

## Antibiotic resistance and integrons in *Escherichia coli* isolated in primary production of beef and pork: a systemic review.

## Resistencia a antibióticos y los integrones en *Escherichia coli* aislada en la producción primaria de cárnicos de res y cerdo: una revisión sistemática.

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### ABSTRACT

*Escherichia coli* is a pathogen of public health concern due to the gastrointestinal diseases it causes. It is present in various food types, with meat serving as a reservoir of multidrug-resistant *E. coli* that can be transmitted to humans through the consumption of contaminated meat. Additionally, it is used as an indicator to monitor antimicrobial resistance (AMR) in the food industry. Therefore, this study conducted a systematic review of articles published between 2013 and 2024, following the PRISMA guidelines. Thirty-four articles were selected for a quantitative analysis of *E. coli* resistance in beef and pork. The report analysis showed resistance to antibiotics from the  $\beta$ -lactam (38.4 %), tetracycline (13.8 %), and aminoglycoside (12.7 %) families. Moreover, the most frequently occurring resistance genes were  $bla_{CTX-M}$  (23.5 %),  $bla_{TEM}$  (15.0 %),  $tet(A)$  (8.9 %),  $tet(B)$  (6.2 %), and  $aacC2$  (5.6 %). Finally, the most common gene arrangements in type 1 integrons were  $dfrA1-aadA1$ ,  $dfrA17-aadA5$ , and  $dfrA12-aadA2$ . This study provides valuable information about the phenotypic and genotypic resistance reported in *E. coli* from pork and beef, and also examines the role of type 1 integrons in the spread of resistance genes.

**KEY WORDS :**  $\beta$ -lactams, intl-1, intl-2, resistance genes.

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## RESUMEN

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*Escherichia coli* es un patógeno de importancia en salud pública, por las enfermedades gastrointestinales que causa, se encuentra en distintos tipos de alimentos, como la carne que, además, es un reservorio de *E. coli* multiresistente, se transmite al humano por el consumo de carne contaminada. Además, es utilizada como un indicador para el monitoreo de la resistencia antimicrobiana (AMR) en la industria alimentaria. Por ello, en este estudio se realizó una revisión sistemática de artículos publicados del 2013 al 2024, siguiendo las guías PRISMA, fueron seleccionados 34 artículos para un análisis cuantitativo, sobre aspectos de la resistencia de *E. coli* en carne de res y cerdo. El análisis de los reportes evidenció resistencia para *E. coli* a antibióticos de las familias de  $\beta$ -lactámicos (38.4 %), tetraciclinas (13.8 %) y aminoglucósidos (12.7 %). Mientras que, los genes con mayor frecuencia reportada fueron  $bla_{CTX-M}$  (23.5 %),  $bla_{TEM}$  (15.0 %),  $tet(A)$  (8.9 %),  $tet(B)$  (6.2 %) y  $aacC2$  (5.6 %). Finalmente, los arreglos de genes más frecuentes en los integrones tipo 1 fueron  $dfrA1-aadA1$ ,  $dfrA17-aadA5$  y  $dfrA12-aadA2$ . El presente estudio revela información relevante referente a la resistencia fenotípica y genotípica que se reporta para *E. coli* en carne de cerdo y de res, e indaga en la importancia que tienen los integrones tipo 1 para la propagación de genes de resistencia.

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**PALABRAS CLAVE:**  $\beta$ -lactámicos, intl-1, intl-2, genes de resistencia.

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### Introduction

Red meat is a typical food in the human diet, providing various macro- and micronutrients essential for energy metabolism and human development (Bonnet & Coinon, 2024; Godfray *et al.*, 2018); additionally, meat production is an important economic activity in developing countries, contributing to food security (Khanal, 2024; Warmate & Onarinde, 2023). The proximate composition of red meat includes up to 19 % protein, 2.5 % fat, 1.2 % carbohydrates, 1.5 % non-protein nitrogenous compounds, and a pH of 5.7, which confer an excellent nutritional profile. However, these same characteristics also make meat an ideal substrate for the growth of various microorganisms, including pathogenic bacteria (Rani *et al.*, 2023; Soepranianondo *et al.*, 2019). Raw meat is a well-known vehicle for pathogens that cause foodborne illnesses (Fegan & Jenson, 2018). Moreover, meat and its byproducts are considered by the CDC (Centers for Disease Control and Prevention) as a route for transmitting antimicrobial-resistant (AMR) bacteria between animals and humans (CDC, 2019; Vikram *et al.*, 2018). This occurs since meat can acquire AMR bacteria during primary processing (mainly during slaughter, evisceration, and skinning), transport, and marketing, which are later transmitted to humans through consumption (Diyantoro & Wardhana,

2019; Niyonzima *et al.*, 2015), thereby promoting resistance through gene exchange among bacterial strains (Endale *et al.*, 2023).

In particular, *E. coli* is a bacterial species frequently associated with meat contamination and also exhibits antimicrobial resistance (Guragain *et al.*, 2024). It is a Gram-negative, facultative aerobic bacillus belonging to the *Enterobacteriaceae* family. While it is part of the mammalian microbiome, including humans, several pathotypes also exist that cause disease, primarily in the gastrointestinal tract (Enciso-Martínez *et al.*, 2022; Gomes *et al.*, 2016; Reyes-Rodríguez *et al.*, 2020). *E. coli* has been reported to be resistant to various families of antibiotics, linked to a wide gene diversity that enables the development of metabolic processes to bypass antibiotic mechanisms of action (Li *et al.*, 2023). Resistance genes in *E. coli* are typically found on plasmids and other genetic elements such as integrons (Jiménez *et al.*, 2017; Reygaert, 2018). Integrons can incorporate foreign genes that confer antibiotic resistance (Ghaly *et al.*, 2020). Although reports on *E. coli* isolates from meat remain limited, their significance is growing due to their role in capturing and expressing gene cassettes that confer resistance (Zhang *et al.*, 2020). In nature, nine classes of integrons have been identified. Types 1, 2, and 3 contain genes associated with antibacterial resistance (Deng *et al.*, 2015), with type 1 being the most common in enterobacteria (Ghaly *et al.*, 2017; Singh *et al.*, 2021). Studying and identifying these are important since over 70 gene cassettes have been described, conferring resistance to  $\beta$ -lactams, aminoglycosides, quinolones, trimethoprim, rifampicin, chloramphenicol, and erythromycin (Kaushik *et al.*, 2018).

