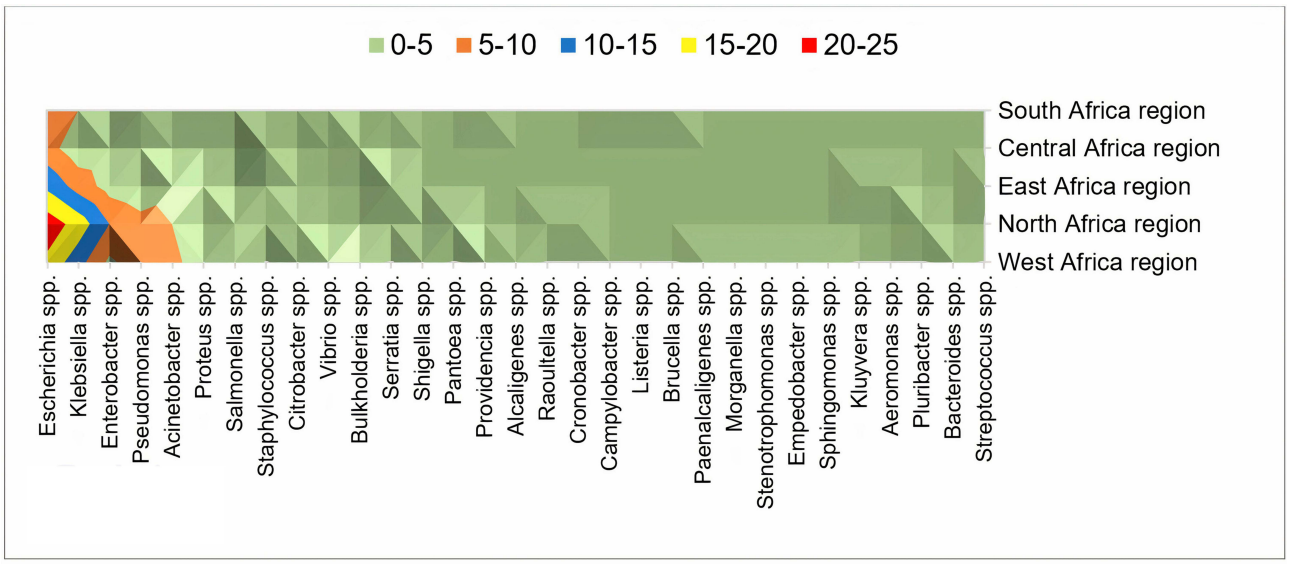

Figure 4 Distribution of articles reporting carbapenem-resistant genera in African regions.

