COWAN, S. T. (1956). *J. gen. Microbiol.* **15**, 345–358

Taxonomic Rank of Enterobacteriaceae ‘Groups’

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SUMMARY: The taxonomic value of the different ‘groups’ into which the Enterobacteriaceae are divided is assessed, and consideration is given to the classification of different groups within the family. No scheme fits the requirements of all workers and two different approaches are made, one for workers in applied bacteriology, and a more logical one for taxonomic purists. For the former scheme it is suggested that common (vulgar) names should be used to describe the groups and their subdivisions. Linnaean binomials are essential for the more systematic scheme, in which the Arizona group is merged with *Salmonella*; Ballerup–Bethesda is combined with *Citrobacter freundii*; Sonne’s bacillus and *Bacillus alcalescens* are included in *Escherichia*; Cloaca and Hafnia (32011) are included as species of *Klebsiella*, and Providence (29911) as a species of *Proteus*. Few of these suggestions are new, but the scheme is a classification of a family and not a collection of ‘groups’.

In taxonomic studies it is convenient to divide organisms into groups and subgroups, leaving the status of rank for each category to be decided when order appears and the work is nearing completion. Problems of rank are met with in all types of organism; they are attacked in different ways in different disciplines, but even in one branch of microbiology there is no uniformity. Among bacteria certain organisms from the intestines of animals present special problems; their morphological and cultural characters are alike, and resemble those of bacteria found in soil, in water and on plants. Though there is nothing to be said in favour of an ecological grouping of bacteria, in practice ecology may determine the primary grouping: a plant pathologist studies those bacteria found in plants, the water bacteriologist studies essentially similar organisms in water, and the clinical pathologist finds them in human or animal excretions. Often these ecologists work in isolation and develop independent taxonomic schemes.

White (1937), writing on the construction of a taxonomic system for bacteria, contrasted determinative keys with systems based on mutual relations and differences. He said that such a system must develop from multiple foci of intensive study, which would gradually widen until they became confluent; only then could an opinion be formed as to the rational groupings of larger size. Of necessity such a system would be built slowly, but it would be laid on sure foundations. White himself laid many of these foundations and, with Kauffmann, Jordan, St John-Brooks, Schütze and Scott of the original *Salmonella* Subcommittee, paved the way by making an intensive study of one group of organisms. Since then the number of groups studied has increased, and the *Salmonella* Subcommittee of the International Committee on Bacteriological Nomenclature has been replaced by an Enterobacteriaceae Subcommittee (E.S.) which covers many more of the ‘multiple foci’. Enlarging

the foci has, as White forecast, resulted in their confluence, and the time seems ripe for an assessment of what are 'rational groupings'.

SUBDIVISIONS OF THE ENTEROBACTERIACEAE

Taxonomic ranks are based on the number of shared characters; higher ranks have few characters in common, lower ranks have many, so that the finest subdivisions, or lowest ranks, may be distinguished by only one or two differences. Intensive study of the enteric bacteria has resulted in the use of minute differences to characterize the various subdivisions, but there remains a lack of uniformity of criteria used in characterization of the different ecological groups. Thus the plant pathogens have been studied along the time-honoured lines of morphology and fermentative ability with little study of their serology or of the characters revealed by the newer tests for deaminases and decarboxylases; the water bacteriologists have concentrated their attention on tests to distinguish between so-called 'faecal coli' and those forms believed to have a different source; while the clinical bacteriologists have, until recently, relied largely on antigenic analysis.

The Enterobacteriaceae Subcommittee (Report, 1954*a*) define the family as Gram-negative non-sporing rods, either motile with peritrichate flagella or non-motile, which grow on ordinary media and ferment glucose rapidly, with or without gas production; nitrates are reduced to nitrites. The Subcommittee (Report, 1954*a, b*) recognizes nine groups, *Salmonella*, *Shigella*, *Arizona*, *Escherichia*, *Alkalescens-dispar*, *Klebsiella*, *Bethesda*, *Proteus*, *Providence*, but does not imply that these should be regarded as genera. Kauffmann (1953) would make further subdivisions and add as groups, presumably of equivalent rank, *Cloaca*, *Morganella* and *Rettgerella*. Møller (1954) created another group which he named *Hafnia*. To these should be added *Erwinia* (and perhaps *Pectobacterium*) and the *Prodigiosus* group (reasons for not using the name *Serratia* are given in Cowan, 1956). Even these groups do not include all the enteric bacteria, and the common lactose-fermenting motile forms with IMViC reactions — — + +, which fail to liquefy gelatin, have no place in the scheme.

