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Review

Enterobacteria in the 21st century: a review focused on taxonomic changes

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Abstract

Introduction: *Enterobacteria* are the main group causing infections in humans. The aim of this review is to present the new genera and the taxonomic changes that the *Enterobacteriacea* family has experienced in recent years.
Methodology: a systematic search of papers published in databases from January 2000 to July 2018 was done. Additionally, the bibliographic references of each document were reviewed and each paper citing the article was reviewed in search of clinical cases.
Results: Nineteen new genera of *Enterobacteria* have been described since 2000. The genera *Yersinia*, *Morganella* and *Erwinia* do not belong to the family *Enterobacteriacea* anymore.
Conclusions: for an adequate clinical and epidemiological interpretation, it is advisable to update the libraries of the commercial systems used for the identification of the microorganisms, as well as to train the staff in the taxonomic changes of microorganisms.

Key words: *Enterobacteriaceae; Escherichia; Enterobacterales; Morganellaceae*.

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Introduction

Enterobacteriaceae is a heterogeneous group of gammaproteobacteria, that are straight rod-shaped and non-sporulated; they are also non-motile or motile by means of peritrichous flagella, facultative anaerobes, oxidase-negative, catalase-positive, nitrate-to-nitrite reducers, glucose-fermentors producing various final products, having simple nutritional requirements. On average they measure 2-4 µm in length by 0.4-0.6 µm in width, with rounded ends, and in vitro generation time between 20 and 30 minutes [1,2].

Members of *Enterobacteriaceae* are widely distributed in nature, and many of their species live in the gut of humans and animals, including insects, where they can cause enteric diseases or remain as commensal organisms. The members of this family play a role as plants pathogens, and biotechnological microorganisms for the heterologous production of proteins [2]. However, not all genera o species within a same genus are pathogen, only a small group of species are considered strict pathogens [3].

Historically, the differentiation of members of this family has been based on biochemical features; with the use of miniaturized tests that contain various carbon and nitrogen sources; and more recently, with the analysis of the sequence of the 16S RNAr gene. However, in some cases, the low discriminatory power of 16S RNAr sequence analysis [4] make it necessary to use additional identification techniques [5] as a result, the taxonomy of the *Enterobacteria* have undergone repeated changes in recent decades.

Recent reclassification of organisms can cause confusion in clinicians and microbiologists, as well as in the regulatory authorities responsible for the monitoring and control of these microorganisms [1,6].

In 2006, Kämpfer *et al*., [7], proposed the genus *Thorsellia* with the species *Thorsellia anophelis*, and in 2015, the authors proposed the family *Thorselliaceae* with the new species *Thorsellia kandunguensis* sp. nov. and the renaming of *Thorsellia anophelis* to *Thorsellia kenyensis*. Based on phylogenetic analysis of rRNA16S, it was found that the *Thorsellia* genus is a separated branch, distinct from the *Enterobacteriaceae* [8]. In 2016, Kämpfer *et al.,* proposed the genus *Coetzeea* as the second member of the family [9].

But the main change in its taxonomic classification came in 2016, when Adelou *et al*., [10] based on phylogenetic analyzes and conserved molecular characteristics analysis, proposed that the *Enterobacteriales* order, which until then, had a one

single *Enterobacteriaceae* family [11], changed its name to order Enterobacterales, and it would be divided into seven families: *Enterobacteriaceae* [12], *Erwiniaceae* fam nov., *Pectobacteriaceae* fam. nov., *Yersiniaceae* fam. nov., *Hafniaceae* fam. nov., *Morganellaceae* fam. nov. and *Budviciaceae* fam. nov. [10]. The order *Enterobacterales* contains the type genus *Enterobacter*, and its description is the same as the *Enterobacteriaceae* family.

The aim of this review is to present the description of new bacterial genera within the *Enterobacteriacea* and describe the taxonomical changes that this family has undergone in the last years.

