WHO Collaborating Centre for Reference and Research on *Salmonella*

ANTIGENIC FORMULAE OF THE *SALMONELLA* SEROVARS

2007

9th edition

Patrick A.D. Grimont & François-Xavier Weill
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WHO Collaborating Centre for Reference and Research on Salmonella
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Role of the WHO Collaborating Centre for Reference and Research on Salmonella (WHOCC-Salm)

WHOCC-Salm is expected to provide the following service:

- Updating the Salmonella serotyping scheme (antigenic factors and serovar nomenclature)
- Technical support for Salmonella National Reference Centres (unusual antigenic structures or biochemical features)
- Updating protocols for the production of antisera
- Research activities on Salmonella (molecular methods for the identification of serovars)
- Contribution to the WHO surveillance program (recommendations, training, participation to Global Salm-Surv)

The historical role of WHOCC-Salm has been to maintain the comprehensive list of known Salmonella serovars. Since the creation of the Salmonella International Centre by Thorwald Madsen, Chairman of the Hygiene Committee of the League of Nations, the following scientists were in charge:

- F. Kauffmann (Statens Serum Institut, Copenhagen, Denmark) : 1934-1965
- L. Le Minor (Institut Pasteur, Paris) : 1965-1989
- M.Y. Popoff (Institut Pasteur, Paris) : 1989-2003

The first publication of the Kauffmann-White scheme (Salmonella Subcommittee, 1934, J. Hyg. 34 :333-350) listed 44 serovars. When F. Kauffmann retired (1964), the scheme contained 958 serovars. L. Le Minor published an annual supplement in the Annales de l’Institut Pasteur which became Research in Microbiology. When L. Le Minor retired, there were 2267 serovars and when M.Y. Popoff left, there were 2555 serovars.

Since L. Le Minor described most of the presently known serovars, we propose to designate the list of antigenic formulae (formerly known as “Kauffmann-White scheme”) as White-Kauffmann-Le Minor scheme.

Validation of new serovars is done at WHOCC-Salm (Institut Pasteur) in collaboration with laboratories in Hamburg (Institut für Hygiene und Umwelt, J. Bockemühl, S. Aleksic, and P. Roggentin) and Atlanta (Centers for Disease Control, F.W. Brenner, L. Gheesling, P. Fields, and M. Mikoleit). Serovars are homologated when these three laboratories agree on their validation.

This scheme which summarizes antigenic formulae of all known Salmonella serovars, is intended for National Reference Centres and other laboratories where all agglutinating sera are available. It is a reference document. Beware of non-authorized copies or translations with a modified content.
We recommend that National Reference Centres make available to local laboratories a simplified scheme limited to the most prevalent serovars in their countries. About 30 serovars may account for more than 90% of *Salmonella* isolates in a given country.

**Acknowledgements**

We thank our above-mentioned colleagues from Hamburg and Atlanta for their fruitful collaboration. Special thanks are due to Martine Guibourdenche for her precise work and the preparation of this document.
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**White-Kauffmann-Le Minor scheme**  

**Alphabetic list of names given to serovars of *S. enterica* subspecies *enterica* with their antigenic formulae**  

**Alphabetic list of serovar names withdrawn from the scheme**
Taxonomy and nomenclature of the genus *Salmonella*


These species and subspecies can be distinguished on the basis of differential characters (table below).

Before the taxonomy of the genus *Salmonella* was established on scientific basis, *S. enterica* subspecies were considered as subgenera and serovars were treated as species. Thus, there were subgenera I (*S. enterica* subsp. *enterica*), II (*S. enterica* subsp. *salamae*), III (former genus Arizona; subdivided in IIIa, *S. enterica* subsp. *arizonae*, and IIIb, *S. enterica* subsp. *diarizonae*), IV (*S. enterica* subsp. *houtenae*), V (*S. bongori*), and VI (*S. enterica* subsp. *indica*).

The way serovars were designated evolved with time. Some serovar names denoted syndrome (*S. typhi*) or relationship (*S. paratyphi* A, B, C). Other names were correlated with syndrome and host specificity which was right in some cases (*S. abortus-ovis, S. abortus-equus*) or wrong in other cases (*S. typhi-murium, S. cholerae-suis*). To avoid possible sources of confusion, names indicating geographical origin of the first strain of a new serovar (*S. london, S. panama, S. telekebir*) were then used. At the International Congress of Microbiology held in Moscow ([Int. J. Syst. Bacteriol.], 1968., 18, 191-196), it was decided that compound names would be hereafter condensed in simple names (*S. typhimurium, S. choleraesuis, S. telekebir*). These names, wrongly considered as species names, were for this reason italicized. They are in fact without taxonomic status, used to name bacteria frequently isolated in human or veterinary medicine. In other bacterial species (*Escherichia coli*, for example) names have not been given to serovars which are only designated by their antigenic formula. However, names of the most frequently encountered *Salmonella* serovars are so familiar that it would be unrealistic to suppress these names and to substitute their antigenic formula. Names were maintained only for subspecies *enterica* serovars which account for more than 99.5% of isolated *Salmonella* strains. These names must no longer be italicized. The first letter is a capital letter. In practice, for *S. enterica* subsp. *enterica*, the subspecies name (subsp. *enterica*) does not need to be indicated as only serovars of this subspecies bear a name. Serovars of other subspecies of *S. enterica* and those of *S. bongori* are designated only by their antigenic formula. Therefore, the following examples are correct: *S. enterica* subsp. *enterica* serovar Typhimurium, or *S. enterica* serovar Typhimurium, or *Salmonella* ser. Typhimurium. Designations such as *S. Typhimurium* or S.I, S.II, S.IIIa, S.IIIb, S.IV, S.VI should be limited to laboratory notebooks since abbreviation (S.) of a genus name (*Salmonella*) cannot stand alone without being followed by a specific epithet (*S. enterica*).
### Differential characters of *Salmonella* species and subspecies