Among the genetic factors linked to antimicrobial resistance in *E. coli*, the most common are *bla* genes, which encode  $\beta$ -lactamases, enzymes capable of hydrolyzing the amide bond of the  $\beta$ -lactam ring, rendering these drugs ineffective (Bharadwaj *et al.*, 2022). *tet* genes confer resistance to tetracyclines mainly through three mechanisms: ribosomal protection, enzymatic inactivation, and efflux pumps (Grossman, 2016; Jahantigh *et al.*, 2020). For *sul* genes, which give resistance to sulfonamides, three main variants are reported (*sul1*, *sul2*, and *sul3*). These genes encode different forms of the enzyme dihydropteroate synthase, the target of these drugs, involved in folic acid biosynthesis (Poey *et al.*, 2019; Venkatesan *et al.*, 2023). Ultimately, enterobacteria such as *E. coli* have a wide range of resistance strategies, making them significant public health threats due to the challenges in treating infections they cause. This is especially critical given the limited treatment options, which can even lead to death.

Therefore, this systematic review aims to analyze data from specialized sources regarding antibiotic resistance in *E. coli* isolated from meat and to describe the frequency of reports related to antibiotics, genes, and integrons involved in resistance. This will provide important insights into *E. coli* resistance in meat production and aid in monitoring the spread of resistance genes associated with this bacterium worldwide.