Methodology

A systematic search of studies published between January 2000 and July 2018 with the descriptors "*Enterobactericaea* gen. nov" was conducted in PubMed, Redalyc and Google Scholar. The search was limited to these databases and search engine, for being the most important sources of scientific literature in English, Portuguese and Spanish languages. Publications referenced in the bibliography were reviewed in search of previous descriptions of each genus. Subsequently, each article citation was searched for reports of clinical cases.

For each publication, we read the title, the abstract, and later the rest of the document. Classifying the information by authors and year of publication. Finally, all the data obtained was compared with the data from the web page of LSPN, List of Prokaryotic Names with Standing in Nomenclature (www.bacterio.net) and with the data from MEDLINE (NCBI Taxonomy Browser - NCBI – (www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi).

Declaration of ethical aspects

The authors declare that in this work no experiments were carried out in humans or animals and that the data do not allow the identification of patients.

Results

Sixty-two publications were identified in the initial search. Only were considered the articles that described new bacterial genera, clinical case reports or new combinations of genera.

Articles referring to genera belonging to unclassified *Enterobacteriales* or unclassified *Enterobacteriaceae* (candidates) were not considered. Simultaneously, publications about the taxonomy and the phylogeny that had been selected as theoretical support of this research were reviewed.

At the time of writing this document, the family *Enterobacteriaceae* contains 32 genera (https://www.ncbi.nlm.nih.gov/Taxonomy/taxonomyhome.html/). The family *Erwiniaceae* with seven genera, the family *Pectobacteriaceae* with five genera, the family *Yersniaceae* with eight genera, the family *Morganellaceae* with eight genera, and the families *Hafniaceae* and *Budviciae* with 3 genera each. The genera *Coetzeea* and *Thorsellia*, are the only genera described for the *Thorselliaceae* family. Even though this review focuses only on genera within the family *Enterobacteriaceae* described during the 21th century, Table 1 shows all the families and genera that belong to the order *Enterobacteriales* [13-21] , in order to show the genera related to *Enterobacteriaceae*.

In Table 1, for the bacterial genera described after the year 2000, the author and year of publication are stated; while for the bacterial genera described before the year 2000, only the year of description is mentioned.

Following is a brief description of the genera belonging to the *Enterobacteriaceae* family that were first described in the 21st century.

Atlantibacter

The name of the genus *Atlantibacter* was given in memory of the city of Atlanta, Georgia, USA. The type species, *Atlantibacter hermannii*, was named after George J. Hermann, former head of the Enteric Section of CDC, and Lloyd G. Herman of the National Institutes of Health, Bethesda.

The genus was created to reclassify isolates of *Escherichia hermannii* and *Salmonella subterranea* as *Atlantibacter hermannii* and *Atlantibacter subterranea*, respectively [22] .

The genus *Atlantibacter* is composed of motile bacteria, indole-positive, urease-negative, that do not decarboxylate ornithine, arginine or lysine. They are H_2S positive and Voges-Proskauer positive.

Clinical importance: *Atlantibacter (Escherichia) hermannii* has been widely reported as an etiological agent of infection in humans [23-25]. There are no reported cases of infection in humans by *Atlantibacter* (*Salmonella*) *subterranea*.

Biostraticola

(bio: live; stratum: layer; cola: inhabitant)"biofilm inhabitant". The type species is *Biostraticola tofi*, named after tufa (calcareous tufa, limestone) [26]. They are non-motile bacilli, non-spore-forming, catalase-positive and oxidase-negative.

Table 1. Genera in the families of the order *Enterobacterales* described before and after the year 2000.