It seems to me that the 'groups' mentioned are not of equal taxonomic rank, and that it would be profitable to consider what rank should be accorded to each. With this in mind I have drawn up a table which shows the majority reactions of different groups in both the old and newer type of biochemical test (Table 1). Some of the 'groups' shown in Table 1 differ slightly from similar groups of the Enterobacteriaceae Subcommittee Reports; for example *Escherichia freundii* is shown separately and is not included with either the *Escherichia* group or the *Bethesda-Ballerup* group. In recording reactions the *Salmonella* group is shown as gas-producing; this is the reaction of the majority of serotypes, but of course it does not imply that all anaerogenic strains should be classified as *Salmonella typhi*. In the same way *Klebsiella pneumoniae* is shown as VP-positive, although a small proportion of strains is VP-negative.

Before discussing the groups in detail it will be convenient to fix the taxonomic rank of one, to which the others can be referred. *Escherichia*, which is based on *Escherichia coli*, would be the group of choice, but the picture is

Motility	Providence	+	d	+	-	d	-	d	-	-	(+)	+	-	*	-	+	+	+	-	-	+	+	d	-	+
Gas from glucose	<i>Proteus rettgeri</i>	+	-	+	+	+	+	-	+	+	d	+	-	*	-	d	+	+	-	-	+	+	+	-	+
Acid from glucose	<i>P. morganii</i>	+	+	+	+	-	-	-	-	-	-	+	+	+	+	+	+	+	(+)	-	+	+	+	-	+
Acid from mannitol	<i>P. mirabilis</i>	+	+	+	+	-	-	-	-	-	-	+	+	+	d	+	+	+	-	-	+	+	+	-	+
Acid from adonitol	<i>P. vulgaris</i>	+	+	+	+	-	-	-	-	+	+	+	+	+	+	+	+	+	-	-	+	+	d	-	+
Acid from dulcitol	Hafnia	+	+	+	+	-	-	-	-	d	x	-	-	+	+	+	-	+	+	(+)	+	+	+	+	-
Acid from inositol	Cloaca	+	+	+	+	d	-	-	d	(+)	+	+	+	*	-	d†	+	+	(+)	+	+	-	+	d	-
Acid from lactose	<i>K. pneumoniae</i>	-	+	+	+	+	d	+	+	+	+	-	-	*	-	+	+	+	+	-	-	+	+	+	-
Acid from sucrose	<i>K. rhinoscleromatis</i>	-	-	+	+	+	-	+	+	+	+	-	-	-	-	+	+	+	-	-	+	+	+	-	-
Indole	<i>Klebsiella ozaenae</i>	-	d	+	+	+	+	-	+	(+)	x	-	-	*	-	+	x	+	-	d	-	-	+	-	-
Gelatin liquefaction	Bethesda-Ballerup	+	+	+	+	-	d	x	x	d	d	-	-	+	+	+	x	+	-	+	d	-	+	+	-
H ₂ S produced	<i>Escherichia freundii</i>	+	+	+	+	-	d	x	+	d	d	-	-	+	+	+	+	+	-	+	-	+	+	d	-
VP	Other shigellas	-	-	+	d	-	d	-	-	-	-	d	-	-	-	+	+	+	+	+	+	-	-	-	-
MR	<i>Shigella sonnei</i>	-	-	+	+	-	-	-	(+)	-	(+)	-	-	*	-	+	+	+	(+)	+	+	+	-	-	-
Urease	A-D group	-	-	+	+	-	d	-	d	d	d	+	-	*	-	+	+	+	+	-	d	+	-	-	-
Nitrates reduced	<i>Escherichia coli</i>	+	+	+	+	-	d	-	+	d	d	+	-	*	-	+	+	+	+	+	d	+	-	-	-
Lysine decarboxylase	Arizona	+	+	+	+	-	-	-	(+)	-	-	-	(+)	+	+	+	+	+	+	+	+	-	+	+	-
Arginine decarboxylase	Other salmonellas	+	+	+	+	-	+	d	-	-	-	-	-	+	+	+	+	+	+	+	+	-	+	-	-
Ornithine decarboxylase	<i>Salmonella typhi</i>	+	-	+	+	-	x	-	-	-	-	-	-	+	+	+	+	+	+	+	-	-	-	-	-
Glutamic acid decarboxylase																									
Growth on KCN																									
Growth on Koser's citrate																									
Malonate																									
Phenylalanine																									

Reactions given are mainly based on Report (1954b), Kauffmann (1954), Edwards & Ewing (1955) and Møller (1954, 1955). Exceptions are *Klebsiella ozaenae*, *K. rhinoscleromatis*, and the decarboxylases of the A-D group, for which detailed descriptions were not found; the results recorded for these organisms are based on tests carried out in the National Collection of Type Cultures (NCTC) by Miss C. Shaw, who also supplied the results of the malonate and phenylalanine tests.

