

What are superintegrons?

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Although integrons have been found in transposons, in plasmids and in bacterial chromosomes, all integrons have the same basic properties, namely an *intI* gene and an *attI* site that allow them to capture gene cassettes¹. When an integron is part of a transposon, as is the case for integron classes 1, 2 and probably 3 (REF. 2), it is obvious that this would vastly increase the capacity of the integron to capture cassettes from a wide range of bacterial sources. However, their location does not make them either structurally or functionally different from the more sedentary integrons found in bacterial genomes.

Mazel and co-workers initially noted that the integron in *Vibrio cholerae* N16961 was different to the integrons that had been described previously because it is found in the chromosome and had a large number (178) of cassettes associated with it, and they referred to it as a ‘superintegron’ (REF. 3). Subsequently, confusion arose because the term superintegron was applied to other integrons that were chromosomally located, even though most of these do not have a large cassette array. Defining a distinct type of integron based on arbitrary features of the cassette array is dangerous because the size and composition of the cassette array associated with an integron can easily change. This variability is necessarily intrinsic to a system that captures and harbours mobile elements, such as gene cassettes. These discrepancies were pointed out by Hall and Stokes¹ who recommended that, as all integrons have the same basic properties, they should all be called integrons.

Despite this recommendation, a recent review⁴ continues to use, and re-defines, the term ‘superintegron’. The three features that are now claimed to make superintegrons a ‘distinct type’ of integron are: first, that there are at least 20 cassettes in the associated array; second, that a single type (over 80% identical) of *attC* site (59-be) is predominantly found in these cassettes; and third, that the integron is not associated with mobile elements⁴. However, in subsequent sections of the review, integrons that do not comply with this definition are also described as superintegrons.

So, what are superintegrons? This latest definition actually applies to only 3 of the integrons for which an analysis is available. The integrons so far found in the chromosomes of Vibrionaceae have more than 20 cassettes associated with them, but only in the case of *V. cholerae* is there a single sequence type for the 59-be (*attC*) associated with the vast majority of these cassettes^{5,6}. Among the remaining chromosomally located integrons for which an analysis of the cassette array has been published^{7–12}, only 3 have over 20 cassettes (TABLE 1). Our analysis of these cassette arrays to determine if there is a single predominant 59-be type at the 80% identity level revealed that only the integrons in *Xanthomonas campestris* and *Treponema denticola* meet this criterion (TABLE 1). Therefore, based on currently available information, integrons with the features of a ‘superintegron’ are rather uncommon.

We continue to believe that the term superintegron is superfluous. The many definitions so far given and the lack of rigour in applying these definitions is creating unnecessary confusion. We recommend that all integrons, no matter what their location, remain simply integrons.

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Table 1 | **Properties of cassette arrays in analysed chromosomally located integrons**

Organism	Strain	GenBank accession number	Intl	Number of cassettes*	Single 59-be type predominant [‡]	Super-integron
<i>Pseudomonas alcaligenes</i>	ATCC055044	AY038186	–	32 (Ref. 7)	No [§]	No
<i>Shewanella oneidensis</i>	MR-1	NC_004347	SO_2039	3 (Ref. 8)	No	No
<i>Nitrosomonas europaea</i>	ATCC19718	NC_004757	NE2189	1 (Ref. 9)	–	No
<i>Treponema denticola</i>	ATCC35405	NC_002967	TDE1844	45 (Ref. 11)	Yes (Ref. 11)	Yes
<i>Xanthomonas campestris</i> pv. <i>campestris</i>	ATCC33913	NC_003902	XCC0344	22 (Ref. 10)	Yes	Yes
<i>Pseudomonas stutzeri</i>	Q	AY129392	–	10 (Ref. 12)	Yes [¶]	No
<i>Pseudomonas stutzeri</i>	BAM17	AY129393	–	14 (Ref. 12)	Yes [¶]	No

*The reference cited contains the published analysis of the number of cassettes in the array. References for the original genome sequences can be found through the GenBank entry. [‡]The similarity of 59-be in the cassettes was analysed here. Predominant was taken to mean over 75% of the cassettes. [§]16 out of 32 cassettes have type 1 59-be (average length 77 bp), 10 have type 2 59-be (average length 89 bp). ^{||}18 out of 22 have the same 59-be type (average length 60 bp). [¶]8 out of 10 and 12 out of 14 cassettes have the same type of 59-be (average length 77 bp). Note this type is the same as type 1 from *P. alcaligenes*, indicating that 59-be types are not necessarily species specific.