Family	Genera described during the 21th century	Genera described before 2000
Enterobacteriaceae (Rahn, 1937, Adeolu *et al.* 2016) [10,12]	*Atlantibacter* (Hata *et al.,* 2016) [22] *Biostraticola* (Verbarg *et al.,* 2008) [26] *Cronobacter* (Iversen *et al.,* 2008) [28] *Enterobacillus* (Patil *et al.,* 2015) [36] *Franconibacter* (Stephan *et al.,* 2014) [37] *Gibbsiella* (Brady *et al.,* 2011) [39] *Izhakiella* (Aizenberg- Gershtein *et al.,* 2016) [41] *Kosakonia* (Brady *et al.,* 2013) [42] *Lelliottia* (Brady *et al.,* 2013) [42] *Limnobaculum* (Baek *et al*., 2018) [46] *Mangrovibacter* (Rameshkumar *et al.,* 2010) [47] *Metakosakonia* (Alnajar & Gupta, 2017) [48] *Pluralibacter* (Brady *et al.,* 2013) [42] *Pseudocitrobacter* (Kampfer *et al.,* 2014) [52] *Pseudoescherichia* (Alnajar & Gupta, 2017) [48] *Raoultella* (Drancourt *et al.,* 2001) [56] *Rosenbergiella* (Halpern *et al.,* 2013) [62] *Shimwellia* (Priest & Barker, 2010) [63] *Siccibacter* (Stephan *et al.,* 2014) [37]	*Buttiauxella* (1982) *Cedecea* (1981) *Citrobacter* (1932) *Enterobacter* (1960) *Escherichia* (1919) ***** *Klebsiella* (1980) *Kluyvera* (1981) *Leclercia* (1987) *Saccharobacter* (1990) *Salmonella* (1900) *Shigella* (1919) *Trabulsiella* (1992) *Yokenella* (1985)
Erwiniaceae (Adeolu *et al.* 2016) [10]	*Phaseolibacter* (Halpern *et al*., 2013) [13] *Mixta* (Palmer *et al*., 2018) [14]	*Buchnera (1991)* *Erwinia (1920)* ***** *Pantoea (1989)* *Tatumella (1982)* *Wigglesworthia (1995)*
Pectobacteriaceae (Adeolu *et al.* 2016) [10]	*Dickeya (*Samson *et al*., 2005) [15] *Lonsdalea (*Brady *et al.,* 2012) [16]	*Brenneria (1999)* *Pectobacterium (1945)* ***** *Sodalis* (1999)
Yersiniaceae (Adeolu *et al.* 2016) [10]	*Chania* (Ee *et al.,* 2016) [17] *Nissabacter (*Mlaga 2017) [18] *Rouxiella* (Le Fleche-Mateos *et al.,* 2015) [19] *Samsonia* (Sutra *et al.,* 2001) [20]	*Ewingella (1984)* *Rahnella (1981)* *Serratia (1823)* *Yersinia (1944)* *****
Hafniaceae (Adeolu *et al.* 2016) [10]		*Edwardsiella* (1965) *Hafnia* (1954) ***** *Obesumbacterium* (1963)
Morganellaceae (Adeolu *et al.* 2016) [10]	*Cosenzaea* (Giammanco *et al*., 2011) [21]	*Arsenophonus (1991)* *Moellerella (1984)* *Morganella (1943)* ***** *Photorhabdus (1993)* *Proteus (1885)* *Providencia (1962)* *Xenorhabdus (1979)*
Budviciaceae (Adeolu *et al.* 2016) [10]		*Budvicia (1985)* ***** *Leminorella (1985)* *Pragia (1988)*
Thorselliaceae (Kämpfer *et al.* 2015) [8]	*Coetzeea (*Kämpfer *et al.* 2016) [9] *Thorsellia (*Kämpfer *et al.* 2006) ***** [7]	

***** Type genus of the family.

The first isolates were obtained from the biofilm of a limestone deposit in a hard water rivulet on the western slopes of the Harz Mountains, Lower Saxony, Germany.

Clinical importance: Unknown. *Biostraticola* has not been reported causing infections in humans.