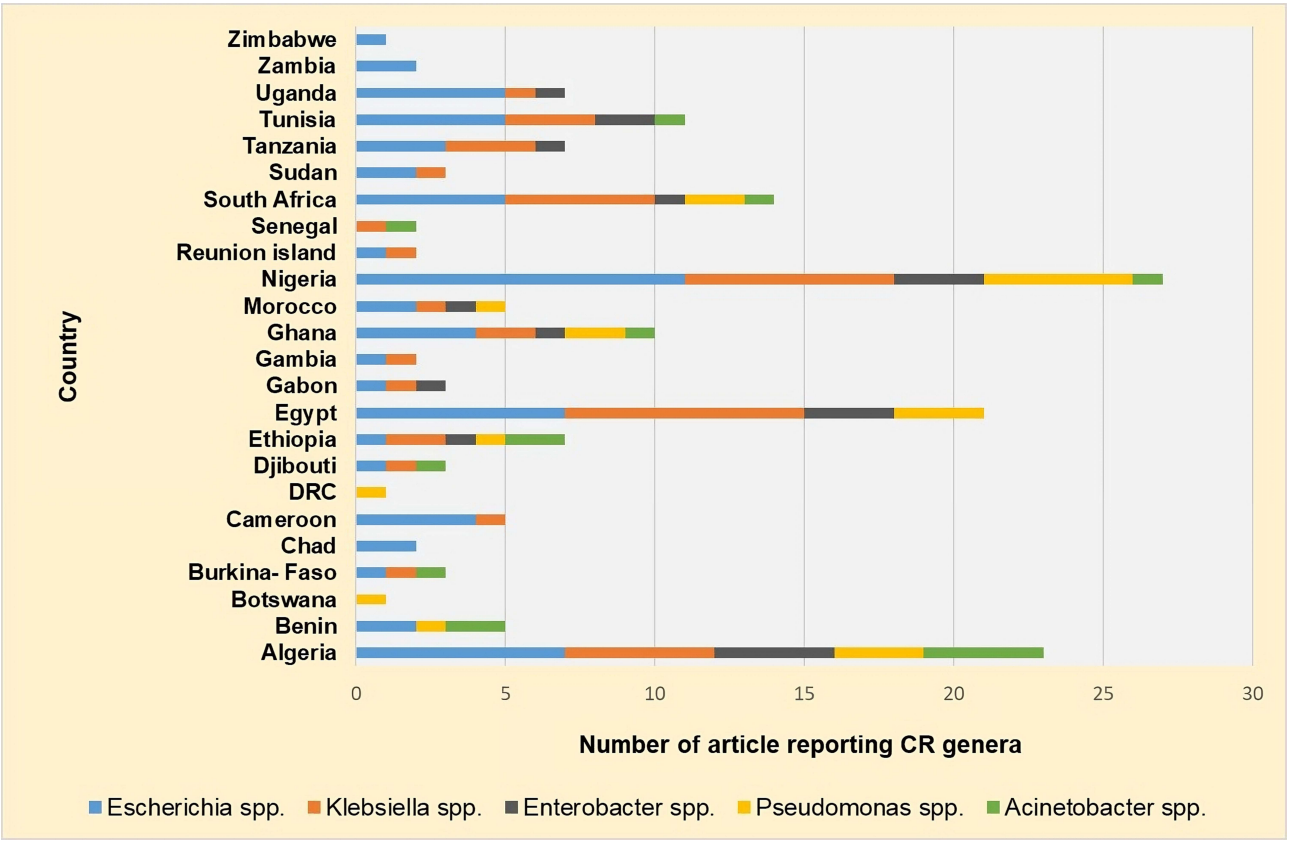

Figure 5 Distribution of articles reporting the most prevalent CRB genera by country.

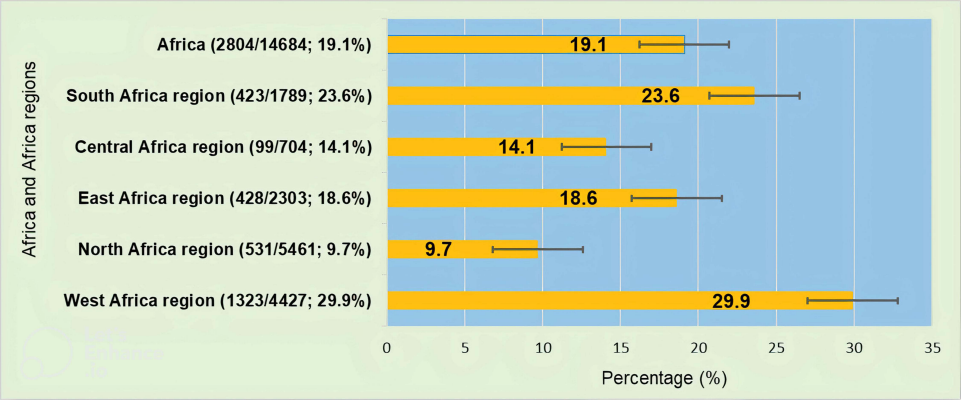

Figure 6 Pooled prevalences of CRBs in Africa and Africa regions.

Flavobacteriaceae, Campylobacteraceae and *Burkholderiaceae* were reported in minority. The distribution of articles reporting CRB genera by African region and country is shown in Figures 4 and 5, respectively.

Prevalence of Carbapenem-Resistant Bacteria

Ninety-five (95) articles out of 137 reported the prevalence of CRBs (the number of CRBs divided by the total number of bacteria tested). Variable prevalence was observed in countries, ranging from 1.1% to 48.5% (Table 1; Figure 6). The regional CRB mean prevalence included West African region (1323/4427; 29.9%; SD=18), South African region (423/1789; 23.6%; SD = 16.7), East African region (428/2303; 18.6%; SD = 16.2), Central African region (99/704; 14.1%; SD = 15.2), and North African region (531/5461; 9.7%; SD = 18.9) (Figure 6). The prevalence of CRBs in West Africa was significantly higher than that reported in the 4 other regions ($p < 0.0001$). According to the 95 articles reviewed, the pooled prevalence of CRBs isolated in Africa from Animal-environment-food from 2009 to 2023 was 19.1% (2804/14,684; SD = 15) (Figure 6).

Distribution of Carbapenemase-Encoding Genes

Eighty-four (84) articles investigated and reported carbapenemase-encoding genes belonging to A, B, C, and D Ambler classes (Figure 7). Carbapenemase-encoding genes belonged to 20 carbapenemase families and included bla_{OXA} (44/84; 52.4%), bla_{NDM} (34/84; 40.5%), bla_{SHV} (23/84; 27.4%); bla_{KPC} (22/84; 26.2%), bla_{VIM} (19/84; 22.6%), bla_{IMP} (12/84; 14.3%), bla_{TEM} (8/84; 9.5%), bla_{GES} (8/84; 9.5%), bla_{CMY} (7/84; 8.3%), bla_{ACT} (6/84; 7.1%), bla_{PER} (3/84; 3.6%), bla_{IMI} (1/84; 1.2%), bla_{MAL} (1/84; 1.2%), bla_{PenA} (1/84; 1.2%), bla_{SFO} (1/84; 1.2%), bla_{SCO} (1/84; 1.2%), bla_{POM} (1/84; 1.2%), bla_{CGB} (1/84; 1.2%), ble_{MBL} (1/84; 1.2%) and bla_{CcrA} (1/84; 1.2%). The distribution of articles reporting carbapenemase families according to regions of Africa is shown in Figure 8. Figure 7 shows the distribution of the carbapenemase families by country. In the OXA family, 27 variants that hydrolyze carbapenems have been reported, including mainly bla_{OXA-48} (28/88; 31.8%), bla_{OXA-23} (12/88; 13.6%), $bla_{OXA-181}$ (7/88; 8%), and bla_{OXA-58} (6/88; 6.8%) (Figure 9). Regarding SHV, 19 variants that hydrolyze carbapenems have been reported, including mainly bla_{SHV-11} (12/45; 26.7%), bla_{SHV-12} (6/45; 13.3%), and bla_{SHV-28} (6/45; 13.3%) (Figure 10). Regarding NDM, bla_{NDM-1} (13/20; 65%), bla_{NDM-5} (6/20; 30%), and bla_{NDM-7} (1/20; 5%) have been reported. In addition, bla_{VIM-1} (5/13; 38.5%), bla_{VIM-2} (4/13; 30.8%), bla_{VIM-4} (2/13; 15.4%), bla_{VIM-5} (2/13; 15.4%) and bla_{KPC-2} (2/3; 66.7%); bla_{KPC-3} (1/3; 33.3%) were reported. Finally, bla_{CMY-2} (n = 7) was the only bla_{CMY} variant reported.