<table>
<thead>
<tr>
<th>Species</th>
<th><em>S. enterica</em></th>
<th><em>S. bongori</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Subspecies</strong></td>
<td><em>enterica</em></td>
<td>salamae</td>
</tr>
<tr>
<td><strong>Characters</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dulcitol</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>ONPG (2 h)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Malonate</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Gelatinase</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Sorbitol</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Growth with KCN</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>L(+)-tartrate&lt;sup&gt;(a)&lt;/sup&gt;</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Galacturonate</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>γ-glutamyltransferase &lt;sup&gt;(*)&lt;/sup&gt;</td>
<td>+&lt;sup&gt;(*)&lt;/sup&gt;</td>
<td>–</td>
</tr>
<tr>
<td>β-glucuronidase</td>
<td>d</td>
<td>d</td>
</tr>
<tr>
<td>Mucate</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Salicine</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Lactose</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Lysed by phage O1</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

**Usual habitat**

- Warm-blooded animals
- Cold-blooded animals and environment

---

<sup>(a)</sup> = *d*-tartrate.

<sup>(*)</sup> = Typhimurium d, Dublin –.

+ = 90% or more positive reactions.

– = 90% or more negative reactions.

d = different reactions given by different serovars.

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### Changes in serovar nomenclature

Some names appearing in previous editions of the scheme were deleted:

- those given to variants converted by lysogenization: *e.g.*, Newhaw is now called Muenster var. 15<sup>+</sup>, Arkansas is now called Muenster var. 15, 34, as they correspond to variants of serovar Muenster converted by phage ε₁₅ or by phages ε₁₅+ε₃₄, respectively. The position of these converted variants is essentially the same as the position of group O:4 (B) strains which express after conversion, factor ₁ and for which no new name had been proposed.

- those given before 1966 to serovars later found not to belong to subspecies *enterica*.

These names, suppressed from the scheme, are listed in appendix II. These names have only a historic interest. This appendix also lists the names of serovars which have been combined with serovars kept in the scheme. For example, Pullorum is considered as one among the biovars of serovar Gallinarum (identical 1,9,12:–:– formula).
Designation of the O groups.

Historically, O groups were first designated by letters. Since there were not enough letters, it was necessary to continue with numbers 51 to 67. It is now more logical to designate each O group using the characteristic O factor. Letters are provisionally kept into brackets. Ex. O:4 (B); O:18 (K). It is advisable to abandon designation-by-letter which is unnecessary.

Old and new designations:

<table>
<thead>
<tr>
<th>Old</th>
<th>New</th>
<th>Old</th>
<th>New</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2</td>
<td>G₁-G₂</td>
<td>13</td>
</tr>
<tr>
<td>B</td>
<td>4</td>
<td>H</td>
<td>6,14</td>
</tr>
<tr>
<td>C₁-C₄</td>
<td>6,7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C₂-C₃</td>
<td>8</td>
<td>I</td>
<td>16</td>
</tr>
<tr>
<td>D₁</td>
<td>9</td>
<td>J</td>
<td>17</td>
</tr>
<tr>
<td>D₂</td>
<td>9,46</td>
<td>L</td>
<td>21</td>
</tr>
<tr>
<td>D₃</td>
<td>9,46,27</td>
<td>M</td>
<td>28</td>
</tr>
<tr>
<td>E₁-E₂-E₃</td>
<td>3,10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E₄</td>
<td>1,3,19</td>
<td>O</td>
<td>35</td>
</tr>
<tr>
<td>F</td>
<td>11</td>
<td>P</td>
<td>38</td>
</tr>
<tr>
<td>Q</td>
<td>39</td>
<td></td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S</td>
<td>41</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>42</td>
<td></td>
<td></td>
</tr>
<tr>
<td>U</td>
<td>43</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>44</td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>47</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Y</td>
<td>48</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Z</td>
<td>50</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Case of factor O:27 in group O:4

Production of factor O:27 in group O:4 was thought to be determined by a converting phage. Therefore, in 1983, several pairs of serovars differing only by the presence of factor O:27 were combined into single serovars. Reeves and coworkers (J Bacteriol. 2002. 184:1669-1677) showed that production of factor O:27 is in fact due to gene *wzy*ₐₕₐₜ, located within the major O-antigen cluster on the bacterial chromosome. To take this into account, we suppressed underlining for this factor and provisionally print factor O:27 into brackets – [27] – to indicate variability when a named serotype includes both formulae (with and without O:27). Population genetic methods will be used before any further revision of the antigenic formula nomenclature associated with factor O:27.