Cronobacter

Cronos: titan of Greek mythology, who ate their children at birth, bacter: rod. A rod-shaped bacterium that can cause infection (death) in newborns. The type species is *Cronobacter sakazakii*, named after the Japanese microbiologist Riichi Sakazaki.

The genus was created as a consequence of the reclassification of strains of *Enterobacter* [27].

Cronobacter comprises gram-negative bacilli, negative oxidase, catalase positive, generally motile, which use citrate, hydrolyze esculin and arginine, are generally positive for the Voges-Proskauer test and negative for the methyl red test. They do not produce hydrogen sulfide, urease, or lysine decarboxylase [28].

C. sakazakii survives in low water activity environments, particularly, in powdered formulas for infants [29-31]. In Syria, Belal *et al*., found *Cronobacter* in food samples: medicinal herbs (32 %), spices (52 %) and liquorici (94%), which indicates that *Cronobacter* is associated with plant-based foods and not only with infant formula, infant food and milk powder. [32]

Clinical importance: since its first description by Farmer in 1980, *Cronobacter* (*Enterobacter*) *sakazakii* has been recognized as an important agent isolated in human clinical specimens such as sputum, feces, and wounds [33-35]. *Cronobacter* has been associated with rare food-borne illnesses; some potentially fatal (meningitis, septicemia, necrotizing enterocolitis) in newborns and premature infants, where infant powdered formulas have been identified as the source of the pathogen [29]. In adittion, the findings of Belal *et al*., suggest that extra precautions should be taken with dietary supplements containing herbs or herbal beverages that are administered to infants or to immunocompromised persons. [32]

Enterobacillus "enteric bacillus"

The type species is *Enterobacillus tribolii*, which received its name for being first isolated from *Tribolium cutaneum* (red flour beetle) [36].

The cells are gram-negative, motile, straight, catalase-positive and oxidase-negative, non-H_2S-producers, non-urease-producer and non-nitrate-reducers. Its clinical importance is still unknown.

Franconibacter

A bacterium named in memory of the microbiologist Augusto Franco-Mora. The type species is *Franconibacter helveticus*, named after the geographical origin of the first isolate (Helvetica, Switzerland).

Its description as a genus was given from the reclassification of *Enterobacter pulveris* and *Enterobacter helveticus* as members of the genus *Cronobacter* [37].

The genus is composed of motile gram-negative bacilli or cocci, single or in pairs; catalase-positive, oxidase-negative or weakly positive; capable of forming convex yellow colonies. The results for the urea, indole and Voges Proskauer tests are always negative.

Clinical importance: Unknown. *Franconibacter* have been isolated from powdered fruits and infant formulas [38].

Gibbsiella

This genus was named in honor of the British forest pathologist John N. Gibbs. The type species is *Gibbsiella quercinecans*, named because the first isolates were obtained from oaks with symptoms of extensive stem bleeding; Quercus (Latin): oak; necare (Latin): kill or "Destroyers of oaks" [39].

These are short gram-negative, oxidase-negative and catalase-positive bacteria, occurring as single cells, in pairs or in groups of four; negative for urease, indole and H_2S production; citrate-utilizing ability and can reduce nitrate to nitrite.

Clinical importance: Unknown. In 2012, Saito *et al*. [40], described isolates from the oral cavity of bears.

Izhakiella

Named in honor of Professor Ido Izhaki, an Israeli ecologist. The type species is *Izhakiella capsodis*, which epithet comes from having been first isolated from the mirid bug *Capsodes infuscatus*.

The genus is composed of gram-negative, catalase-positive and oxidase-negative bacilli; with the ability to hydrolyze urea and reduce nitrate to nitrite. They do not produce indole, nor H2S [41].

Its clinical importance remains unknown, no isolate has been reported in humans.

Kosakonia

Kosakonia species (former Enterobacter species) have been isolated from the environment, including from soil and trees.

The genus name was given in honor of Y. Kosako, for his contribution to the bacterial taxonomy. The type species is *Kosakonia cowanii*, which epithet comes from S.T. Cowan, the British bacteriologist.