Mobile Genetic Elements Carrying Carbapenemase-Encoding Genes

Nineteen (19) articles investigated and reported mobile genetic supports carrying carbapenemase-encoding genes, including plasmids (16/19; 84.2%), integrons (3/19; 15.8%), transposons (3/19; 15.8%), and insertion sequences (2/19; 10.5%) (Table 1). The reported plasmids carried bla_{OXA} carbapenemase-encoding genes (8/19; 42.1%), bla_{NDM} (6/19; 31.6%), bla_{KPC} (2/19; 10.5%), bla_{VIM} (2/19; 10.5%), and bla_{CMY} (1/19; 5.3%) (Table 1). bla_{OXA-48} was often carried by

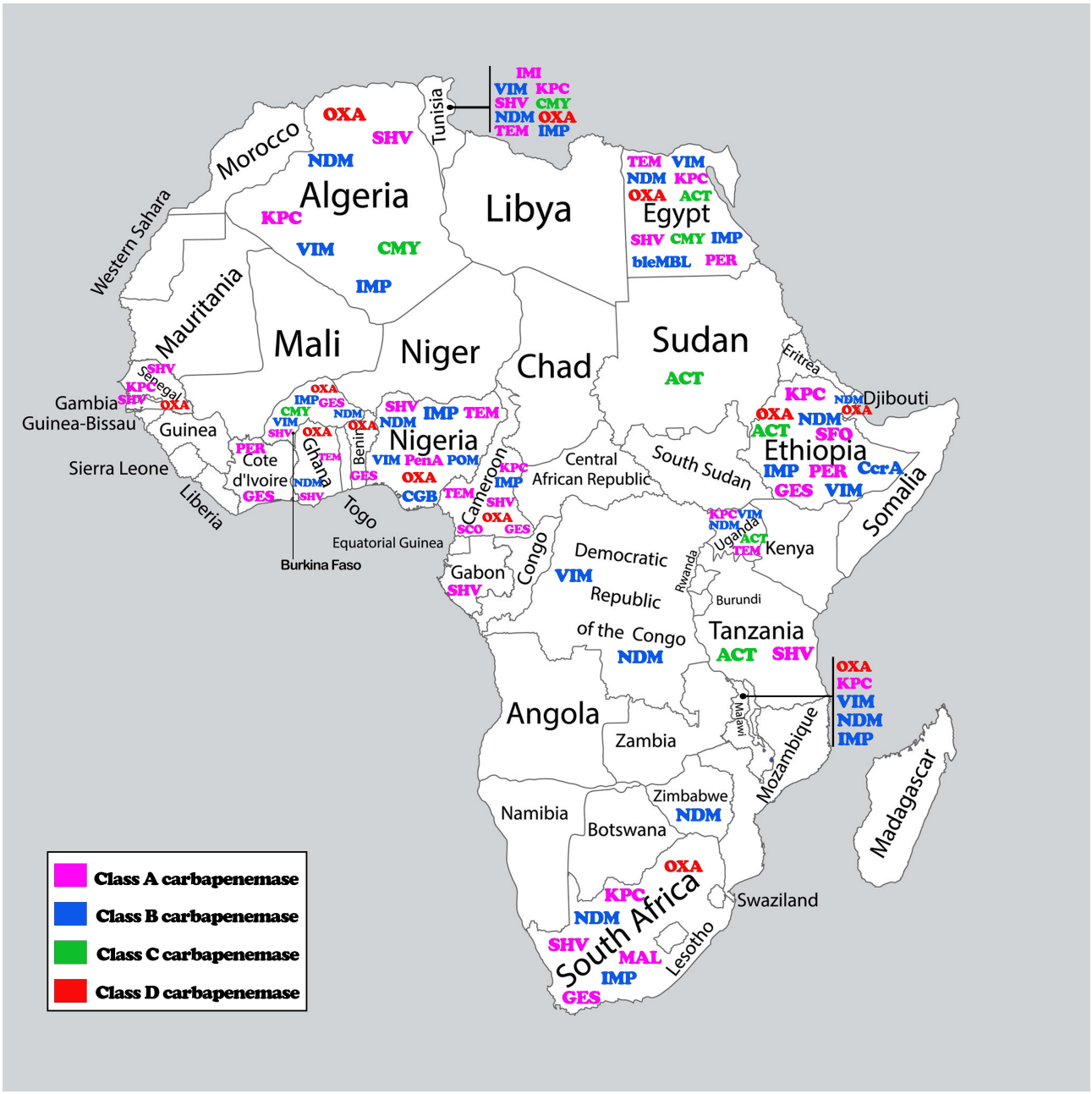

Figure 7 Carbapenemase-encoding gene families detected in Africa in animals, the environment, and foods.