## Material and Methods

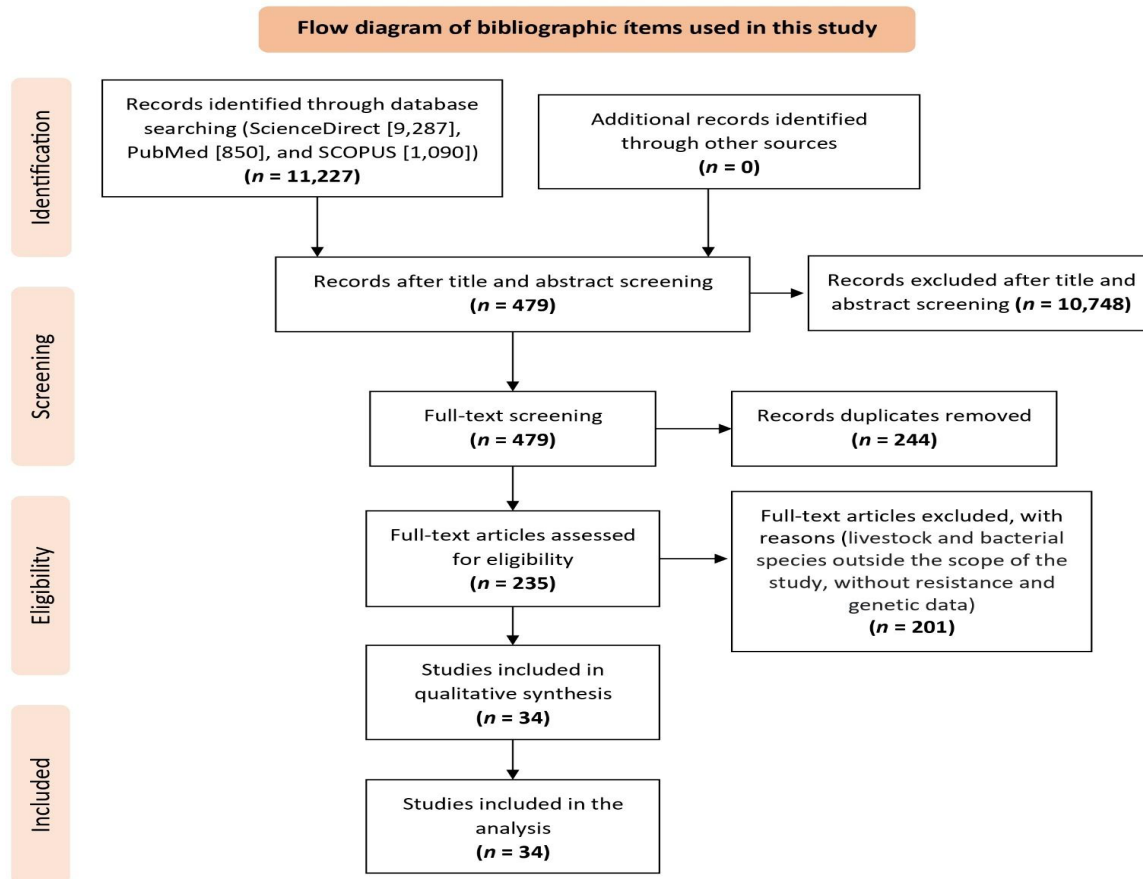
### Search strategy

A systematic search of scientific reports was conducted in accordance with the PRISMA guidelines (Hutton *et al.*, 2015; Moher *et al.*, 2009). The search strategy was based on the keywords “*Escherichia coli*”, “Ground meat”, “Antibiotic resistance”, “Multi-drug resistance”, “Multiresistance”, “Integrons *Int1-1* and *Int1-2*.” From these keywords, six input queries were defined for the search engines: 1) (*Escherichia coli* OR *E. coli*) AND (Meat) AND (Antibiotic resistance); 2) (*Escherichia coli* OR *E. coli*) AND (Meat) AND (Multi-drug resistance OR multiresistance) AND (Integrans); 3) (*Escherichia coli* OR *E. coli*) AND (Meat) AND (Multi-drug resistance OR multiresistance) AND (Integrans OR *Int1-1* OR *Int1-2*); 4) (*Escherichia coli* OR *E. coli*) AND (Ground beef) AND (Multi-drug resistance OR multiresistance); 5) (*Escherichia coli* OR *E. coli*) AND (Ground lamb) AND (Multi-drug resistance OR multiresistance); 6) (*Escherichia coli* OR *E. coli*) AND (Ground pork) AND (Multi-drug resistance OR multiresistance). The search entries were designed to progress from general to specific, identifying reports related to beef, pork, and lamb. Searches were conducted in three databases: ScienceDirect (<https://www.sciencedirect.com/>), PubMed (<https://pubmed.ncbi.nlm.nih.gov/>), and SCOPUS (<https://www.scopus.com/home.uri>), with institutional access through the Universidad Autónoma del Estado de Hidalgo. The search was carried out in February 2024 across all three platforms. The systematic strategy focused on evaluating the detection of *E. coli* in meat matrices, genetic characterization of multidrug resistance, and determination of integrans.

### Inclusion criteria

The resources identified in the search were evaluated according to the PRISMA flow diagram, which encompasses the phases of identification, screening, eligibility, and inclusion (Figure 1). For final inclusion, each record had to meet the following criteria, established according to the scope of this study:

1. Articles published between 2013 and February 2024.
2. Studies reporting the isolation of *E. coli* from commercial meat.
3. Reports containing data on antibiotic resistance and describing resistance profiles.
4. Articles presenting quantitative variables related to the number of resistant strains and the number of strains carrying integrans.



**Figure 1. Flow diagram describing the management phases for bibliographic resources according to PRISMA guidelines.**

The 34 studies included in the analysis of this systematic review are: (Ahmed *et al.*, 2015; Ahmed *et al.*, 2023; Awosile *et al.*, 2021; Badi *et al.*, 2018; Barrios-Villa *et al.*, 2018; Belotindos *et al.*, 2022; Cebeci, 2022; Clemente *et al.*, 2021; Fang *et al.*, 2019; Hemeg, 2018; Inat *et al.*, 2023; Kanokudom *et al.*, 2021; Kim *et al.*, 2018; Krizman *et al.*, 2017; Liu *et al.*, 2015; Mehdi *et al.*, 2020; Moawad *et al.*, 2017; Nguyen *et al.*, 2016; Okubo *et al.*, 2020; Pehlivanlar *et al.*, 2015; Pungpian *et al.*, 2021; Rebbah *et al.*, 2017; Sabala *et al.*, 2021; Sánchez *et al.*, 2021; Skočková *et al.*, 2015; Srichumporn *et al.*, 2022; Sun *et al.*, 2021; Tadesse *et al.*, 2018; Vikram *et al.*, 2019; Vogt *et al.*, 2014; Wang *et al.*, 2020; Xedzro *et al.*, 2023; Xu *et al.*, 2014; Zhang *et al.*, 2022).

Source: own elaboration based on Moher *et al.* (2009).

## Exclusion criteria

Bibliographic sources were excluded when identified as books, reviews, book chapters, extended conference proceedings, meta-analyses, conference abstracts, systematic reviews,

patents, encyclopedias, or when the articles did not provide valuable data for extracting variables related to *E. coli* resistance and genetic characterization.

### **Data extraction**

The bibliographic elements were reviewed based on their titles and abstracts. Items that aligned with the scope of the objective were downloaded from online repositories. In the second stage, the full texts were examined to confirm they met the inclusion criteria for each item. When the criteria were satisfied, the articles advanced to a third stage, which involved importing them into the Mendeley® bibliographic manager, version 1.19.8 for desktop. This software was used to remove duplicates ( $n \geq 2$ ). Ultimately, 34 articles were eligible for the study. Data such as Author, Year, Country, Origin, Number of Strains, Antibiotic, Number of Resistant Strains, Antibiotic Family, MDR (Multidrug-resistant), XDR (Extensively drug-resistant), PDR (Pan-drug-resistant), Int1-1 (cassette gene), Int1-2 (cassette gene), Type of Resistance Gene, and Number of Strains with the Resistance Gene were extracted. This information was used to build the database for analysis, and any discrepancies between authors were resolved through joint review.

### **Data analysis**

The extracted data were processed in .csv format using Microsoft Office Excel® 2019. Graphical representations were created using Sankey plots in VisualParadigm®, illustrating the frequency of occurrence across antibiotic families, resistance gene types, and genes associated with *E. coli* resistance. Multidrug resistance (MDR), extensive drug resistance (XDR), and pan-drug resistance (PDR) were evaluated in terms of frequency and geographic distribution by country, utilizing TomTom® as an Excel® map chart tool. Finally, integron reports and associated gene arrays were summarized in a tabular format.