Case of group O:54

Heterogenous group O:54 is provisionally kept. It has been demonstrated that O factor 54 is plasmid-determined in 8 serovars. If the plasmid is lost, factor O:54 is no longer expressed (Ann. Inst. Pasteur, 1985, 136 B, 169-179). The serovars listed below may be considered:

- Tonev as a variant 54⁺ of Minnesota
- Winnipeg as a variant 54⁺ of Ferruch
- Poeseldorf as a variant 54⁺ of Kentucky
- Ochsenwerder as a variant 54⁺ of Thompson
- Steinwerder as a variant 54⁺ of Orion var. 15⁺
- Canton as a variant 54⁺ of Hadar
- Barry as a variant 54⁺ of Mbandaka
- Newholland as a variant 54⁺ of Banana

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Otherwise the formula of Uccle (3,54:g,s,t-) corresponds to the formula of an undescribed serovar 3...g,s,t-. As Orion var 15+, Steinwerder can express both factors 34 and 12, after conversion by phage ε14.

**Flagellar (H) antigens of the e,n,x/e,n,z15 complex**

**Composition of H antigens e,n,x and e,n,z15**

<table>
<thead>
<tr>
<th>Salmonella</th>
<th>H formula in scheme</th>
<th>Actual H factors</th>
<th>Factor x present</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. enterica</em> subsp. <em>enterica</em></td>
<td>e,n,x</td>
<td>e,n,x,z16</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>e,n,x</td>
<td>e,n,x,z17 (very rare)</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>e,n,z15</td>
<td>e,n,z15,z17</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>e,n,x,z15</td>
<td>e,n,z15,z16</td>
<td>-</td>
</tr>
<tr>
<td><em>S. enterica</em> subsp. <em>salamae</em></td>
<td>e,n,x</td>
<td>e,n,z16</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>e,n,z15</td>
<td>e,n,z15,z17</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>e,n,x,z15</td>
<td>e,n,z15,z16</td>
<td>-</td>
</tr>
<tr>
<td><em>S. enterica</em> subsp. <em>diarizonae</em></td>
<td>e,n,x</td>
<td>e,n,z16</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>e,n,x,z15</td>
<td>e,n,z15,z16</td>
<td>-</td>
</tr>
<tr>
<td><em>S. enterica</em> subsp. <em>houtenae</em></td>
<td>e,n,x</td>
<td>e,n,x,z17</td>
<td>+</td>
</tr>
<tr>
<td><em>S. enterica</em> subsp. <em>indica</em></td>
<td>e,n,x</td>
<td>e,n,x,z17</td>
<td>+</td>
</tr>
<tr>
<td><em>S. bongori</em></td>
<td>e,n,z15</td>
<td>e,n,z15,z17</td>
<td>-</td>
</tr>
</tbody>
</table>

Most e,n,x phases of *S. enterica* subsp. *enterica* (subspecies I) strains contain both factors x and z16, and their formula is in fact e,n,x,z16. Exceptionally, e,n,x phases can occur without z16 and with z17. In contrast, factor x never occurs in strains of subspecies *salamae* (II) and *diarizonae* (IIIb) even if the WKLM scheme indicates e,n,x or e,n,x,z15. The so-called factor x in their formula is in fact z16.

All e,n,z15 phases have, in addition, factor z17. Factor z17 never occurs with e,n,x,z15 (which is in fact, e,n,z15.z16).

**Differential characters of serovars having the same global antigenic formula**

Historically, different names have been given to serovars having the same antigenic formula and differing by either biochemical characters, pathogenicity, or habitat.
**Differentiation of serovars with formula 6,7:c:1,5 (Table below)**

<table>
<thead>
<tr>
<th></th>
<th>Dulcitol</th>
<th>H₂S</th>
<th>Mucate</th>
<th>Agglutination of H:c in sera</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S1</td>
</tr>
<tr>
<td>Paratyphi C (Vi⁺ or Vi⁻)</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Choleraesuis</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Choleraesuis var. Kunzendorf</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Choleraesuis var. Decatur</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Typhisuis</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

S1 = Serum anti-Choleraesuis var. Decatur absorbed with Choleraesuis var. Kunzendorf.
S2 = Serum anti-Choleraesuis var. Decatur absorbed with Paratyphi C.
S3 = Serum anti-Choleraesuis var. Decatur absorbed with Choleraesuis.

Typhisuis is a serovar adapted to pigs. Colonies are small. Dulcitol, L+(= d)tartrate negative in contrast to the four other serovars.


**Differentiation of serovars with formula 1,9,12:a:1,5**

Serovars Miami and Sendai are both kept in this scheme because they might be different. Biochemical characters formerly used for their differentiation (xylose, arabinose, rhamnose, H₂S) can only be used to define biovars. The differentiation is now based on an essential character: Sendai, which is adapted to man, is auxotrophic, i.e. does not grow on a minimal medium with glucose or on Simmons's citrate agar. On the contrary, Miami, which is ubiquitous, is prototrophic, i.e. grows on such minimal media.