(60–65kb) IncL/M pOXA-48 plasmids while $bla_{\text{NDM-5}}$ was often carried by (45–50kb) IncX-type plasmids (Table 1). The reported integrons were class 1 and carried $bla_{\text{VIM-1}}$ and $bla_{\text{VIM-2}}$. The transposons identified were Tn*2006* carrying $bla_{\text{OXA-23}}$, Tn*402* carrying $bla_{\text{VIM-5}}$, and Tn*4401d* carrying $bla_{\text{KPC-3}}$ (Table 1).

Virulent and Hypervirulent CRBs Isolated from Animal-Environment-Food

Twenty-five (25) articles investigated and reported virulent and hypervirulent CRBs that carried multiple virulence genes. These studies were from North Africa (14/25; 56%); East Africa (4/25; 16%); West Africa (3/25; 12%); South Africa (3/25; 12%) and central Africa (1/25; 4%) (Table 1). Almost all of these CRBs carrying virulence genes belonged to *Enterobacteriaceae* and were isolated from animal, environmental, and food samples. The virulence genes reported included adhesins (18/76; 23.7%) (*fimH, mrkD, fimC, safC, eae, CsgA, Kpn, sefB*); toxins (16/76; 21.1%) (*Cnf1, hlyF,*

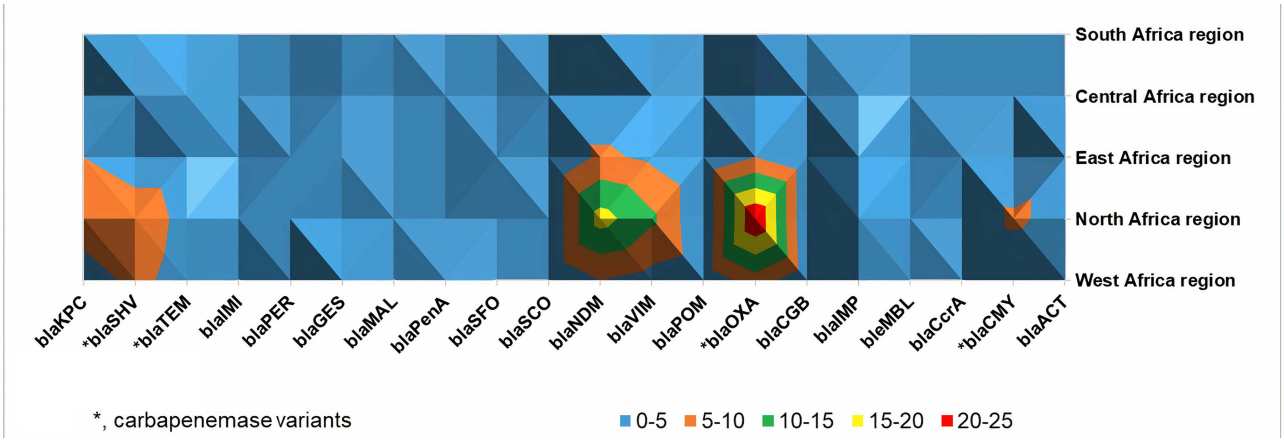

Figure 8 Distribution of articles reporting carbapenemase families in animals, the environment and foods in Africa regions.