Notation used is that of Kauffmann, Edwards & Ewing (1956), viz. + = positive 1-2 days; (+) = delayed positive (3-4 days, occasionally later); x = late and irregularly positive or negative (mutative); - = negative; d = different strains, each consistent in itself, give different reactions (e.g. a single serotype may have strains giving +, (+), x or - reactions). Other symbols * = negative in ferrous chloride gelatin medium, positive when adequate sulphur source available (see Clarke, 1953); † = negative by Hormaeche's method at 45° (personal communication).

complicated by the fact that although the Enterobacteriaceae Subcommittee (Report, 1954*b*), Kauffmann (1954), and Edwards & Ewing (1955) separate *E. freundii* from the *Escherichia* group, they retain the generic name *Escherichia* for the species and thus make it appear that the group is an emasculated genus. I shall discuss the *Escherichia* group presently, and for the moment would prefer to fix the taxonomic rank of the *Salmonella* group. Most bacteriologists now look upon this group as a genus (see, for example, *Bergey's Manual*, 1948; *Topley and Wilson's Principles*, 1955), and it can, without difficulty, be given generic rank. Therefore, in the sequel, I shall assume that the *Salmonella* group forms the basis of a genus, *Salmonella*.

Salmonella and Arizona groups

In the *Salmonella* group *Salmonella typhi* is in a class of its own; its constant anaerogenic habit and its lack of ornithine decarboxylase distinguish it from the other motile salmonella species or serotypes. Most of the aerogenic salmonellas share a biochemical pattern; this is similar to that of Arizona strains, except that the latter liquefy gelatin, ferment lactose slowly, and do not ferment dulcitol. The malonate test distinguishes Arizona strains from the more typical salmonellas, but some gelatin-liquefying salmonellas (e.g. *S. dar-es-salaam*) are, like Arizona strains, malonate-positive (Shaw, 1956), and thus form a link. Antigenic overlapping is so great that *Salmonella* diagnostic antisera can be used as substitutes for many of the Arizona antisera (Edwards & Ewing, 1955). As Seligmann & Saphra (1951) and Edwards & Ewing (1955) pointed out, the allocation of some strains to *Salmonella* or Arizona is quite arbitrary, and the problem is to decide whether the Arizona group is equivalent in rank to *Salmonella* or only to part of *Salmonella*.

The Enterobacteriaceae Subcommittee Reports of 1950 and 1953 (Report 1954*a, b*) describe *Salmonella* and Arizona separately, and this arrangement is followed by Kauffmann (1954) and by Edwards & Ewing (1955). However, this usage has become established because it is more convenient to have two antigenic schemes than to combine them. It seems to me that in a systematic classification the Arizona group is equivalent only to a part of the *Salmonella* group, of which it should be regarded as a major subdivision, equivalent in rank, *vis à vis* other salmonellas, to *Salmonella typhi*, i.e. to a species. The species thus created, *Salmonella arizonae*, is divisible into the serotypes of the Arizona group.

The nomenclatural problems of *Salmonella* are complex. The name *Salmonella* received official recognition when the *Salmonella* Subcommittee was appointed (Report, 1937). The acceptance by the *Salmonella* Subcommittee (1934) of *S. cholerae-suis* as type species created difficulties that were not foreseen at the time. With increasing knowledge of the permutations and combinations of antigens of the group there is less willingness to regard each combination as a species; these are now viewed as serotypes of a relatively small number of species. Three solutions of the nomenclatural difficulty present themselves: (i) all aerogenic salmonellas can be named *S. cholerae-suis* and individuals distinguished by subspecific epithets or numbers; (ii) the aerogenic

salmonellas can be divided into two species as suggested by Borman, Stuart & Wheeler (1944) and by Kauffmann & Edwards (1952); (iii) each combination of antigens, or serotypes, can be given a common name, as *Salmonella* London. The difficulty arises because of the necessity to report *Salmonella* spp. or serotypes in such a way that their significance will be apparent to a number of people with different professional backgrounds. To a clinician the name *S. cholerae-suis* var. *paratyphi-B* would be extremely confusing, as would *S. cholerae-suis* var. *pullorum* to a veterinarian. Fortunately the needs of the clinician, veterinarian, medical officer of health, sanitary inspector and general practitioner can be met by the use of common rather than scientific names. This is in fact the procedure at present adopted, though the use of italic type and lower-case initial letter for the place name gives the false impression of a specific binomial. For the systematist the suggestions of Borman *et al.* (1944) and of Kauffmann & Edwards (1952) provide the better solution; in considering these proposals it should be borne in mind that the epithet *kauffmannii* has priority over *enterica*.