**Differentiation of serovars with formula 4,12:a:1,5**

Serovars Hessarek (4,12,27 :a :1,5) and Fulica (4,[5],12 :a :[1,5]), which formula could be similar, are not combined because they differ by biochemical characters. Rhamnose, gas production from glucose, dulcitol, trehalose, Simmons citrate, L(+) tartrate (= d-tartrate), mucate, H₂S, and tetrathionate-reductase are positive for Hessarek and negative for Fulica. This latter serovar is very rare.
Presentation of the scheme. Symbols

In the first column of the table, are reported:

- the name of the serovar for *S. enterica* subsp. *enterica*;

- for other subspecies of *S. enterica*, the subspecies to which belongs the serovar is indicated by the following symbol:
  - II for serovar of *S. enterica* subsp. *salamae*
  - IIIa for serovar of *S. enterica* subsp. *arizonae*
  - IIIb for serovar of *S. enterica* subsp. *diarizonae*
  - IV for serovar of *S. enterica* subsp. *houtenae*
  - VI for serovar of *S. enterica* subsp. *indica*

- for serovars of *S. bongori*, symbol “V” was retained to avoid confusion with serovar names of *S. enterica* subsp. *enterica*.

The subfactors of O factors 40, 47, 48 and 50 are no longer mentioned as their identification is unnecessary in current practice. O and H factors having the same symbol in the White-Kauffmann-Le Minor scheme are always related, but not always identical in different serovars. This table of antigenic formulae is a scheme designed for identification purposes. Details that are unnecessary for the identification of serovars are not given in this scheme.

___ = Underlined O factors are determined by phage conversion (e.g. 6,14,18). They are present only if the culture is lysogenized by the corresponding converting phage. These factors are added to the factors present in non-converted strain (for example 6,7 → 6,7,14) except in group O:3,10 (see below). These underlined factors are mentioned in the table for serovars in which they were found. It is probable that this situation may be encountered for all serovars in the same O group.

{} = O-factors indicated in curly brackets are exclusive. In a given serovar, factors in curly brackets cannot coexist with other factors in curly brackets. Some factors may be phage-determined (underlined). In group O:3,10, factors O:15 or O:15,34, when present, replace O:10. To indicate this fact, the following symbols are used, O:3,{10},{15},{15,34}.

[ ] = O (not underlined) or H factor that may be present or absent without relation to phage conversion. Example: factor [5] of group O:4 (B). When H factors are in square brackets, this means that they are exceptionally found in wild strains. For example, most strains of Paratyphi A possess a monophasic antigen phase 1 (a). In rare cases, diphasic strains with phase 2 H:1,5 may be isolated. For this reason, [1,5] is mentioned in square brackets in the formula of this serovar.

( ) = O or H factor weakly agglutinable. H factor k, in *S. enterica* subsp. *arizonae*, is weakly agglutinable by the standard k serum (prepared against *S. enterica* subsp. *enterica*), but is normally agglutinable by polyvalent k serum (see "Guidelines for the preparation of *Salmonella* antisera").

Groups formerly called C_1 (O:6,7,14), E_2 (O:3,15), and E_3 (O:3,15,34) contained respectively serovars of group C_1 lysogenized by phage 14 (O:6,7 → O:6,7,14), and serovars of groups E_1,

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lysogenized by phage $\varepsilon_{15}$ (O:3,10 $\rightarrow$ O:3,15), or by phages $\varepsilon_{15}$ and $\varepsilon_{34}$ (O:3,10 $\rightarrow$ O:3,15,34). Serovars of these groups are included in group O:7 (C₁) and O:3,10 (E₁).

Presence or absence of accessory O factors (underlined or in square brackets) does not interfere with serovar identification. These factors are only interesting as epidemiological markers within a given serovar.

Lower case letter "l" and number "1" are difficult to distinguish in print. Associated with another letter, it is letter "ell" (e.g. l,w). When associated with a number, it is number "one" (ex. 1,2).

**Designation of "R phases" of H antigens.**

These "abnormal" specificities of H antigens described by Kauffmann and first reported by him for Typhi (Z. Hyg., 1936, 119, 103) were designated by R followed by the factor symbol, e.g. $R_j$ for Typhi, $R_{z_{66}}$ for Muenchen. The genetic basis of these « R phases » is only known in a few cases. Factor $j$ is the product of gene $fliC-j$ which is Typhi $fliC-d$ with a 261-nucleotide deletion. Factor $z_{66}$ of Typhi is an additionnal phase (coded by neither $fliC$ nor $fljB$) the gene of which is on a plasmid (Baker, S. et al., 2007, PLoS Pathogens, 3 :e59). In the scheme, three columns are now devoted to H antigens, and R phases and third phases are given in the third column. Since many R phases are agglutinable by anti-1,2 - 1,5 - 1,6 - 1,7 sera but not by anti-2 - 5 - 6 - 7 sera, these are now all designated by $R_1$. The subdivision $R_1,10$ - $R_1,11$ ... is no longer used, being of little interest.

"R phases" of H antigens are uncommon. Their identification is usually done only by Reference Centres. However, corresponding antisera are useful for phase inversion.

**Information and references concerning the first isolation of each serovar.**

They were collected in two books by E. Kelterborn:

Present number of serovars in each species and subspecies

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<th>Species</th>
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<td><strong>Total (genus Salmonella)</strong></td>
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WHITE-KAUFFMANN-LE MINOR SCHEME

ANTIGENIC FORMULAE
VALIDATED AS OF JANUARY 1st, 2007
# Group O:2 (A)

<table>
<thead>
<tr>
<th>Type</th>
<th>Somatic (O) antigen</th>
<th>Flagellar (H) antigen</th>
<th>Phase 1</th>
<th>Phase 2</th>
<th>Other</th>
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**Group O:4 (B)**

Presentation of factor O:27 was modified. See page 8.