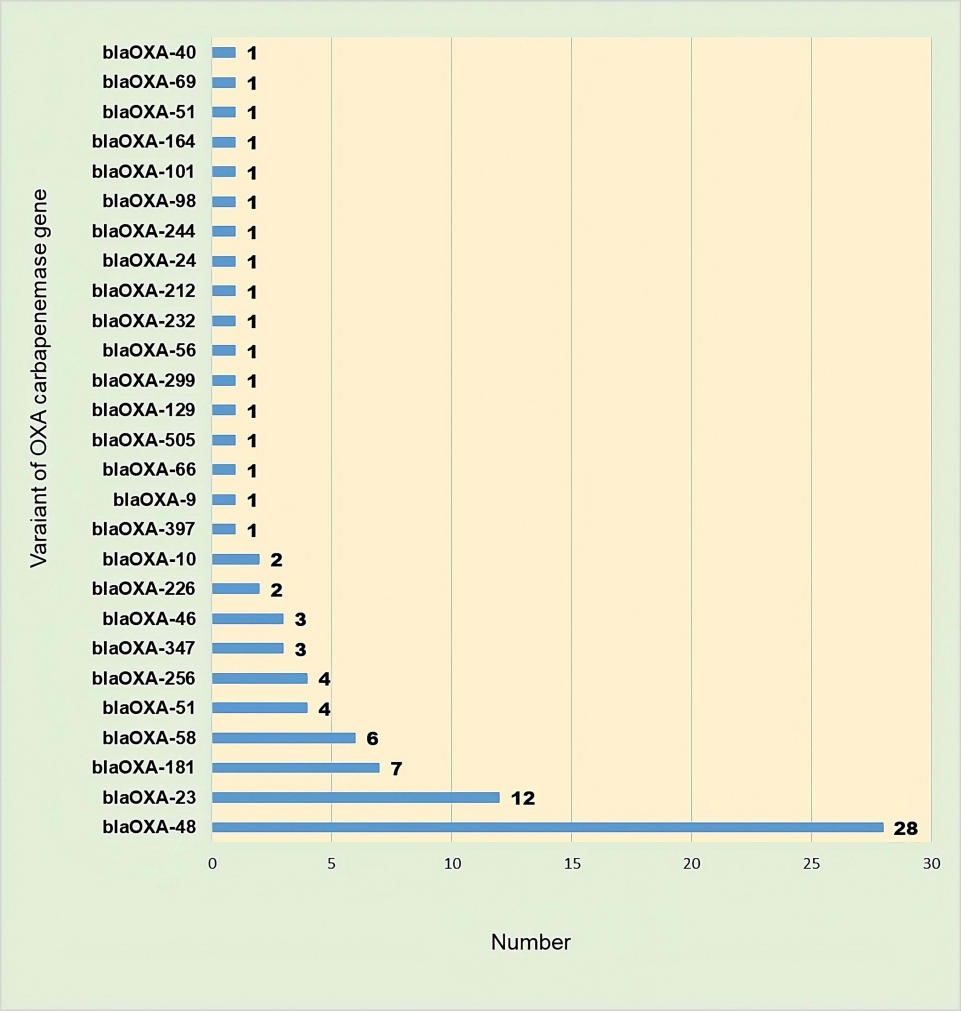

Figure 9 Number of studies reporting OXA-carbapenemase-encoding genes.

hlyA, CvaC, exoS/exoT/exoY, stx, elt/est, toxA, stn); iron acquisition systems (14/76; 18.4%) (*entB, irp-1, iroN, kfu, ybtS, iutA, PAI IV536, fyuA*); protectins (14/76; 18.4%) (*iss, zapA, uge, ugeF, WabG, ipaH, kpsMTII, rfbE, flicH7, ompT*); virulence factors involved in the metabolism, transcriptional and activation pathways (8/76; 10.5%) (*ureA, ureC, cat2,*

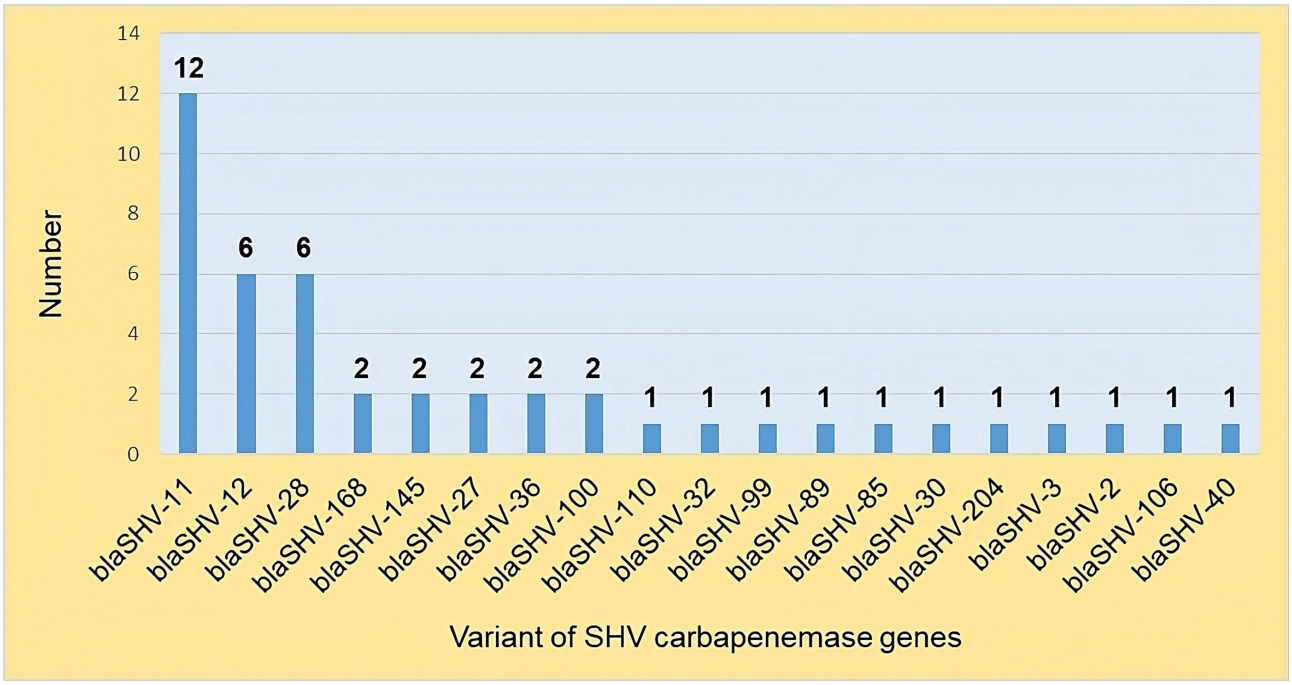

Figure 10 Number of studies reporting SHV-carbapenemase-encoding genes.