Escherichia and *Alkaescens-dispar* (A-D) groups

The *Escherichia* group, as defined in Enterobacteriaceae Subcommittee Reports, consists of organisms classified as *Escherichia coli* and its varieties, including *E. coli-mutabile* and anaerogenic strains. Although the fermentation of lactose is regarded as a main character of the species *E. coli* it is not requisite for inclusion in the *Escherichia* group (Kauffmann, 1954). Should *E. coli* be limited to strains which ferment lactose promptly, another species would have to be designated for the slow fermenters or non-fermenters of lactose that have other characters of the *Escherichia* group; such a species was defined and named *Paracolobactrum coliforme* by Borman *et al.* (1944).

The *Escherichia* group, based on *Escherichia coli* and including both lactose-fermenters and non-fermenters, clearly forms a group of rank equal to the salmonellas. It remains to be decided: (i) whether a species is justified for the late or non-lactose-fermenters; (ii) whether there are species from other groups to be transferred to the genus *Escherichia*.

Kauffmann (1954) would not exclude non-lactose fermenters from *Escherichia coli*, and indeed several strains of his serotypes do not ferment the sugar; the Enterobacteriaceae Subcommittee (Report, 1954*a, b*) also supports the inclusion of the non-lactose fermenting strains. At the present time there is not enough evidence that the lactose fermenters differ significantly from the non-fermenters to justify creating a species based on *Paracolobactrum coliforme* (Borman *et al.* 1944), but, as in all these problems, future work may demand a change in outlook.

A whole 'group' to be included in the genus *Escherichia* is the *Alkaescens-dispar* (A-D) group, composed of anaerogenic, non-motile organisms with O and K antigens of the *Escherichia* group. The recognition of one or two species within this group depends on the importance placed on lactose fermentation; *dispar* is a lactose-fermenter (prompt or delayed) and *alkaescens* does not ferment lactose, but there are many strains difficult to assign to one or other

species; it is, therefore, advisable to combine them, as in the Subcommittee's Reports. *Bacillus alkalescens* and *B. dispar* were both described and named in the same paper (Andrewes, 1918) and priority, decided by the order of their appearance, makes *alkalescens*, changed to *alkalescens* in conformity with the accepted views on transliteration, the correct specific epithet for the combined species. Information on the biochemical reactions of the A-D group is scanty, and I have not found a paper describing their decarboxylases; those observed in a limited number of strains by Miss C. Shaw are shown in Table 1. It is convenient to draw attention here to Sonne's bacillus (*Shigella sonnei*), the indole-negative biochemical counterpart of *Bacillus dispar*; its decarboxylases, except for a quantitative difference in lysine production, are the same as those of *Escherichia coli*, and differ from those of the other *Shigella* species or serotypes. The biochemical and serological characters of Sonne's bacillus are similar to those of the motile coliform C27 (Ferguson & Henderson, 1947; Schmid, Velaudapillai & Niles, 1954), and it seems logical that it should be regarded as an *Escherichia* species, but neither C27 nor Sonne's bacillus has any of the *Escherichia* O antigens 1-130 (Edwards & Ewing, 1955).

Thus, while the transfer of Sonne's organism to the genus *Escherichia* is logical and probably desirable systematically, it is hardly practicable as its membership of the *Shigella* group has become so firmly established. Furthermore, its inclusion in the genus *Escherichia* would be opposed by those who regard the *Shigella* group not as a bacteriological entity but as the dysentery group of bacteria (Bensted, 1956). However, if ever bacterial systematics are allowed to become logical, this is one of the transfers that could profitably be made, and I have made it in the systematic scheme at the end of this paper.

Shigella group

The other *Shigella* spp. form a homogeneous group related to the *Escherichia* group both by biochemical and serological reactions. Their decarboxylase activities are often weak, but the pattern of all shigellas, except Sonne's bacillus, is indistinguishable (Møller, 1954). Many shigella serotypes cross-react with *escherichia* antisera (Ewing, 1953; Edwards & Ewing, 1955) but the majority have, in addition, specific antigens by which they can be recognized, and which justify the genus *Shigella*. It is debatable whether *S. boydii* should be a distinct species or a variety of *S. flexneri*; the serotypes of *S. flexneri* are not biochemically homogeneous and except by serology cannot be distinguished from *S. boydii*; it is probably more systematic to recognize two varieties of *S. flexneri*, namely var. *flexneri* and var. *boydii*.