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1. Rhamnose, gas from glucose, dulcitol, trehalose, Simmons citrate, L(+) tartrate (= d-tartrate), mucate, H_2S, and tetrathionate-reductase : + for Hessarek, – for Fulica. This latter serovar is very rare.

2. L(+) tartrate (= d-tartrate) positive variant is often referred to as var. Java.

3. Gelatinase +, dulcitol –.

4. R1... : R phases agglutinated by anti-1,2 - 1,5 - 1,6 - 1,7 sera and not by anti-2 - 5 - 6 - 7 sera.
Group O:7 (C₁)

Strains in this group can be lysogenized by phage 14 (O:6,7 —> O:6,7,14, former group C₄).

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<th>Type</th>
<th>Somatic (O) antigen</th>
<th>Flagellar (H) antigen</th>
<th>Phase 1</th>
<th>Phase 2</th>
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1. See table "Differential characters of serovars having the same global antigenic formula" (chapter Taxonomy and nomenclature of the genus *Salmonella*).

2. Plasmid-controlled factor O:54 may occur and mask factors O:6,7,14.

3. R1... : R phases agglutinated by anti-1,2 - 1,5 - 1,6 - 1,7 sera and not by anti-2 - 5 - 6 - 7 sera.
**Group O:8 (C\textsubscript{2}-C\textsubscript{3})**

Groups O:6,8 (C\textsubscript{2}) and O:8 (C\textsubscript{3}) which differed only by the presence or absence of factor O:6, were lumped together in a single group O:8.

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1 R1...: R phases agglutinated by anti-1,2 - 1,5 - 1,6 - 1,7 sera and not by anti-2 - 5 - 6 - 7 sera.
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1. Sendai (adapted to man) is auxotrophic, Miami is prototrophic.

2. Rare strains can have, as phase 1, H :j instead of H :d (261-nucleotide deletion in gene fliC). Independently, rare strains can have an additional phase H :z66 determined by a plasmid-borne gene.

3. In addition to factors H:g,ln, some strains may have factor H:p or H:f or H:t. Exceptional strains can have antigen H:1,7 as second phase.

4. R1…: R phases agglutinated by anti-1,2 - 1,5 - 1,6 - 1,7 sera and not by anti-2 - 5 - 6 - 7 sera.
Group O:9,46 (D$_2$)

In this group, strains also have factors O:3 and (O:10), the latter being weak. They can be lysogenized by phages $\varepsilon_{15}$ and $\varepsilon_{34}$. When doubly lysogenized, they become strongly agglutinable (like group E strains) by sera O:34 and O:12$_2$.

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### Group O:9,46,27 (D₃)

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**Group O:3,10 (E₁)**

In this group, strains can be lysogenized by phage ε₁₅ (O:3,10 —–> O:3,1₅, former group E₂) then by phage ε₃₄ (O:3,1₅ —–> O:3,1₅,3₄, former group E₃). **In these cases, factors O:1₅ or O:1₅,3₄ replace factor O:1₀ which is no more detected.** Factors O:1₀, O:1₅ and O:1₅,3₄ are given in curly brackets {} to indicate exclusivity. Factors O:1₅ and O:1₅,3₄ are given in the scheme when occurring naturally.

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1 R1...: R phases agglutinated by anti-1,2 - 1,5 - 1,6 - 1,7 sera and not by anti-2 - 5 - 6 - 7 sera.

### Group O:54

This classification is provisional (see page 8).

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\(^1\) Factor O:54 is plasmid-controlled. In serovar Montevideo, factors O:6,7,14 are expressed in the absence of O:54.
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1 R1…: R phases agglutinated by anti-1,2 - 1,5 - 1,6 - 1,7 sera and not by anti-2 - 5 - 6 - 7 sera.
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Abaetetuba 11  
Aberdeen 11  
Abidjan 39  
Ablogame 16  
Abobo 16  
Abony 1,4,[5],12,27  
Abortusequi 4,12  
Abortusovis 4,12  
Abuja 11  
Accra 1,3,19  
Ackwepe 9,46  
Adabraka 3,10  
Adamstown 28  
Adamstua 11  
Adana 43  
Adelaide 35  
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Aderike 28  
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Adjame 13,23  
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| Maastricht         | 11|    |     | z_41|     |     |     |     | 1,2 |     |     |     |     |     |     |     |
| Macallen           | 3 | 10|     | z_36|     |     |     |     |     |     |     |     |     |     |     |     |
| Macclesfield       | 9 | 46|     | g   | m   | s   |     |     | 1,2 | 7   |     |     |     |     |     |     |
| Machaga            | 1 | 3 | 19  | i   |     |     |     |     | e   | n   | x   |     |     |     |     |
| Madelia            | 1 | 6 | 14 | 25  | y   |     |     |     | 1,7 |     |     |     |     |     |     |
| Madiago            | 1 | 3 | 19  | c   |     |     |     |     | 1,7 |     |     |     |     |     |     |
| Madigan            | 44|    |     | c   |     |     |     |     |     | 1,5 |     |     |     |     |     |
| Madison            | 21|    |     | d   |     |     |     |     |     |     |     |     |     |     |     |
| Madjorio           | 3 | 10|     | d   |     |     |     |     |     |     |     |     |     | e   | n   | z_15|     |
| Madras             | 4 | 5 | 12  | m   | t   |     |     |     |     |     |     |     |     |     |     |     |
| Magherafelt        | 8 | 20|     | i   |     |     |     |     | l   | w   |     |     |     |     |
| Magumeri           | 1 | 6 | 14 | 25  | e   | h   |     |     |     |     |     |     |     |     |     |     | 1,6 |     |</p>
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ALPHABETIC LIST OF SEROVAR NAMES WITHDRAWN FROM THE SCHEME