## **Results and Discussion**

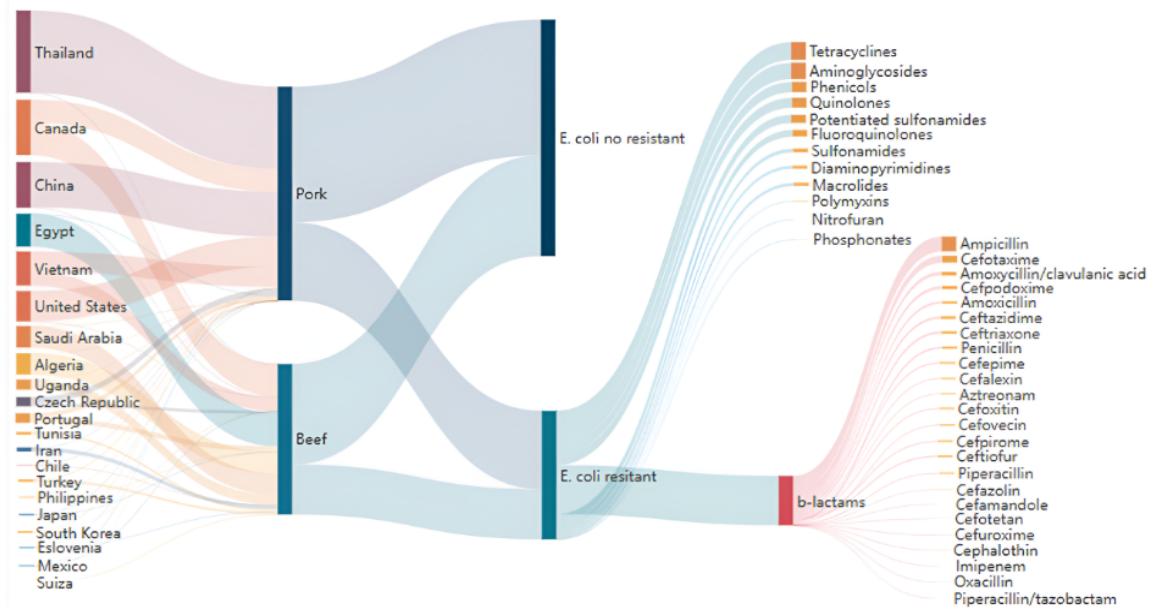
### **Study characteristics**

The database search yielded a total of 11,227 studies, of which 1,090 were identified by the SCOPUS search engine, 850 by PubMed, and 9,287 by ScienceDirect. Of these, 479 studies were significant for the present research, based on a review of the title and abstract, with 208 studies from SCOPUS, 182 studies from PubMed, and 89 studies from ScienceDirect. From the 479 bibliographic resources, a screening was conducted to identify elements suitable for inclusion in the quantitative analysis. As a result of this stage, 445 elements were excluded for the following reasons: duplication (244 articles), studies with multiple variables in terms of the origin of the sample or the bacterial species analyzed, without discriminating between them, making data extraction unfeasible (134 articles), only phenotypic resistance was evaluated (34 articles), sampling was not performed at the point of sale or slaughterhouse (15 articles), the sample did not correspond to raw meat (11 articles), the origin of the sample was not specified (4 articles), resistance was expressed only in its molecular determination (2 articles), and resistance

to disinfectants was evaluated (1 article). Finally, this study was limited to analyzing 34 articles that initially met the inclusion and exclusion criteria (Figure 1).

### **Resistance patterns of *E. coli***

This review analyzed 34 studies assessing the phenotypic and genotypic resistance of *E. coli* isolated from two types of meat (pork and beef). A total of 1,944 *E. coli* isolates were examined, with 1,091 from pork and 853 from beef. These reports originated from 21 countries. The countries contributing the most isolates were Thailand (383), Canada (286), China (248), the United States (146), Vietnam (168), Egypt (190), Algeria (102), and Saudi Arabia (120), indicating more monitoring efforts for this pathogen in these regions compared to others. Thailand, China, and the United States predominantly tested pork isolates, representing 100 %, 97.9 %, and 99.3 %, respectively, while Algeria and Saudi Arabia tested 100 % of beef isolates (Figure 2). This may be related to the high level of production and consumption in each country, which may be associated with greater attention to *E. coli* monitoring. For example, in 2023, per capita consumption of these meats was reported in countries such as China at 28 kg of pork and 4.8 kg of beef, and Thailand at 6.4 kg of pork and 1.2 kg of beef (OECD, 2024). Consumption in these countries tends toward a single type of protein, specifically pork, and is related to the fact that they are the countries with the highest reports of *E. coli* isolates from pork. While Saudi Arabia reported a consumption of 4.1 kg of beef and 0.3 kg of pork, it has also been reported that in Algeria, red meat consumption is based on beef production (Kardjadj & Luka, 2016), which is also related to the fact that these countries only evaluated beef. On the other hand, 48.7 % of *E. coli* isolates showed resistance to 13 families of antibacterials, of which 38.4 % were resistant to  $\beta$ -lactam compounds, followed by tetracyclines with 13.8 %, aminoglycosides with 12.7 %, phenicols with 7.9 %, quinolones with 7.7 %, potentiated sulfonamides with 6.2 %, and fluoroquinolones with 5.1 %. The resistance of *E. coli* to  $\beta$ -lactam compounds is evident. This resistance is linked to the production of  $\beta$ -lactamase enzymes, particularly extended-spectrum  $\beta$ -lactamases (ESBLs), which are considered the primary mechanism of resistance to  $\beta$ -lactams in enterobacteria (Abayneh *et al.*, 2019; De Angelis *et al.*, 2020). Of all the antibiotics evaluated, tetracycline was the antibiotic with the highest percentage of resistant isolates, at 12.6 %. On the other hand, among the  $\beta$ -lactam compounds, the antibiotics with the highest percentage of resistant isolates were ampicillin (11.5 % of isolates), followed by cefotaxime (5.3 % resistant isolates), amoxicillin with clavulanic acid (2.7 %), cefpodoxime (2.3 %), ceftazidime (2.0 %), and ceftriaxone (1.9 % resistant isolates). The antibiotics gentamicin and streptomycin had the highest number of resistant isolates among the aminoglycosides, with 5.3 % and 4.5%, respectively. Among the phenicols, chloramphenicol had 7.2 % resistant isolates. Among the quinolones, nalidixic acid had 5.1 %. Finally, sulfamethoxazole with trimethoprim had 6.2 % resistant isolates, which corresponds to the group of potentiated sulfonamides (Figure 2).