The removal of Sonne's bacillus from *Shigella* leaves that genus as a group of organisms divided biochemically into two subgroups, but this subdivision based on mannitol fermentation is not without exception; Ewing has found mannitol-fermenting strains of *S. dysenteriae* serotype 3, and non-mannitol-fermenting strains of *S. flexneri* serotypes 1-6, and of *S. boydii* serotypes 3 and 6 (Ewing, 1954; Edwards & Ewing, 1955). In a personal communication, Ewing suggests that any revision of shigella classification should combine all existing species.

The modification of the Enterobacteriaceae Subcommittee's (Report, 1954*a*) classification of shigellas proposed in the fourth edition of *Topley and Wilson's Principles* (1955) is likely to increase confusion; in this three species are recognized in the non-mannitol fermenting subgroup A, and one of them, the Large-Sachs group, is named *S. ambigua*, a name previously attached to Schmitz's bacillus.

Shigella nomenclature has been the subject of an Official Opinion (no. 11) of the Judicial Commission (1954). For the taxonomic scheme suggested here for systematists, there are only two species and Sonne's bacillus is translated to *Escherichia*. However, it is realized that neither clinicians nor clinical pathologists would welcome this improvement in its systematic position, and for their specialized use the name *S. sonnei* would be retained.

Bethesda-Ballerup and freundii group

The Enterobacteriaceae Subcommittee (Report, 1954*b*) regard the Bethesda group as the slow lactose-fermenting counterpart of the indole-negative cultures classified as *Escherichia freundii*, and include both lactose fermenters and non-fermenters in the 'Bethesda (Bethesda-Ballerup) group'. Kauffmann (1954) used the same arrangement but designated the group as a species, '*Escherichia freundii* (including Bethesda-Ballerup)'. The decarboxylases of the group are unlike those of the *Escherichia* group, and in these, as in the KCN test, the reactions of the group more closely resemble those of the *Klebsiella* group. The lactose fermenters form the two species *Citrobacter freundii* and *C. intermedium* (Werkman & Gillen, 1932), distinguished mainly by H₂S production; under suitable conditions both are H₂S-positive (Clarke, 1953) and I have combined them in Table 1. Antigenic overlapping between the *Escherichia* serotypes and *Escherichia freundii* seems to be unusual, but a Bethesda strain related to *Escherichia* serotype O111:B4 has been described (Ørskov, Schmid & Velaudapillai, 1953). Kauffmann (1954), in his table 1, shows *E. freundii* as a species of *Escherichia*, but in his table 3, which is based on the KCN test and decarboxylases, it is grouped with *Klebsiella*, *Cloaca* and *Hafnia*, all of which are KCN positive and can use citrate as a carbon source; in these characters they differ from *E. coli*. There seems to be good reason for including *E. freundii* in the Bethesda group, and for excluding the combined group from *Escherichia*, according it equal (i.e. generic) rank with that group (Kauffmann, 1953). This solution raises a minor problem of nomenclature best disposed of here: *E. freundii* is a synonym of *Citrobacter freundii* (Braak) Werkman & Gillen (1932), and this name antedates *Bethesda ballerupensis* Kauffmann & Edwards (1952) and *Bethesda freundii* (Kauffmann, 1953). Consequently, the generic name valid for the group is *Citrobacter* Werkman & Gillen, and the type species is *Citrobacter freundii*. The Bethesda-Ballerup organisms, which are slow or non-fermenters of lactose, could correctly be given the name *Citrobacter ballerupensis* Kauffmann & Edwards, nov. comb., although such a segregation of lactose fermenters and non-lactose fermenters is not consistent with the policy developed so far in this classification.

Klebsiella, Cloaca and Hafnia groups

The *Klebsiella* group is primarily divided by differences in the capsular antigens. Motile forms are excluded (Report, 1954*b*), but neither Kauffmann (1954) nor Edwards & Ewing (1955) regard this as a satisfactory solution of a difficult problem. Edwards & Fife (1955) found that 19 motile strains gave Quellung reactions with *klebsiella* antisera; 17 of these strains liquefied gelatin and all had the general biochemical reactions of the 128 motile strains studied. Edwards (Edwards & Ewing, 1955; Edwards & Fife, 1955) would redefine the genus *Aerobacter* with *Aerobacter cloacae* as the type species; I shall discuss this proposal presently.