(Symbols: =, identical to … ; =>, combined with …)
Abortusbovis => Abony
Abortuscanis => Paratyphi B
II Acres = II 1,13,23:b:[1,5]:z_{42}
II Alexander = II 3,10:z:1,5
II Alsterdorf = II 1,40:g,[m],[s].t:[1,5]
II Angola = II 1,9,12:z:z_{6}
Anie => Mesbit
Ardwick = Risen var. 14^{*}
IV Argentina = IV 6,7:z_{36}:-
Arkansas = Muenster var. 15^{*},34^{*}
II Artis = II 56:b:[1,5]
II Askraal = II 51:l,z_{28}:z_{6}
Atherton = Waycross
Atlanta => Mississippi
II Atra = II 50:m,t:z_{6}:z_{42}
II Bacongo = II 6,7:z_{36}:z_{42}
V Balboa = V 48:z_{41}:-
Bambesa => Miami
Bantam = Meleagridis
II Baragwanath = II 6,8:m,t:1,5
II Basel = II 58:1,z_{13},z_{28}:1,5
Batavia = Lexington
II Bechuana = 1,4,12,27:g,[m].t:[1,5]
II Bellville = II 16:e,n,x:1,(5),7
II Beloha = II 18:z_{36}:-
IV Bern = IV 40:z_{4},z_{52}:-
II Betioky = II 59:k:z_{65}
II Biltoven = II 47:a:1,5
Binza = Orion var. 15^{*}
II Blankenese = II 1,9,12:b:z_{6}
II Bleadon = II 17: g.t: [e, n, x, z₁₅]
II Bloemfontein = II 6,7: b: e, n, x: z₄₂
IV Bockenheim = IV 1,53: z₃₆, z₃₈:
II Boksburg = II 40: g, m, s, t: e, n, x
IV Bonaire = IV 50: z₄, z₃₂:
V Bongor = V 48: z₃₅:
VI Bornheim = VI 1,6,14,25: z₁₆, 1, (2), 7
Bornum = Lille var. 14⁺
II Boulders = II 1,13,23: m, t: z₄₂
II Bremen = II 45: g, m, s, t: e, n, x
V Brookfield = V 66: z₄₁:
Broxbourne = Wien
Buenosaires = Bonariensis
II Bulawayo = II 1,40: z: 1,5
II Bunnik = II 43: z₄₂: 1,5, 7
Cairo => Stanley
II Caledon = II 1,4,12, 1, 22: g, [m], [s], t: e, n, x
II Calvinia = II 6,7: a: z₄₂
Cambridge = Meleagris var. 15⁺
V Camdeni = V 44: r: -
II Canastel = II 9,12: z₅₀, 1, 5
Canoga = Westhampton var. 15⁺, 34⁺
II Cape = II 6,7: z₆, 1, 7
Cardiff => Thompson
II Carletonville = II 38: d: [1, 5]
II Ceres = II 28: z: z₃₉
IV Chameleon = IV 16: z₄, z₃₂:
II Chersina = II 47: z: z₆
II Chinovum = II 42: b: 1, 5
II Chudleigh = II 3,10: e, n, x: 1, 7
Clichy = Goelzau var. 15⁺
II Clifton = II 13,22: z₉₇, 1, 5
II Clovelly = II 1,44:z_{36};e,n,x,z_{15}
Congo => Agbeni
II Constantia = II 17:z:1,w:z_{42}
Cook => Champaign
Dalat => Ball
II Daressalaam = II 1,9,12:1,w:e,n,x
Decatur => Choleraesuis
II Degania = II 40:z_{4},z_{24};z_{39}
II Detroit = II 42:z:1,5
Drypool = Amsterdam var. 15'
II Dubrovnik = II 41:z:1,5
II Duivenhoks = II 9,46:g,[m],[s],t:[e,n,x]
II Durbanville = II 1,4,12,22;z_{39};1,[5],7
II Eilbek = IIIb 61:i:z
Eimsbuettel = Livingstone var. 14'
II Ejeda = II 45:a:z_{10}
II Elsiesrivier = II 16:z_{42}:1,6
II Emmerich = II 6,14:m,t:e,n,x
II Epping = II 1,13,23:e,n,x:1,[5],7
II Erlangen = II 48:g,m,t:-
Eschersheim = Souza var. 15'
II Etosha = II 48:d:1,2
II Fandran = II 1,40:z_{35};e,n,x,z_{15}
II Faure = II 50:z_{42}:1,7
Ferlac = VI 1,6,14,25:a:e,n,x
II Finchley = II 3,10:z:e,n,x
IV Flint = IV 50:z_{4},z_{23}:-
II Foulpointe = II 38:g,t:-
II Fremantle = II 42:g,t:-
II Fuhlsbuettel = II 3,10:1,v:z_{6}
Gelsenkirchen = Gdansk var. 14'
II Germiston = II 6,8:m,t:e,n,x
II Gilbert = II 6,7:z_{39}:1,5,7
II Glencairn = II 11:a:z_{6};z_{42}
Goerlitz = Vejle var. 15^*
II Gojenberg = II 1,13,23:g,t:1,5
II Goodwood = II 13,22:z_{29}:e,n,x