They are are straight and motile gram-negative bacilli that do not produce indole and are Voges Proskauer positive [42].

Clinical importance: in 2017, Bhatti *et al*., published the first case of human infection by *Kosakonia radicintans*, which was detected by hemoculture in a patient with suspected sepsis [43].

Lelliottia

Named after of R.A. Lelliott, who greatly contributed to the understanding of bacterial diseases in plants. The type species is *Lelliottia nimipressuralis*, which epithet means "with excessive pressure" (Latin *nimis*: excessive and *pressuralis*: pressure) [44].

The re-evaluation of species of *Enterobacter* gave origin to this genus.

Lelliottia are straight gram-negative bacilli that are glucose fermenters and nitrate-to-nitrite reducers, positive for Voges-Proskauer and ornithine decarboxylase; but negative for lysine decarboxylase, indole and H_2S production.

Lelliottia species have been isolated from from food products, water and from elms with symptoms of wetwood disease.

Clinical importance: some species of *Lelliotia* have been sporadically associated with infections in humans [44,45].

Limnobaculum

Limnobaculum parvum was isolated from isolated from aquatic environment [46].

Clinical importance: unknown

Mangrovibacter

The first isolates came from wild rice roots associated with mangrove, collected in the Pichavaram mangrove forest in India. (*Mangrovibacter*: mangrove bacillus).

The type species is *Mangrovibacter plantisponsor*, a diazotroph, that received this name due to its potential plant-growth promoting effect [47].

Species of the genus are gram-negative, motile, oxidase-negative and catalase-positive bacilli that are negative for decarboxylate ornithine and Voges-Proskauer reaction.

Clinical importance: unknown

Metakosakonia

Genus named for its phylogenetic proximity with the genus *Kosakonia*. The type species is *Metakosakonia massiliensis*, named after Massilia, Latin name of the city of Marseille (France).

The genus originated from the reclassification of *Enterobacter massiliensis* isolates due to comparative phylogenomic studies. Gender comprises gram-negative, glucose-fermenter, indole positive, catalase positive, and oxidase negative bacilli that are positive for the arginine dihydrolase pathway [48].

Clinical importance: unknown

Pluralibacter: "bacteria from many sources"

The type species is *Pluralibacter gergoviae*, named after the city of Gergovie (Gergovia), France, where it was first isolated.

Its description as a genus was based on the reclassification of isolates of *Enterobacter* [42].

Cells are straight, motile and rod-shaped, which reduce nitrate to nitrite, positive for Voges-Proskauer and ornithine decarboxylase; but negative for arginine dihydrolase, and production of indole from tryptophan.

Isolates of *Pluralibacter* have been detected from environmental samples and from brown leaf spots on pear trees.

Clinical importance: *Pluralibacter* (*Enterobacte*r) *gergoviae* is an important opportunistic pathogen, associated with sepsis, endophthalmitis, pneumonia and intra-hospital outbreaks [49-51].

Pseudocitrobacter: or "false Citrobacter"

The type species is *Pseudocitrobacter faecalis*, named after being isolated from fecal samples. The first isolates of the genus correspond to four strains from hospitalized patients and outpatients who attended two military hospitals in Rawalpindi, Pakistan, in 2010 and 2011 [52].

They are short and motile gram-negative bacilli; negative for oxidase, indole, H2S production and urease. They decarboxylate lysine and ornithine, but not arginine. They can reduce nitrate to nitrite.

Clinical importance: unknown.

Pseudoescherichia: "false Escherichia"

The type species is *Pseudoescherichia vulneris*, named after being isolated from wounds (Latin *vulneris*: wounds).

This genus originated from the reclassification due to phylogenomic analysis of *Escherichia vulneris* isolates [48].

The genus is composed of motile gram-negative bacilli, which are negative for Voges-Proskauer reaction, indole production, urea hydrolase, H2S production, citrate utilization, ornithine decarboxylase, phenylalanine deaminase and DNase; and positive for methyl red.