If, for the moment, we restrict our consideration to the non-motile forms (i.e. the *Klebsiella* group of the ES reports) the majority of strains are aerogenic and have the IMViC reactions — — + +, but there is a sufficiently large proportion of anaerogenic strains, and strains with different IMViC reactions (Ørskov, 1955) to suggest that the group might be divided on the basis of these reactions. The aerogenic — — + + forms consist of strains which are typical of *Aerobacter aerogenes* and of Friedländer's bacillus (*Klebsiella pneumoniae*) and, as these cannot be distinguished either by biochemical or serological tests, (Report, 1954*b*) they are now usually considered together, often without species designation (Kauffmann, 1953, 1954; Edwards & Ewing, 1955; Edwards & Fife, 1955). It will be less confusing to say at once that if we accept the *Klebsiella* group as a genus, these aerogenic — — + + organisms form a species whose correct name is probably *Klebsiella pneumoniae-crouposae* (Zopf) nov.comb. (see Cowan, 1954) but which has become well established as *Klebsiella pneumoniae*, by which name I shall refer to it here.

Strains with other IMViC reactions are distributed among many capsule serotypes but are especially frequent in types 1, 2, 3, 4 and 5; Edwards & Fife (1955) found 81 of 173 strains of these serotypes were MR-positive, VP-negative, and of these 52 of 59 were types 4 and 5. It is not easy to determine from published data the distribution of anaerogenic strains among the different serotypes; for strains of known serotypes examined in this Collection (NCTC) the frequency was as follows:

Serotype	Aerogenic	Anaerogenic
1	9	2
2	15	3
3	7	6
4	17	3
5	8	0
6	9	0

Serotype 3 anaerogenic strains have other characters which segregate them from other *klebsiella* strains (Goslings, 1934), and these undoubtedly represent *Klebsiella rhinoscleromatis*, which can be described as citrate-negative, lactose-negative, malonate-positive and lysine-negative, whereas the aerogenic strains of type 3 are lactose-positive and lysine-positive.

Klebsiella ozaenae, represented by types D, E and F of Goslings & Snijders

(1936), or types 4, 5 and 6 in the newer terminology, are either aerogenic or anaerogenic, MR-positive, VP-negative, citrate-positive and malonate-negative.

The motile strains with IMViC reactions — — + + may or may not liquefy gelatin. In describing *Bacillus cloacae*, Jordan (1903) reported that all strains were actively motile, that most liquefied gelatin slowly, that 14 of 21 strains fermented lactose, but often this was slow. Kauffmann (1953, 1954) would resurrect the genus *Cloaca*, Castellani & Chalmers (1919), for these organisms, but Edwards & Fife (1955) prefer to redefine *Aerobacter*, basing it on a new type *A. cloacae*. Another possibility not considered by these authors is to make the motile forms, both liquefying and non-liquefying, a species of *Klebsiella*, i.e. *Klebsiella cloacae* (Jordan) nov.comb., and this is what I propose to do here. This has the advantage that motile and liquefying strains which react with klebsiella capsule antisera can be typed as *Klebsiella* species, whereas it would be confusing to describe a strain as *Cloaca cloacae* Klebsiella type X, or *Aerobacter cloacae* Klebsiella type Y. Unfortunately this kind of designation has sometimes to be made to describe certain antigenic overlaps, e.g. some strains of *Escherichia coli* have salmonella antigens.

Stuart's 32011 type (Stuart, Wheeler, Rustigian & Zimmerman, 1943; Stuart & Rustigian, 1943) forms part of the species *Paracolobactrum aerogenoides* (Borman *et al.* 1944) and falls within the *Hafnia* group of Møller (1954) with the type species *Hafnia alvei* (Bahr) Møller. These bacteria resemble *Klebsiella pneumoniae* in being IMViC — — + +, KCN-positive, malonate-positive and having a strong lysine decarboxylase; they differ in being motile, lactose-negative, urease-negative and having an ornithine and a weak arginine decarboxylase. They also resemble the *Cloaca* group (*K. cloacae*), of which they might be considered the non-lactose fermenting, gelatin-negative counterpart. Eventually the *Cloaca* and *Hafnia* groups may be combined, but for the moment I propose to regard *Hafnia* as a species of *Klebsiella*, with the name *K. alvei* (Bahr) nov.comb. Thus, I have arranged the motile — — + + forms in two species, *K. cloacae* and *K. alvei*, differing mainly on the fermentation of lactose. There are forms which are gelatin-positive and lactose-negative, by Jordan's circumscription these are regarded as *K. cloacae*, as are the gelatin-negative, lactose-positive motile forms. Consideration was given to the possibility of creating another species for the gelatin-negative, lactose-positive form but as the gelatin liquefaction test must have an arbitrary time limit and is greatly influenced by the type of gelatin used and the method of sterilization (Report, 1956*b*), such a new species would be based on much too flimsy grounds and there would be a likelihood that strains would drift from *K. cloacae* to the new species as they gradually lost their gelatin-liquefying power on subculture.