II Grabouw = II 11:g,[m],s,t:z_{39}
II Greenside = II 50:z:e,n,x
II Grunty = II 1,40:z_{39};1,6
II Gwaai = II 21:z_{4};z_{24};-
II Haarlem = II 9,46:z:e,n,x
II Haddon = II 16:z_{4};z_{23};-
II Hagenbeck = II 48:d:z_{6}
Halmstad = Westhampton var. 15^*
II Hamburg => II 1,9,12:g,m,[s],t:[1,5,7]:[z_{42}]
Hamilton = Vejle var. 15^*,[Rz_{27}]
II Hammonia = II 48:e,n,x,z_{15}:z_{6}
IV Harmelen = IV 51:z_{4};z_{23};-
II Heilbron = II 6,7:1,z_{28};1,5:[z_{42}]
II Helsinki = II 1,4,12:z_{29};e,n,x
Heves = 6,14,[24]:d:1,5
II Hillbrow = II 17:b:e,n,x,z_{15}
Hirschfield = Paratyphi C
II Hooggraven = II 50:z_{10};z_{6};z_{42}
IV Houten = IV 43:z_{4};z_{23};-
II Hueningen = II 9,12:z:z_{39}
II Huila = II 11:1,z_{28};e,n,x
II Humber = II 53:z_{4};z_{23};-
Illinois = Lexington var. 15^*,34^*
II Islington = II 3,10:g,t;-
Italiana => Panama
Iwojima = Kentucky
II Jacksonville = II 16:z_{29};e,n,x
Jaja = Stanleyville var. 27+
Java = Paratyphi B var. L(+) tartrate (= d-tartrate)+
Joenkoeping => Kingston
II Kaltenhausen = II 28:b:z₆
Kanda = Meleagridis
Kaposvar => Reading
II Katesgrove = II 1,13,23,m,t:1,5
II Khami = II 47:b:e,n,x,z₁₅
Khartoum = Oxford var. 15⁺,34⁺
II Kilwa = II 4,12:l,w:e,n,x
Kinshasa = Uganda var. 15⁺
II Klapmuts = II 45:z:z₉₉
II Kluetjenfelde = II 4,12:d:e,n,x
II Kommetje = II 43:b:z₄₂
II Kraaifontein => II 1,13,23:g,m,[s],t:[e,n,x]
IV Kralendyk = IV 6,7:z₄,z₂₄:-
II Krugersdorp = II 50:e,n,x:1,7
II Kuilsrivier = II 1,9,12:g,m,s,t:e,n,x
Lanka = Weltevreden var. 15⁺
II Lethe = II 41:g,t:-
II Lichtenberg = II 41:z₁₀:z₆
II Limbe = II 1,13,22:g,m,t:[1,5]
II Lincoln = II 11:m,t:e,n,x
II Lindrick = II 9,12:e,n,x:1,[5],7
II Llandudno = II 28:g,(m),[s],t:1,5
II Lobatsi = II 52:z₄₄:1,5,7
II Locarno = II 57:z₂₉:z₄₃
IV Lohbruegge = IV 44:z₄,z₃₂:-
II Louwbester = II 16:z:e,n,x
II Luanshya = II 1,13,23:g,m,[s],t:[e,n,x]
II Lundby = II 9,46:b:e,n,x
II Lurup = II 41:z10:e,n,x,z15
II Luton = II 60:z:e,n,x
II Maarssen = II 9,46:z4,z24;z39;z42
III Maartensdijk = IIIa 40:g,z51:
II Makoma = II 1,4,[5],12,27:a:e,n,x
II Makumira = II 1,4,12,27:e,n,x:1,[5],7
V Malawi = V 66:z65:
II Manica => II 1,9,12:g,m,[s],t:[1,5,7]:[z42]
Manila = Lexington var. 15*
II Manombo = II 57:z39:e,n,x,z15
V Maregrosso = V 66:z35:
IV Marina = IV 48:g,z51:
IV Maritza => Salford
II Matroosfontein = II 3,10:a:e,n,x
Menhaden = Give var. 15*,34*
II Merseyside = II 16:g,t:[1,5]
Mexicana => Muenchen
II Midhurst = II 53:l,z28;Z39
Minneapolis = Anatum var. 15*,34*
Mission => Isangi
II Mjimwema = II 1,9,12:b:e,n,x
II Mobeni = II 16:g,[m],[s],t:[e,n,x]
II Mondeor = II 39:l,z28:e,n,x
II Montgomery = II 11:a:d:e,n,z15
II Mosselbay = II 43:g,m,[s],t:[z42]
II Mpila = II 3,10:z38;z42
II Muizenberg => II 1,9,12:g,m,[s],t:[1,5,7]:[z42]
IV Mundsburg = IV 11:g,z51:
II Nachshonim = II 1,13,23:z:1,5
II Nairobi = II 42:r:-
II Namib = II 50:g,[m],s,t:[1,5]
Nancy = Nchanga var. 15+
II Neasden = II 9,12:g,s,t:e,n,x
II Negev = II 41:z_{10}:1,2
II Ngozi = II 48:z_{10}:[1,5]
Newbrunswick = Give var. 15+
Newhaw = Muenster var. 15+
Newington = Anatum var. 15+
Nienstedten = Ohio var 14+