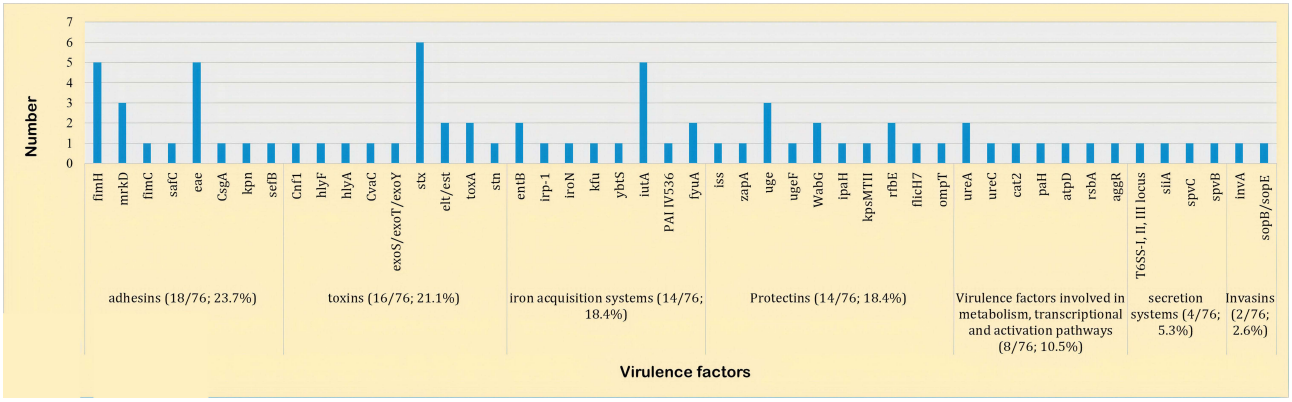

Figure 11 CRB's virulence genes reported in animals, the environment and foods in Africa.

paH, atpD, rsbA, aggR); secretion systems (4/76; 5.3%) (T6SS-I, T6SS-II, T6SS-III locus, *siiA, spvC, spvB*) and invasins (2/76; 2.6%) (*invA, sopB/sopE*) (Figure 11). Moreover, many cases of hypervirulent *K. pneumoniae* (hvKp) strains have been reported.

Discussion

In this review, we reported the current state of carbapenem resistance in animal-environment-food in Africa based on a systematic review.

This review reported CRBs belonging to 31 genera and 17 bacterial families. This suggests that carbapenem resistance in animal-environment-food is not limited to certain bacterial families. Additional genomic investigations would identify more implicated carbapenem-resistant genera and families. In addition, the five most frequently reported bacterial genera were *Escherichia* spp. (68/127; 53.5%); *Klebsiella* spp. (45/127; 35.4%); *Pseudomonas* spp. (20/127;

15.7%), *Enterobacter* spp. (19/127; 15%) and *Acinetobacter* spp. (15/127; 11.8%). Sung et al[166] rather reported *K. pneumoniae* (45.9%), *E. cloacae* complex (29.3%), *E. coli* (13.5%), *R. ornithinolytica* (5.3%), and *C. freundii* (2.3%) isolated from the streams in Republic of Korea.

In this study, the pooled prevalence of CRBs isolated from animal-environment-food in Africa from 2009 to 2023 was 19.1% (2804/14,684; SD=15). The prevalence of CRBs in animal-environment-food in West Africa (1323/4427; 29.9%) was significantly higher than that reported by Dossouvi et al[13] in clinical CRBs from West Africa (1902/41,635; 4.6%) ($p < 0.0001$). It seems that in Africa, CRBs are more prevalent in animal-environment-food than in humans. This would confirm that animal-environment-food systems are reservoirs of CRBs. Our current data are insufficient to precisely determine the causes of the significant difference ($p < 0.0001$) between the prevalence of CRBs of animal-environmental-food origin in North Africa (531/5461; 9.7%) and in West Africa (1323/4427; 29.9%). Furthermore, the prevalence of CRBs among bacterial strains isolated from Chinese rivers (16.3%)[167] was similar to those obtained in the Central and East African regions in our study.

This review reported 20 families of carbapenemases involved in CRBs of animal-environment-food origin, including mostly carbapenemase-encoding genes from the bla_{OXA} (44/84; 52.4%), bla_{NDM} (34/84; 40.5%), bla_{SHV} (23/84; 27.4%), bla_{KPC} (22/84; 26.2%), bla_{VIM} (19/84; 22.6%), and bla_{IMP} (12/84; 14.3%) families. Worldwide, the prevalence trends of carbapenemase-encoding genes in animal-environment-food seem to be different from those observed in this review. In fact, the carbapenemase-encoding genes of CRBs isolated from South Korean streams were bla_{KPC} (n = 37; 41.1%), bla_{NDM} (n = 36; 40%), bla_{GES-5} (n = 10; 11.1%), and bla_{OXA-48} (n = 7; 7.8%).[166] In addition, bla_{NDM} (50%) and bla_{KPC-2} (50%) were the most prevalent carbapenemase genes in CRBs isolated from Chinese rivers.[167] In Spain, Jiménez-Belenguer et al,[168] rather reported bla_{VIM} (26.7%), bla_{IMP} (23.6%), bla_{OXA-48} (17.4%), bla_{CMY-2} (8.1%), and bla_{KPC} (4.3%) in CRBs isolated from fresh vegetables. Interestingly, SHV-type carbapenemases, which are often neglected in humans, are well represented (third rank) in animal-environment-food, with 19 variants in this study.

