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Revised Nomenclature for Transposable Genetic Elements

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Abstract

Transposable DNA elements occur naturally in the genomes of nearly all species of prokaryotes. A proposal for a uniform transposable element nomenclature was published prominently in the 1970s but is not, at present, available online even in abstract form, and many of the newly discovered elements have been named without reference to it. We propose here an updated version of the original nomenclature system for all of the various types of prokaryotic, autonomous, transposable elements excluding insertion sequences, for which a nomenclature system already exists. The use of this inclusive and sequential Tn numbering system for transposable elements described here recognizes the ease of interspecies spread of individual elements, and allows for the naming of mosaic elements containing segments from two or more previously described types of transposons or plasmids. It will guard against a future necessity to rename elements following changes in bacterial nomenclature which occurs constantly with our increased understanding of bacterial phylogenies and taxonomic groupings. It also takes into account the increasing importance of metagenomic sequencing projects and the continued identification of new mobile elements from unknown hosts.

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Introduction

Reports of prokaryotic transposable elements proven by experiment or inferred from sequence homology or their diverse positions in prokaryotic genomes (bacterial and archaeal) have proliferated dramatically in the last two decades (Berg and Howe, 1989; Craig *et al.*, 2002). Although classical elements, such as insertion sequences (IS), comprise only a small fraction (less than 1–2%) of the genomes of *Escherichia coli* and many other microbial species, no obvious uniform rule appears to determine their distribution; for example early studies showed that IS*1*-like elements were far more abundant in certain strains of *Shigella* than in closely related *E. coli* strains (Ohtsubo *et al.*, 1981). When all potential mobile elements or foreign DNA within a particular genome are considered, they can make up much of that genome. For example, sequencing projects have revealed that mobile elements comprise approximately 11% and 25% of the genome of strains of *Clostridium difficile* and *Enterococcus faecalis,* respectively (Sebaihia *et al.*, 2006; Paulsen *et al.*, 2003). Recently the genome sequence of *Orientia tsutsugamushi* revealed that 46.7% of the genome was occupied by sequences derived from an integrative and conjugative element (ICE), 10 types of transposable element and other repetitive regions of unknown origin (Nakayama *et al.*, 2008).

Transposons are borne both by plasmids and the chromosome and have an enormous variation in their genetic organization, the genes responsible for their insertion and excision and in the accessory or passenger genes they carry. Transposable elements are also able to interact, by recombination between elements and / or by transposition into other elements, forming novel chimeric elements.

Given the many genome sequencing projects now underway or planned, there is good reason to believe that new transposable elements will continue to be discovered. Although a proposal for a uniform bacterial transposable element nomenclature had been developed and published 30 years ago (Campbell *et al.*, 1979a; Campbell *et al.*, 1979b), that proposal is not available online and many newly discovered elements have been named without reference to it. In consequence, a myriad of systems have been devised for naming newly discovered prokaryotic transposable elements, which has resulted in a complex and potentially confusing array of names. Much as at the beginning of the transposable element era, nearly 40 years ago, we believe that scientific understanding would benefit from re-implementation of a universal system for naming new transposable elements.

A Historical Perspective

A committee assembled during the meeting on DNA Insertions at Cold Spring Harbor in 1976 proposed a set of rules to be used for the nomenclature of transposable elements. These rules were themselves modified from an initial proposal from D. E. Berg and W. Szybalski (Department of Biochemistry and the McArdle Laboratory for Cancer Research, respectively, University of Wisconsin, USA; Campbell *et al.*, 1977). They were revised further to cope with, and include, the then recent development of DNA sequencing (Campbell *et al.*, 1979a; Campbell *et al.*, 1979b). The authors proposed a system whereby IS elements (IS elements contain a single gene whose protein product catalyses transposition to new genomic sites; reviewed in Mahillon and Chandler 1998) were named IS*1*, IS*2*, etc, with a parallel system for transposable elements (not including IS elements) whereby they would be designated with a prefix of Tn and assigned a sequential number e.g. Tn*1*, Tn*2*, Tn*3*, etc. The allocation of numbers and database administration was carried out by the late Dr Esther Lederberg from Stanford University Medical School, CA, USA. Lists for the registry of Tn number allocations were subsequently published (Lederberg 1981; 1987) taking the continuous system up to Tn*4685*. However, Tn numbers up to and above Tn*5500*

were allocated but a list of these has not been published. The allocation of Tn numbers stopped with the retirement of Dr Lederberg and gradually a variety of rules were adopted for naming newly discovered transposons. At the same time new types of transposable elements, such as the mobilizable and conjugative transposons, were being discovered. Additionally, interactions between different elements including transposition and/or recombination events led to novel chimaeric transposons. These exacerbated the nomenclature problem.

Subsequent nomenclature systems have become complicated, with different systems being adopted for related elements by different research groups. In the case of insertion sequences (IS), the numbers have become very large and a rational nomenclature system is already in place (www-IS.biotoul.fr), although unfortunately is not yet used by all authors. For all other autonomous mobile DNA elements where a nomenclature system does not exist (Table 1), we propose here to return to a version of the early nomenclature system, much like that initially administered by Dr Lederberg (Campbell *et al.*, 1979a; 1979b). We are not including non-autonomous elements (such as integron cassettes and MITEs) in this scheme but stress there is a need for such nomenclature schemes to be worked out for these elements.