Clinical importance: *Pseudoescherichia* (*Escherichia*) *vulneris* is considered an important opportunistic pathogen, involved in cases of complicated diarrhea, sepsis, septic arthritis and queratitis, among others [53-55].

Raoultella

This genus comprises of encapsulated, non-motile, gram-negative bacilli, capable of fermenting glucose and lactose. Most strains utilize citrate, and the Voges-Proskauer test is always positive [56].

The genus was named after the French bacteriologist Didier Raoult, Marseille, France; and the type species is *Raoultella planticola*.

The reclassification of isolates previously identified as *Klebsiella* spp., lead to the creation of the genus.

Raoultella has been isolated from soil and plants, and it is considered an important bacterial pathogen that can cause sepsis, osteomyelitis, tissue necrosis, among others [57-60]. In Colombia, Arteta *et al*., evaluated the vesicular microbiota in patients with gallstones from two populations who underwent cholecystectomy and who did not present symptoms of acute inflammation. When the tissue of the gallbladder and bile had positive cultures, *Raoultella terrigena* was one of the two most frequent bacteria, suggesting differences in the microbiota between the populations [61].

Rosenbergiella

The first isolations were obtained in 2009 from floral nectar of *Amygdalus communis* (almond) and *Citrus paradisi* (grapefruit) in Israel. *Rosenbergiella* was named to honor Professor Eugene Rosenberg, a microbiologist of Israeli origin; and the type species is *Rosenbergiella nectarea*, which specific epithet refers to being isolated from nectar [62].

The members of this genus are motile, rod-shaped, yellow-orange pigmented, gram-negative bacilli. Their clinical importance remains unknown.

Shimwellia

The first isolates came from reused brewery yeast.

Shimwellia was named after J. L. Shimwell, who isolated the bacteria for the first time. The type species is *Shimwellia pseudoproteus* (false *Proteus*).

They are straight, non-motile, gram-negative bacilli that do not produce H2S. They are catalase positive, but this reaction may appear weak and delayed [63]. Its clinical importance is still unknown.

Siccibacter: "dry bacilli" (siccus: dry).

The type species, *Siccibacter turicensis*, was named after the latin name of Zurich: Turicum, where it was first isolated.

The genus originated due to the reclassification of isolates of *Enterobacter turicensis*.

They are motile, gram-negative, catalase-positive, weakly oxidase-positive cocci or bacilli occurring single or in pairs. Negative for indole production, urea hydrolase, Voges-Proskauer and H2S production. Isolates form convex, yellow colonies [37].

Clinical importance: unknown. *Siccibacter* (*Enterobacter*) *turicensis* has been isolated from fruit powder [38].

Discussion

The bacterial taxonomy is changing as a consequence of the separation of microorganisms into new or existing taxa, as well as for combining the taxa. The use in this century of a greater number of constitutive genes as genetic markers has determined a greater degree of taxonomic segregation within the *Enterobacteriaceae* family. The accelerated development of genomics will continue to introduce frequent changes within the classification of this family.

Although automated rapid miniaturized biochemical identification system (Phoenix, VITEK, Microscan, API) and mass spectrometric analysis of proteins (MALDI-TOF) are the most widely used for the identification of microorganisms in laboratories; it is important to note that the identification of reclassified bacterial species has only been possible by molecular techniques. Many of these organisms are not included in databases of commercial identification systems and in some other cases, the updates of the database corresponds to disused names [36,37,52].

It is imperative having updated databases that allow the identification of bacteria with the current species name, which is critical to assess the clinical and epidemiological importance of the findings in cases of colonization or infection in humans.

It is also important the permanent training of laboratory personnel involved in the identification of microorganisms, concerning the taxonomic changes of critical species, and to provide access to more robust methods that allow to confirm the identification of species when needed.

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