**Figure 2. Sankey plot illustrating the relationship between the origin of resistant *E. coli* isolates and their antibiotic resistance patterns.**

Source: own elaboration.

### Multidrug resistance in *E. coli*

For each country, the presence of *E. coli* isolates with multidrug resistance (MDR), extensive drug resistance (XDR), and pan-drug resistance (PDR) was determined (Figure 3). Thailand, which reported the highest number of isolates, also showed the highest proportion of MDR strains: of 383 isolates analyzed, 260 (67 %) were MDR, along with 25 XDR isolates (6.5 %) and 10 PDR isolates (0.26 %). The second country with the highest number of MDR strains was China, with 162 (65.3 %) of 248 isolates classified as MDR, and 9 isolates (3.6 %) as PDR. Algeria ranked third, with 86 of 102 isolates (84.3 %) identified as MDR and 16 (15.6 %) as XDR. In the United States, among 148 isolates, 38 (26.0 %) were MDR and 33 (22.6 %) were PDR, making this country the one with the highest number of PDR strains. Egypt was the second country with the most significant number of PDR isolates, with 16 (8.4 %) of 190, in addition to 17 MDR isolates (8.9 %) and 4 XDR isolates (2.1 %). In other countries such as Canada, Mexico, Uganda, Japan, the Philippines, Slovenia, Switzerland, and the Czech Republic, the presence of MDR strains was also reported, although at lower percentages (Figure 3).



**Figure 3. Distribution of *E. coli* isolates and their multi-drug resistance characteristics. The circle size indicates the total number of isolates evaluated for MDR, XDR, and PDR per country.**

Source: own elaboration.

### Genetics of multidrug resistance in *E. coli*

The antibiotic resistance genes were classified into two groups: *bla* resistance genes and other resistance genes (ORG) (Figure 4). Among the resistance determinants most frequently reported in *E. coli*, the *bla* genes predominated. Within this group, the most abundant were members of the CTX-M enzyme family, encoded by the *bla*<sub>CTX-M</sub> gene, with a frequency of 498 positive isolates (25.6 %) out of 1,944 analyzed. The variants included CTX-M-1, CTX-M-112, CTX-M-136, CTX-M-14, CTX-M-15, CTX-M-161, CTX-M-176, CTX-M-2, CTX-M-227, CTX-M-24, CTX-M-27, CTX-M-28, CTX-M-3, CTX-M-32, CTX-M-55, CTX-M-58, CTX-M-64, CTX-M-65, CTX-M-79, and CTX-M-9. The second most common group was the *bla*<sub>TEM</sub> genes, encoding TEM-type  $\beta$ -lactamases, with 319 positive isolates (16.4 %) reported for variants such as TEM-1, TEM-104, TEM-176, TEM-1B, and TEM-1C. In third place were *bla*<sub>SHV</sub> genes, coding for SHV-type enzymes, detected in 97 isolates (4.9 %). Other *bla* genes were detected at lower frequencies:

*bla*<sub>CMY-2</sub> (43 isolates, 2.2 %), while each of *bla*<sub>AmpC</sub>, *bla*<sub>CITM</sub>, *bla*<sub>NDM</sub>, *bla*<sub>ADC</sub>, *bla*<sub>OXA</sub>, and *bla*<sub>VIM</sub> was below 1 %. The ESBLs most frequently reported in *Enterobacteriaceae* belong to the TEM (named after patient Temoneira, with 243 variants), SHV (sulfhydryl variable, with 228 variants), and CTX-M (cefotaxime hydrolyzing, with 230 variants) families, the latter considered the dominant ESBL enzyme (Castanheira *et al.*, 2021; De Angelis *et al.*, 2020).

These enzymes are encoded by the *bla*<sub>TEM</sub>, *bla*<sub>SHV</sub>, and *bla*<sub>CTX-M</sub> genes, respectively (Saliu *et al.*, 2017), in agreement with the three most prevalent families identified in the *E. coli* isolates analyzed in this work. These genes are located on plasmids and other mobile genetic elements that facilitate dissemination among clinically relevant *Enterobacteriaceae* such as *E. coli* (Tooke *et al.*, 2019). ESBL production is also closely linked to multidrug resistance, as these enzymes can hydrolyze a broad spectrum of antibiotics, including penicillins, monobactams, and first-, second-, and even third-generation cephalosporins (Zhong *et al.*, 2021).