Definition of Transposable Elements

Transposable elements will be defined as “specific DNA segments that can repeatedly insert into one or more sites in one or more genomes”. This definition is modified from that used in the original nomenclature proposal (Campbell *et al.*, 1979a; 1979b) to allow it to include the many different types of transposable elements that have been discovered since that proposal was published.

The movement of most of the elements used in formulating the original definition was mediated by IS-like DD(35)E transposases, in which DD(35)E represents a catalytic triad of acidic amino acids located in the transposase that is essential for transposition activity (Fayet *et al.*, 1990; Kulkosky *et al.*, 1992). However, not all transposases contain this catalytic triad (Mahillon and Chandler, 1998; Chandler and Mahillon; 2002; Curcio and Derbyshire, 2003), as there are a host of alternative enzymes which are able to catalyse the movement of the elements encoding them. For example, the transposases of the IS*91* family [including the recently described IS*CR* (Insertion Sequence with a Common Region) elements] show significant similarity to enzymes associated with replicons that use a rolling-circle replication mechanism (Mendiola *et al.*, 1982; Toleman *et al.*, 2006). These enzymes are known as the Y2 transposases. In addition, members of the IS*200*/IS*605* group encode tyrosine transposases of only about 150 amino acids which resemble relaxase proteins of conjugative plasmids and are the smallest transposases known (Guynet *et al.*, 2008; Barabas *et al.*, 2008).

The transposition of IStrons, a chimeric ribozyme originally found in *Clostridium difficile,* is also likely to be catalyzed by a protein related to the transposase of IS*605* (Braun *et al.*, 2000). The movement of other transposable elements depends on tyrosine and serine recombinases. For example, the conjugative transposon (for definitions of the various transposable elements see Table 1) Tn*916*, the integrative and conjugative element (ICE) pSAM and the integrative and mobilisable element (IME) SGI1 all rely on a tyrosine recombinase to carry out the excision and insertion reactions (Poyart-Salmeron et al,. 1989; Boccard *et al.*, 1989; Doublet *et al.*, 2005). Similarly, both conjugative (Tn*5397*) and mobilisable (Tn*4451*) transposons encode serine recombinases that are responsible for their insertion and excision (Wang and Mullany, 2000; Adams *et al.*, 2004; Adams *et al.*, 2006). Many tyrosine and serine recombinases have been shown to require accessory factors to

control the directionality of the recombination reactions they catalyze (insertion versus excision) (Lewis and Hatfull, 2001) however this is not true of all recombinases e.g. TndX from Tn*5397* (Wang and Mullany, 2000). Pathogenicity islands also encode both tyrosine and serine recombinases which carry out the insertion and excision reactions e.g. the HPI $_{YPS}$ pathogenicity island from *Yersinia pseudotuberculosis* encodes a tyrosine recombinase (Buchrieser *et al.*, 1998) and the *SCCmec* resistance islands from *Staphylococcus aureus* encode a serine recombinase (Hanssen and Ericson Sollid, 2006). Furthermore, the genomes of most temperate phages insert into the genome of their hosts using tyrosine or serine site-specific recombinases or a DD(35)E transposase; we therefore consider these as transposable genetic elements. Furthermore, it is worth noting that other proteins can be responsible for the translocation of certain mobile elements. These include reverse transcriptases that mediate the movement of group II introns, and endonucleases that mediate the movement of group I introns and inteins.

Target-site specificity during transposition reactions also varies among enzymes belonging to the same family (DD(35)E, tyrosine or serine) which may catalyze integration/transposition reactions with a high or a low specificity (specific examples of this for each family are given in table 2). Studies have also revealed that some elements (e.g. Tn*5397*) use specific sites in one host and multiple sites in a different host if the preferred site is not present (Wang *et al.*, 2000), this has also been shown to be the case for Tn*916* in different strains of *C. difficile* (Hussain *et al.*, 2005).

Therefore all elements specifying their own integration could be considered as transposable elements, regardless of the underlying mechanism. The different types of elements that this definition pertains to are shown in Table 1, with details of specific examples described in Table 2.