Nissii => Ohio
II Nordenham = II 1,4,12,22:z:e,n,x
II Noordhoek = II 16:1,1,w:z_{6}
II Nuernberg = II 42:z:z_6
IV Ochsenzoll = IV 16:z_4,z_{23}:-
II Odijk = II 30:a:z_{39}
II Oevelgoenne = II 28:r:e,n,z_{15}
Omderman = Amersfoort var. 14+
Oregon => Muenchen
II Ottershaw = II 40:d:-
II Oysterbeds = II 6,7:z:z_{42}
Pankow = Shangani var. 15+
IV Parera = IV 11:z_4,z_{23}:-
II Parow = II 3,10,15:15:g,m,s,t:-
II Perinet = II 45:g,m,t:e,n,x,z_{15}
II Phoenix = II 47:b:1,5
Pikine => Altona
Portsmouth = London var. 15+
II Portbech = II 42:1,v:e,n,x,z_{15}
Pueris => Newport
Pullorum => Gallinarum
II Quimbamba = II 47:d:z_{39}
II Rand = II 42:z:e,n,x,z_{15}
II Rhodesiense = II 9,12:d:e,n,x
II Roggeveld = II 51:-1,7
II Rooikrantz = II 1,6,14:m,t:1,5
Rosenthal = Butantan var. 15^*,34^*
IV Roterberg = IV 6,7:z_{4},z_{23};:-
II Rotterdam = II 1,13,22:g,t:1,5
II Rowbarton = II 16:m,t:[z_{42}]
Ruki => Ball
Rutgers => Give
IV Sachsenwald = IV 1,40:z_{4},z_{23};:-
Saka => Sya
Sakai = Postdam
II Sakaraha = II 48:k:z_{39}
Salinatis => Duisburg
II Sarepta = II 16:1,z_{28};z_{42}
Schottmuelleri = Paratyphi B
II Seaforth = II 50:k:z_{6}
Selandia = Nyborg var. 15^*
IV Seminole = IV 1,40:g,z_{51};:-
II Setubal = II 60:g,m,t:z_{6}
II Shomron => IIIa 18:z_{4},z_{32};:-
Siegburg = Cerro var. 14^*
II Simonstown = II 1,6,14:z_{16};1,5
Simsbury => Senftenberg
Sladun => Abony
II Slangkop = II 1,6,14:z_{16};z_{6};z_{42}
II Slatograd = II 30:g,t:-
IV Soesterberg = IV 21:z_{4},z_{23};:-
II Sofia = II 1,4,12,27:b:[e,n,x]
II Soutpan = II 11:z:z_{39}
II Springs = II 40:a:z_{39}
VI Srinagar = VI 11:b:e,n,x
II Stellenbosch = II 1,9,12:z:1,7
II Stevenage = II 1,13,23:[z_{42}]:1,[5],7
II Stikland = II 3,10:m,t:e,n,x
II Suarez = II 1,40:c:e,n,x,z_{15}
II Suederelbe = II 1,9,12:b:z_{39}
Suez = Shubra
Supestifer = Choleraesuis
II Sullivan = II 6,7:z_{42}:1,7
II Sunnydale = II 1,40:k:e,n,x,z_{15}
II Sydney => IIIb 48:i:z
II Tafelbaai = II 3,10:z:z_{39}
Taihoku = Meleagridis
Thielallee = Oranienburg var. 14^+
Thomasville = Orion var. 15^+,34^+
Tim => Newington
II Tokai = II 57:z_{42}:1,6:z_{53}
II Tosamanga = II 6,7:z:1,5
Tournai = Stockholm var. 15^+
II Tranoroa = II 55:k:z_{39}
Tuebingen = Amager var. 15^+
IV Tuindorp = IV 43:z_{42},z_{32}:-
II Tulear = II 6,8:a:z_{52}
II Tygerberg = II 1,13,23:a:z_{42}
II Uphill = II 42:b:e,n,x,z_{15}
II Utbremen = II 35:z_{29},e,n,x
II Veddel = II 43:g,t:-
Venusberg => Nchanga
II Verity = II 17:e,n,x,z_{15}:1,6
IV Volksdorf = IV 43:z_{36},z_{38}:-
II Vredelust = II 1,13,23:1,z_{28},z_{42}
VI Vrindaban = VI 45:a:e,n,x
II Wandsbek = II 21:z_{10}:z_{6}
IV Wassenaar = IV 50:g,z_{51}:
II Westpark = II 3,10:1,z_{28}:e,n,x
Wildwood = Meleagris var. 15°,34°
II Wilhemstrasse => II 52:z_{44}:1,5,7
II Winchester = II 3,10:z_{39}:1,\{5\},7
II Windhoek = II 45:g,m,s,t:1,5
II Woerden = II 17:c:z_{39}
Womba => Altendorf
II Woodstock = II 16:z_{42}:1,(5),7
II Worcester = II 1,13,23:m,t:e,n,x
Wuerzburg => Miami
II Wynberg = II 1,9,12:z_{39}:1,7
Zagreb => Saintpaul
II Zeist = II 18:z_{10}:z_{6}
II Zuerich = II 1,9,12,46,27:c:z_{39}