Several studies have precisely characterized the sequences of MGEs carrying genetic determinants of carbapenemases in this study. The international 60–65kb pOXA-48 plasmid reported in humans, animals, environments, and foods worldwide[169–172] has been reported a lot in this review. As in this study, 45–50kb IncX-3 type plasmids carrying bla_{NDM-5} have been worldwide reported in clinical CREs from Togo,[173] China;[174–176] retail meats samples from China,[177] and environmental samples from France.[178] As in this review, bla_{OXA-23} was reported in Tn*2006* in clinical CRBs in China[179,180] and bla_{VIM-2} has also been reported in class 1 integrons in clinical CRBs isolated in South America and Asia.[181–183] It seems that MGEs carrying carbapenemase-encoding genes in clinical and animal-environment-food CRBs are similar or related. Comparative studies of clinical CRB genomes and CRB genomes of animal-environment-food origin would provide interesting conclusions.

This review also reported 25 articles that characterized virulent and hypervirulent CREs in animal-environmental-food. This is very concerning because these genetic determinants of virulence risk to be quickly transmitted horizontally to other bacterial populations as reported by previous studies.[184–188] If no major action is taken, Africa could experience outbreaks of hypervirulent CRBs, as is currently the case in Asia.[10,11,189–191] Like in this review, Ahlstrom et al[192] reported hypervirulent CR *K. pneumoniae* isolates from wild birds in Spain and Ukraine.

Recommendations and Perspectives for Better Control of Carbapenem Resistance in Africa

As global surveys show that in 2019, antimicrobial resistance killed more people than HIV/AIDS or malaria,[29,30] improving surveillance, investigation, and in particular prevention of MDR- and XDR-associated infections must be a priority of public health authorities.

Prevention of Human CRB-Associated Infections

One of the objectives of this review was to provide comprehensive data that could help prevent human CRB-associated infections in Africa. Key reservoirs/samples included the hospital environments (beds, surfaces, doors, taps, sinks, water, wastewater, and hospital devices), currency coins, ready-to-eat meats, household meals, companion animals, water (well

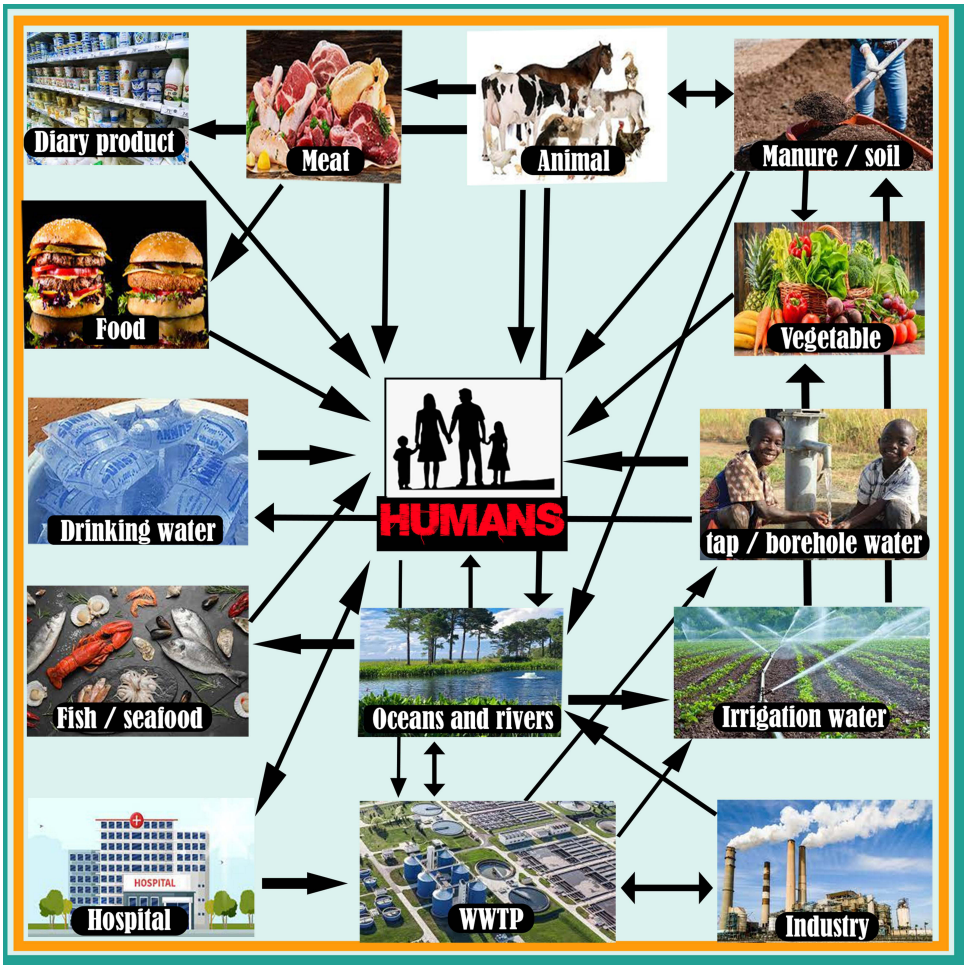

Figure 12 Spread of CRBs between humans, animals, the environment, and foods in Africa.

water, tap water, borehole water), milk and dairy products, fresh vegetables and lettuce, insects (cockroach, human head lice), and seafood (mussels, clams, bivalves) (Figure 12).