Regarding ORG genes, those conferring resistance to tetracyclines were the most common, especially the *tet(A)* gene, with a frequency of 190 (9.7 %) positive strains out of 1,944 analyzed. This was followed by the *tet(B)* gene with 132 (6.7 %) positive strains. The *tet(X4)*, *tet(E)*, *tet(M)*, and *tet(G)* genes had frequencies of less than 1 %. These antibiotics are widely used in the production of animals intended for human consumption (Kaur *et al.*, 2024; Roberts & Schwarz, 2016), particularly in livestock, where they are applied to treat respiratory, gastrointestinal, and skin infections (Kim & Ahn, 2022). Intensive use of these drugs has driven the emergence of tetracycline resistance (Fontana *et al.*, 2021). Resistance is mediated by the diverse *tet* genes, of which 46 have been identified across Gram-positive and Gram-negative bacteria, mostly located on plasmids and conjugative transposons that promote dissemination (Ortega-Balleza *et al.*, 2024; Roberts & Schwarz, 2016). The most frequently reported in *E. coli* are *tet(A)* and *tet(B)* (Shin *et al.*, 2015), although *tet(C)*, *tet(D)*, *tet(E)*, and *tet(G)* have also been described at lower frequencies. These genes encode efflux pumps that expel the drug (Jahantigh *et al.*, 2020; Kallau *et al.*, 2018), while *tet(X)* encodes an NADP+-dependent monooxygenase that degrades tetracyclines (Wang *et al.*, 2022), and *tet(M)* encodes ribosomal protection proteins with broad taxonomic distribution across both Gram-positive and Gram-negative bacteria (La Plante *et al.*, 2022; Roberts & Schwarz, 2016). The second most frequent group was the *sul* genes, conferring sulfonamide resistance, detected in 157 isolates (8.0 %). Within this group, *sul1* and *sul2* were found in 60 isolates (3.0 %), while *sul3* occurred in 37 isolates (1.9 %). Sulfonamide resistance is mediated by *sul* genes (*sul1*, *sul2*, *sul3*, and *sulA*) (Chen *et al.*, 2023), which encode resistant variants of dihydropteroate synthase (DHPS). Commonly, *sul2* is co-located with *strA-strB* genes on transposon Tn5393, and *sul3* is associated with insertion sequence IS 15Δ/26 (Duijkeren *et al.*, 2017; Okubo *et al.*, 2019). Regarding aminoglycoside resistance, several genes were reported: *aacC2* (5.6 %), *aac(6')-Ib-cr* (0.3 %), *aac(3)* (1.2 %) in six variants (*aac(3)-I*, *aac(3)-II*, *aac(3)-IIa*, *aac(3)-IId*, *aac(3)-IV*, *aac(3)-Via*), *aadA* (2.4 %) with variants (*aadA1*, *aadA2*, *aadA12*, *aadA17*, *aadA24*), *aphA1* (0.7 %), *aph(3')* (0.3 %), and *str* (0.5 %), including *strA*, *strA/B*, and *strB*. Aminoglycosides are particularly relevant due to rising resistance rates among *Enterobacteriaceae* (Ojdana *et al.*, 2018). In this review, they ranked third (12.7 %) in resistance in *E. coli* isolates, which is primarily attributed to the production of aminoglycoside-modifying enzymes (AMEs) (Foudraine *et al.*, 2021).

The most frequent AMEs are N-acetyltransferases (AAC), O-nucleotidyltransferases (AAD/ANT), and O-phosphotransferases (APH), which in turn are classified and named according to the position of the aminoglycoside they modify, followed by a Roman numeral and a letter if more enzymes modify the same position (Cameron *et al.*, 2018; Krause *et al.*, 2016). Misuse of aminoglycosides is associated with the genetic diversity observed for *aac*, *aadA*, and *aph* genes in *E. coli* isolates. It should be noted that *strA* is considered a synonym of *aph(3'')-Ib* and *strB* of *aph(6)-Id*; these phosphotransferases are the most common in *E. coli* and confer streptomycin resistance, typically found together with *aph(3'')-I/II* genes that confer kanamycin resistance (Okubo *et al.*, 2019; Poirel *et al.*, 2018).

On another note, potentiated sulfonamides accounted for 6.2 % of resistance in the *E. coli* isolates analyzed. These are sulfamethoxazole and trimethoprim compounds, which are involved in the biosynthesis of folate. Sulfonamides act on dihydropteroate synthase (DHPS), competing with para-aminobenzoic acid (PABA), while trimethoprim competitively inhibits dihydrofolate reductase (DHFR) (Dennis *et al.*, 2018; He *et al.*, 2020). On the other hand, resistance to trimethoprim is associated with the production of replacement DHFR enzymes on which trimethoprim cannot exert its mechanism of action. These genes are called *dfr* and are subdivided into two families: *dfrA*, which encodes DHFR homologues of ~160 amino acids, and *dfrB*, which encodes homologues of 78 amino acids, where *dfrA* is the main cause of resistance to this drug (Jiang *et al.*, 2023; Kneis *et al.*, 2023). The genes associated with trimethoprim resistance analyzed in this study were *dfrA* (3.9 %) in the variants *dfrA1*, *dfrA5*, *dfrA7*, *dfrA8*, and *dfrA12*, and *dhfrI* (0.05 %).