Proteus and Providence groups

Within recent years the genus *Proteus* has been defined with urease production as the main diagnostic character (Rustigian & Stuart, 1945; Cook, 1948). However, *Proteus* species are not the only members of the Enterobacteriaceae to produce urease; many strains of *Klebsiella* spp., and some strains of *Escherichia* and *Citrobacter* spp. are urease-positive. A more specific distinguishing

character is the ability of *Proteus* spp. to deaminate phenylalanine (Henriksen, 1950). The test, originally described by Henriksen & Closs (1938), is one of the simplest of biochemical tests and, among the Enterobacteriaceae, is positive only in the *Proteus* and *Providencia* groups.

Fulton (1943) proposed that Morgan's No. 1 bacillus should be made the type of a new genus *Morganella*, a suggestion repeated by Kauffmann (1953) together with the removal of Rettger's bacillus from *Proteus* and the creation of a new genus *Rettgerella*. Kauffmann (personal communication) still prefers to separate Morgan's and Rettger's bacilli from *Proteus*, but in his book (Kauffmann, 1954) he does not press this solution. Proom & Woiwod (1951) would not only remove Rettger's bacillus from *Proteus* but Proom (1955) would combine it with the *Providencia* group. On the other hand, several workers (Singer & Bar-Chay, 1954; Buttiaux, Osteux, Fresnoy & Moriamez, 1954; Shaw & Clarke, 1955) have pointed to the relation between *Providencia* and *Proteus* cultures, although only a few *Providencia* cultures are urease-positive. Buttiaux *et al.* (1954) and Shaw & Clarke (1955) made formal proposals that the *Providencia* group, which is the 29911 type of Stuart (Stuart *et al.* 1943; Stuart, Wheeler & McGann, 1946), should be included in the genus *Proteus*. Buttiaux *et al.* (1954) proposed the very appropriate name *P. stuartii*, but Shaw & Clarke (1955) found that a culture of *Bacillus inconstans* belonged to this group and this strain probably represented the oldest described species of what is now the *Providencia* group. The inclusion of the *Providencia* group in the genus *Proteus* subordinates the urease to the phenylalanine test, a test which, among the Enterobacteriaceae, is specific for the five species of *Proteus* as circumscribed here.

The *Prodigious* group consists of those peritrichously flagellated Gram-negative rods which produce a pink or red pigment; several species are described but the criteria on which species separation is made are of doubtful value. Dr E. Hormaeche drew my attention to the fact that in biochemical tests many of these organisms resemble the *Cloaca* group. Finally the plant pathogens have not been considered and have been left out of Table 1 as so little is known of their biochemical reactions; aerogenic strains have, in general, the characters of the *Cloaca* group, but the anaerobic strains are more distinctive.

CONCLUSIONS

This discussion of the classification and nomenclature of the enteric bacteria clearly shows that a logical and systematic classification would not adequately fill the needs of those who work with this group. These specialists are handling cultures sent to them by bacteriologists in certain applied fields, as clinical pathology and water bacteriology, and the reports of the specialists must be readily understood by an even greater variety of people, some of whom have little or no biological background. Thus, there is unfortunately a need for two classifications, one scientific, the other applied.

The taxonomic scheme on which a scientific classification is based is always subject to change as additional knowledge is gained, and this may be reflected

by changes in nomenclature. To the applied scientist such changes are anathema and it is, therefore, better that he should use a scheme that can easily be modified without a consequent change of nomenclature. This can be best done by using common (or vulgar) names for the bacteria being classified; unfortunately many of these common names have some semblance to the Linnaean binomials used in a systematic scheme. The simplest common nomenclature is based on aetiology or ecology, for example, 'the typhoid bacillus' or 'faecal-coli', but, except for pathogens, the plan rapidly breaks down. A compromise has to be made, as in the scheme for coliform bacteria (Report, 1956*a*) in which latinized binomials are used; some, as *Escherichia coli* and *Citrobacter freundii*, are nomenclaturally correct but others, as *Klebsiella aerogenes*, are a compromise between the usage of water bacteriologists and the correct *K. pneumoniae-crooposae*.