CRBs disseminated in the hospital environment are the major cause of hospital-acquired infections (HAI).[193–196] Therefore, the eradication of CRBs from hospital environments will lead to a considerable reduction in the occurrence of HAIs. The hospital CRB reservoirs reported in this review included (beds, surfaces, doors, taps, sinks, water, wastewater, and hospital devices). It is therefore necessary to improve and adapt hand, surface, and hospital device cleaning protocols; improve the treatment of hospital wastewater; improve the microbiological quality of tap water distributed in hospitals; and prevent aerial dissemination of bacteria.

Moreover, it is necessary to systematically screen for CRBs in high-risk patients (patients from the intensive care units, patients with postoperative complications, hospitalized elderly and newborn patients, immunocompromised patients, and patients hospitalized in oncology and hemo-oncology departments). Finally, public health authorities will have to regularly improve awareness among healthcare staff and the population regarding appropriate and prohibited actions in hospitals.

In addition to the actions to be taken in hospitals, four actions seem imperative for the better prevention of CRB-associated infections (Figure 12). First, public health authorities will need to improve public awareness regarding CRB reservoirs so that the population can adopt a hand-washing and hygiene habit, as several cases of CRBs have been reported on currency coins, pets, human head lice and cockroaches. Second, the population must be regularly made aware of the importance of cooking food properly and cleaning fruits and vegetables properly before consumption, since several cases of CRBs have been reported in household meals, fresh meat and fish, fruits, tomatoes, and lettuce. Furthermore,

raw and undercooked mussels must be prohibited. Third, because several strains of CRBs have been isolated from well water, boreholes, and tap water, public health authorities will have to improve the microbiological quality of tap water, and the population will have to be better educated on water treatment techniques for wells and borehole water intended for consumption. Finally, several cases of ready-to-eat meals, milk and dairy products sold in supermarkets have been mentioned as CRB carriers. This is alarming because the aforementioned products, sold in supermarkets, are consumed without cooking. The policy of investigation and control of ready-to-eat meals and dairy products sold in supermarkets needs to be improved.

These preventive measures will undoubtedly improve the results of antimicrobial resistance control.

WGS as a Powerful Tool for Monitoring and Investigating Carbapenem Resistance in Africa

In this review, we assessed the current state of carbapenem resistance in animals, the environment, and food in Africa. However, it would be interesting to compare CRB strains of human origin to those of animal-environmental-food origin to identify the real sources, vectors, and platforms of propagation of CRB epidemics in humans. Hence, the WGS of CRBs is important.

WGS is a powerful tool for investigating, monitoring, and controlling antimicrobial resistance.[197,198] Indeed, WGS provides exact information on sequence types, clonal and phylogenic origins, resistance genes, resistance mechanisms involved, virulence, metabolism, MGE, and mutations. Unfortunately, only 19 of 137 articles reported in this review (13.9%) performed WGS. It is clear that the maximum amount of information concerning CRBs was not reported in the 118 studies (86.1%) that did not perform WGS. Therefore, the actual extent of carbapenem resistance in animal-environment-food in Africa would be more staggering than the results reported in this systematic review. Therefore, we invite African research teams to use WGS techniques more frequently. We also invite African public health authorities to invest more in the acquisition of sequencing and bioinformatics platforms and the training of competent personnel. Finally, we invite funders to direct more funding towards studies including the WGS of bacterial strains isolated in Africa.

Conclusion

The data presented in this review confirm the generalization of CRBs in animal-environment-food ecosystems in Africa. Based on the data reported in this review, animal-environment-food ecosystems would constitute reservoirs of CRBs involved in human infections. However, further epidemiological and genotypic studies are required to gain better understanding. Currently, public health authorities should focus their efforts on preventing the transmission of CRBs from animal-environment-food ecosystems to humans and invest more in the acquisition and use of genomics platforms in Africa. The One Health approach and constant collaboration between governments are necessary to drastically reduce the mortality rates linked to antimicrobial resistance.

Abbreviations

CPB, carbapenemase-producing bacteria; CRB, carbapenem-resistant bacteria; CRE, carbapenem-resistant *Enterobacteriaceae*; ESBL, extended spectrum beta-lactamase; hvKp; hypervirulent *Klebsiella pneumoniae*; MDR, Multidrug-resistant bacteria; MGE, mobile genetic element; WHO, World Health Organization; XDR, extensively drug-resistant bacteria.

Author Contributions

All authors made a significant contribution to the work reported, whether that is in the conception, study design, execution, acquisition of data, analysis and interpretation, or in all these areas; took part in drafting, revising or critically reviewing the article; gave final approval of the version to be published; have agreed on the journal to which the article has been submitted; and agree to be accountable for all aspects of the work.

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