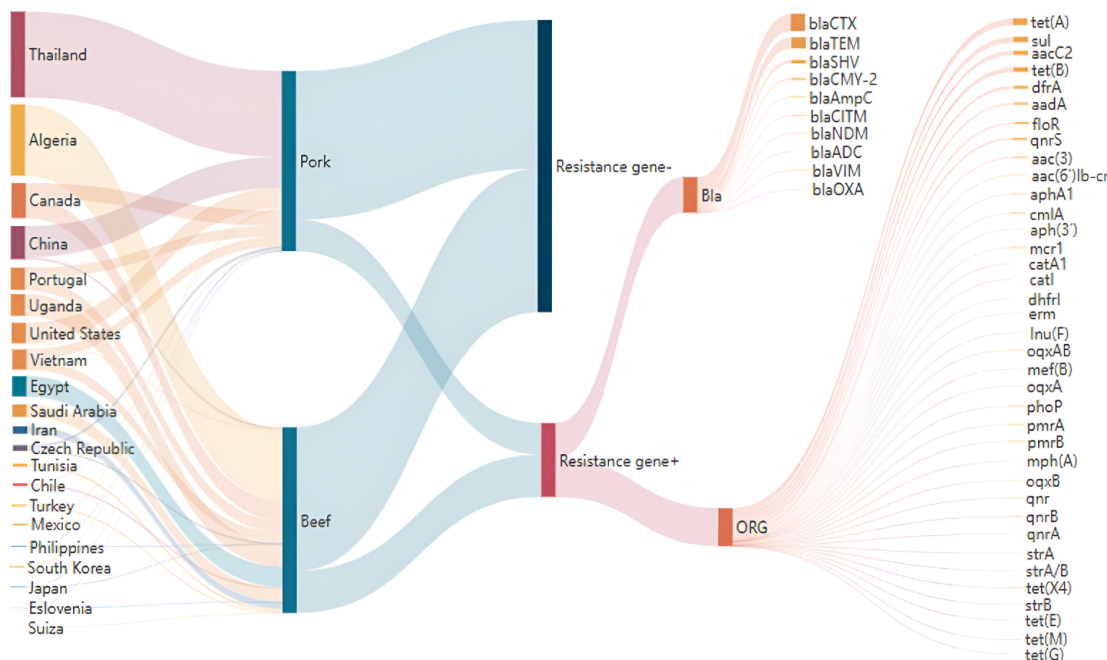
On the other hand, 7.9 % of all isolates showed resistance to the phenicol group, and the genes reported were *cat* (0.09 %) (specifically the *catI* and *catAI* genes), *cmIA* (1.0 %), and *floR* (2.1 %). These compounds are not frequently used in human medicine due to their toxicity; however, they are still used in veterinary medicine with certain restrictions. Chloramphenicol is restricted for use in pets and non-food-producing animals, while florfenicol is exclusively for use in food-producing animals (Poirel *et al.*, 2018; Roberts & Schwarz, 2016). Resistance mechanisms include chloramphenicol acetyltransferases (CAT) encoded by *cat* genes (Huang *et al.*, 2017), and efflux pumps encoded by *cmIA* (chloramphenicol) and *floR* (florfenicol) (Zhou *et al.*, 2023).

Resistance to quinolones and fluoroquinolones was also significant, accounting for 7.7 % and 5.1 % of all resistant strains. The genes reported to be associated with resistance to this family of antibiotics are of the *qnr* type, which confer resistance to quinolones: *qnrS* (2.6 %), *qnrB* (0.6 %), and *qnrA* (0.09 %). Resistance to these drugs can occur due to mutations at the target site (*gyrA* and *parC*) or mediated by plasmids, where the main mechanism is the production of Qnr-like proteins (*qnrA*, *qnrB*, *qnrC*, *qnrD*, and *qnrS*) that prevent the compound from binding to the target site (Dias *et al.*, 2020; Machuca *et al.*, 2017).

Additional plasmid-mediated mechanisms include AAC(6')-Ib-cr N-acetyltransferases (modifying ciprofloxacin and enrofloxacin) and efflux pumps encoded by *oqxAB* (Poirel *et al.*, 2018). Resistance to colistin (polymyxins) was linked to *mcr1* (0.9 %), *phoP* (0.8 %), *pmrA* (0.8 %), and *pmrB* (0.8 %). Resistance to macrolides involved *erm* (0.1 %), *mef(B)* (0.1 %), and *mph(A)* (0.09 %). Resistance to lincosamides was associated with *Inu(F)* (0.1 %). Efflux pump genes *oqxA*

(0.3 %), *oqxB* (0.4 %), and *oqxAB* (0.5 %) were also detected, conferring resistance to multiple drugs (Figure 4).

This overview highlights the importance of the genetic diversity of resistance determinants found in *E. coli*. The success of horizontal gene transfer among commensal and pathogenic species is largely due to its localization in mobile genetic elements such as plasmids (facilitating transfer between bacteria), as well as transposons, insertion sequences, and integrons, which can mobilize within bacterial genomes (Partridge *et al.*, 2018; Rozwandowicz *et al.*, 2018).



**Figure 4. Sankey plot of the relationship between the origin of the *E. coli* isolates and the evaluation of resistance genes in strains.**

Source: own elaboration.

## Antibiotic resistance and its relationship with integrons

From the 34 articles included in this review, 13 determined the presence of class 1 and/or class 2 integrons (Table 1). Class 1 integrons were detected in 161 isolates, while class 2 integrons were identified in only 13 isolates. Among the 13 studies that investigated integrons, 10 reported the genes or gene cassette arrays carried by them. The most common were *dfrA* and *aadA*, either as single genes or in arrays. Frequently observed arrays included *dfrA1-aadA1*, *dfrA17-aadA5*, and *dfrA12-aadA2*. Less frequent arrays included *aadA2-linF*, *aacA4-cmlA*, *dfrA1-*

*orf*, *aadB-aadA1-cmlA6*, and *aadB-aadA*. Additional reported genes included *sul2*, *tet(B)*, and *qacEΔ1*.