Most of this paper has been concerned with the scientific scheme which attempts to systematize the classification of these organisms, and this is summarized in the third column of Table 2. The other scheme must be a

Table 2. *Correlation of classification and nomenclature of: (1) reports of the Enterobacteriaceae Subcommittee; (2) a compromise scheme for applied bacteriology; (3) a scheme for the taxonomic purist*

E.S. Reports	Compromise scheme	Systematist's scheme
Salmonella	<i>Salmonella typhi</i> (typhoid bacillus) <i>S. cholerae-suis</i> (hog cholera bacillus) <i>S. typhi-murium</i> (mouse typhoid bacillus) Salmonella London	<i>Salmonella typhi</i> <i>S. cholerae-suis</i> <i>S. kauffmannii</i> var. <i>typhi-murium</i> <i>S. kauffmannii</i> var. London
Arizona	Arizona + serotype or antigenic formula	<i>S. arizonae</i> + serotype
Escherichia	<i>Escherichia coli</i>	<i>Escherichia coli</i>
Alcalescens-Dispar or A-D group	Alcalescens-dispar (or A-D) + serotype	<i>E. alcalescens</i>
Shigella	<i>Shigella sonnei</i> (Sonne's bacillus) <i>S. dysenteriae</i> { Shiga's bacillus Schmitz's bacillus Large-Sachs' bacilli } <i>S. flexneri</i> (Flexner's bacilli) <i>S. boydii</i> (Boyd's bacilli)	<i>E. sonnei</i> <i>Shigella dysenteriae</i> <i>S. flexneri</i> var. <i>flexneri</i> <i>S. flexneri</i> var. <i>boydii</i>
Bethesda	<i>Bethesda ballerupensis</i> }	<i>Citrobacter freundii</i>
Escherichia freundii	<i>Citrobacter freundii</i> }	
Klebsiella	<i>Klebsiella pneumoniae</i> <i>Klebsiella</i> + serotype <i>K. aerogenes</i> (water bacteriology)	{ <i>Klebsiella pneumoniae</i> <i>K. rhinoscleromatis</i> <i>K. ozaenae</i>
Cloaca	<i>Cloaca cloacae</i>	<i>K. cloacae</i>
Hafnia	<i>Hafnia alvei</i> or 32011 group	<i>K. alvei</i>
Proteus	<i>Proteus vulgaris</i> <i>P. mirabilis</i> <i>P.morganii</i> (Morgan's bacillus) <i>P. rettgeri</i> (Rettger's bacillus)	<i>Proteus vulgaris</i> <i>P. mirabilis</i> <i>P.morganii</i> <i>P. rettgeri</i>
Providence	Providence + serotype or 29011 group	<i>P. inconstans</i>

compromise and need not be good systematics. Although it would be difficult to improve on the detail of its Reports (1954*a, b*), the Enterobacteriaceae Subcommittee has never published a comprehensive classification. The first column of Table 2 shows the groups of the E.S. Reports, and the second column shows a slight re-arrangement which occupies, I think, a position midway between the working groups of the Subcommittee and the systematist's genera and species. Thus, in the compromise scheme, organisms of the Salmonella group would be known and reported as *Salmonella typhi*, *S. paratyphi-B*, or *Salmonella* London, the last preferably with an initial capital for the place name and printed in roman. Until the antigenic scheme for the Arizona group is fully integrated with the Salmonella group it will be convenient to retain the two. The only major divergence from the nomenclature used by the E.S. Reports concerns the subgroup named *Escherichia freundii*; these organisms are clearly different from the *E. coli* and it would be wiser to adopt now the nomenclaturally correct, *Citrobacter freundii*. In the Klebsiella group, a subgroup or species *Klebsiella aerogenes* is suggested for organisms isolated by water bacteriologists, who would create considerable confusion and dismay among the public if they reported a human pathogen (*K. pneumoniae* or Friedländer's bacillus) in a potable water supply. The Cloaca and Hafnia groups are not further subdivided, and, in this scheme, Providence is separated from Proteus.

Applied bacteriologists are not willing to be treated as chaff and blown hither and thither at every change in taxonomic breeze, and it is our duty to recognize them as the producers of seed which provides us, the taxonomic purists, with our plants for further study.

This paper owes any merits it possesses to a series of discussions with many bacteriologists, to all of whom I want to express my thanks; they include Lt.-Col. H. J. Bensted, Brigadier J. S. K. Boyd, Dr R. E. Buchanan, Dr K. P. Carpenter, Dr P. R. Edwards, Dr W. H. Ewing, Dr E. Hormaeche, Dr F. Kauffmann, Miss Constance Shaw, Dr Joan Taylor, Dr E. Windle Taylor and Dr G. S. Wilson. For the views expressed here I am alone responsible.

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(Received 20 April 1956)