The study of integrons has gained relevance due to their role in the dissemination of resistance genes and their contribution to the emergence of Gram-negative MDR, XDR, and PDR bacteria (Liu *et al.*, 2022). Integrons are composed of three elements that enable the capture and expression of gene cassettes: a gene encoding the integrase (*intl*), an *attI* recombination site where cassettes integrate through site-specific recombination, and a promoter ( $P_c$ ) for expression of the integrated genes (Zhang *et al.*, 2020). Type 1 integrons are the most common in *E. coli* and enterobacterial isolates. This type of integron can recombine with a wide range of *attC* sites, which are nucleotide sequences that serve as recognition sites for type 1-specific integrase. These sites can be disparate and can also bind to nucleotide sequences with less similarity (Kaushik *et al.*, 2018). They are also located in plasmids (a characteristic that allows them to be classified as “mobile integrons”), unlike type 2 integrons, which are present at the chromosomal level (Fuentes *et al.*, 2013). Another relevant aspect of type 1 integrons is that they consist of two conserved regions and one variable region (where the resistance genes are located). The first conserved region contains the *IntI1* (encoding type 1 integrase), *attI1* (a binding segment that captures cassette genes), and promoter genes. The second conserved region contains the *qacEΔ1* (which confers resistance to disinfectants and ammonium compounds) and *sul1* (resistance to sulfonamides) (Wan & Chou, 2015), indicating that whenever type 1 integrons are present, the *sul1* gene will also be present. Therefore, the study and presence of integrons is relevant in other areas of microbial control. It has been reported that type 1 integrons, in conjunction with the *sul1* gene, are found in multidrug resistance plasmids that carry *bla* genes encoding ESBLs (Poirel *et al.*, 2018). Furthermore, both class 1 and class 2 integrons frequently harbor *dfrA* and *dfrB* genes associated with insertion sequences CR1 or CR2 (Ambrose & Hall, 2019; Jiang *et al.*, 2023), as well as *aadA* genes commonly identified as cassettes (Zárate *et al.*, 2018). This aligns with the gene cassette arrays reported in *E. coli* isolates, particularly *dfrA1-aadA1*, *dfrA17-aadA5*, and *dfrA12-aadA2* (Liu *et al.*, 2022; Poey *et al.*, 2019). The analyzed evidence highlights the crucial role of integrons in the dissemination of antimicrobial resistance in bacteria of major importance to both animal health and public health.

**Table 1. Record of *E. coli* strains isolated from meat that reported the presence of integrons.**

Author	Year	Country	Origin	No. strains	<i>Int-1</i>	Cassette gene	<i>Intl-2</i>	Cassette gene
Vogt <i>et al.</i>	2014	Suiza	Beef	1	1	<i>dfrA17, sul2, tet(B)</i>	0	Not reported
Ahmed <i>et al.</i>	2015	Egypt	Beef	21	6	<i>aadA1</i> <i>dfrA1-aadA</i> <i>dfrA12-orf-aadA2</i> <i>dfrA17-aadA5</i>	1	<i>dfrA1-sat2-aadA1</i>

Continuation  
**Table 1. Record of *E. coli* strains isolated from meat that reported the presence of integrons.**

Author	Year	Country	Origin	No. strains	<i>Int-1</i>	Cassette gene	<i>Intl-2</i>	Cassette gene
Liu <i>et al.</i>	2015	China	Pork	11	9	aadA22 dfrA17-aadA5 dfrA12-aadA2 aadA2-linF aacA4-cmlA1	0	Not reported
Moawad <i>et al.</i>	2017	Egypt	Beef	6	1	dfrA1 dfrA1-orf	0	Not reported
Rebbah <i>et al.</i>	2017	Algeria	Beef	102	69*	Not reported	10*	Not reported
Kim <i>et al.</i>	2018	South Korea	Pork	6	5	aadA1, aadA5, dfrA17, qacEΔ1	0	Not reported
Fang <i>et al.</i>	2019	China	Pork	180	19	aadB-aadA1-cmlA6	0	Not reported
Barrios-Villa <i>et al.</i>	2018	Mexico	Pork	5	3	aadB-aadA dfrA1-aadA1 dfr12-aadA2	0	Not reported
Wang <i>et al.</i>	2020	China	Pork	8	3	aadA2, aadB	0	Not reported
Pungpian <i>et al.</i>	2021	Thailand	Pork	216	10	aadA1 dfrA1-aadA1 dfrA12- aadA2 dfrA17-aadA5	0	Not reported
Clemente <i>et al.</i>	2021	Portugal	Beef	26	16	Not reported	1*	Not reported
			Pork	23	13	Not reported	1*	Not reported
Xedzro <i>et al.</i>	2023	Japan	Beef	4	3	aadA1	0	Not reported
			Pork	4	1	aadA5-dfr17	0	Not reported
İnat <i>et al.</i>	2023	Turkey	Beef	4	2*	Not reported	0	Not reported

\* These resources reported the presence of integrons; however, the gene arrangement was not reported.

Source: own elaboration.

## Conclusions

The consumption of pork and beef shows different trends across various regions worldwide. In areas with high production and consumption, increased monitoring of multidrug-resistant *E. coli*

strains has been reported, particularly in countries such as Thailand, China, the United States, Algeria, and Egypt. Still, monitoring of *E. coli* remains a global public health concern.

Among the reports analyzed, the production of extended-spectrum  $\beta$ -lactamases was the most common resistance mechanism observed. Often, this was accompanied by additional mechanisms conferring resistance to other antibiotic groups, such as *tet* and *sul* genes, which grant resistance to tetracyclines and sulfonamides, respectively. Both pork and beef products were identified as potential carriers for *E. coli* resistance genes. This transmission can occur among food-producing animals, humans, and other bacterial species. Therefore, studying phenotypic and genotypic resistance in *E. coli* is essential for helping healthcare professionals in both animals and humans manage infections caused by this pathogen.

Lastly, class 1 and class 2 integrons were found at low frequencies, despite their well-known role in spreading resistance genes and the emergence of MDR strains. Continued monitoring of microorganisms with significant public health impact, such as *E. coli*, should be maintained, with a greater focus on incorporating integrons to better understand their specific role in *E. coli* antimicrobial resistance.

## Author Contributions

Work conceptualization: C.L.A.P., R.R.N.E., and M.J.V.M.; Methodology: C.L.A.P., A.P.V.J.O.; Software: A.P.V.J.O.; Validation: R.R.N.E., M.J.V.M., and V.S.V.; Formal analysis: C.L.A.P.; Data curation: A.P.V.J.O.; Writing-original draft preparation: C.L.A.P.; Writing-review and editing: R.R.N.E., M.J.V.M., V.S.V., B.L.J., and O.L.I.

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## Conflict of Interest

The authors declare no conflict of interest.

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