Proposed Nomenclature System

It is proposed that newly discovered bacterial and archaeal autonomous transposable elements (unit and composite transposons, mobilizable transposons / integrative mobilizable elements, conjugative transposons / integrative conjugative elements and mobile genomic islands; see Table 1 for definitions) be designated with a sequential Tn number, written in italics to conform with previous guidelines, e.g. Tn*3* or Tn*5397*. A registry for the assignment of Tn numbers has been set up on the UCL website (http://www.ucl.ac.uk/eastman/tn/) where researchers can request as many Tn numbers as needed and log details (e.g. description, accession numbers and references) of newly discovered, fully sequenced and /or functional transposons in the registry. It is envisaged that the website will eventually include sequence and ORF data of each element and will be interfaced with ISfinder for cross-referencing. Existing names for transposons will not be altered, as they are so entrenched that any change could cause confusion. Additionally, and due to their prolific use in the literature, the terms ICE and IME for integrative conjugative element and integrative mobilizable element are interchangeable with the terms CTn for conjugative transposon and MTn for mobilizable transposon, respectively. For example, if an element was designated Tn5999 and subsequently shown to be conjugative it can be subsequently named CTn5999 or ICE5999. The same is true for elements found to be mobilisable, a MTn or IME prefix can be substituted. However each number will only ever be issued once. In time it is also planned to complete a historical database on the website of all elements whose sequence is known and deposited in sequence databases.

When essentially the same mobile element is found in different hosts it is proposed that it be designated with the first-used name provided that the entire element has been sequenced and the nucleotide identity is 100% identical to that of the original element. This threshold has

been chosen as it is important for both epidemiological purposes and studies on the evolution of transposable elements, further more; if very closely related elements are given the same name there is likely to be only one representative readily available in the various sequence databases, thus making it difficult to access this data and impeding research. New individual Tn numbers should be given to elements showing < 100% deduced nucleotide sequence similarity to their closest relatives, or to elements that contain novel resistance, virulence, catabolic or other accessory genes, or novel combinations of genes or modules. If functionality is demonstrated (excision, insertion, transposition or transfer) but the entire sequence of the element is not determined the element may still be assigned a Tn number provided the known sequence is sufficiently different from previously determined sequences, as described above. The rules governing the requesting of Tn numbers are summarised in figure 1.

We appreciate that other elements (integrated or transposable prophage and satellite prophage, group I and II introns, IStrons, inteins, and insertion sequences) fit our definition of a transposable element. However, in most cases there is already a coherent nomenclature system in place and any change would cause confusion. If a novel element is found which fails to qualify for the established nomenclature schemes a Tn number can be used.

Conclusions and Perspectives

The issue of nomenclature for any group of entities, transposable elements included, is often subject to lively discussion. In an earlier system for new integrative and conjugative elements, Burrus *et al.* (2002) proposed to use the prefix ICE followed by the initials of the name of the bacterial genus and species and a number corresponding to the rank of the discovery (e.g. ICE*St1* for the first ICE found in *Streptococcus thermophilus*). Subsequently, Burrus *et al.* (2006) further proposed inclusion of three letters to identify the country of origin, followed by a number to distinguish between different isolates of the same species and country. For example, the first ICE of the SXT/R391 family found in *V. cholerae* isolated in Mexico was designated ICE*VchMex*1 (Burrus *et al.*, 2006a). However, the continued use of the sequential and continuous numbering system for transposable elements, as described here, is simpler and recognizes the ease of interspecies spread of individual elements and international spread of microbes that carry them, and allows for the naming of mosaic elements containing segments from two or more previously described types of transposons or plasmids; this should diminish the need for further reclassification of elements with changes in the understanding of bacterial phylogeny and taxonomic groupings. Additionally most bacterial species have not been successfully cultivated in the laboratory. For example, it is estimated that 99% or more of species in the soil are currently uncultivable (Amann *et al.*, 1995; Gans *et al.*, 2005). However, such microbes are increasingly amenable to genome sequencing approaches (metagenomics), as illustrated by the shotgun sequencing of Sargasso sea bacterial DNA and the identification of over 1000 open reading frames annotated as “mobile and extrachromosomal element functions” (Venter *et al.*, 2004). When a novel putative transposable element is discovered using this approach it is not known if the element is actually mobile, and often no other sequences on the same DNA fragment or contig are sufficiently informative phylogenetically to identify the element’s host species. The Tn nomenclature system proposed here does not require species identifiers, and thus accommodates metagenomic findings and the continued identification of new mobile elements from unknown hosts. Researchers must however, endeavour to ensure any metagenomic mobile element actually exists in their sample and is not results of *in-silico* recombination between separate sequences.

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Weil J, Signer ER. Recombination in bacteriophage lambda. II. Site-specific recombination promoted by the integration system. J Mol Biol. 1968; 34:273–279. [PubMed: 5760459]

1. **Has excision, insertion, transposition and / or transfer been demonstrated?**

   Yes; go to 3

   No; go to 2

2. **Has the entire DNA sequence been determined and the putative ends delineated?**[a]

   Yes; go to 4

   No; go to 6

3. **Is any part of the DNA sequence of the element known?**

   Yes; go to 4

   No; go to 6

4. **Is the nucleotide sequence <100% identical to known sequences over any one predicted protein?**

   Yes; go to 7

   No; go to 5

5. **Is synteny conserved over the entire sequence compared to database sequences?**

   Yes; got to 6

   No; got to 7

6. **A Tn number is inappropriate at this stage**

7. **A Tn number is appropriate**

[a]in the case of composite transposon flanked by IS elements transposition or different insertion sites need to be demonstrated, as it is possible that the majority of these have never transposed.

Figure 1. Key for determining if a Tn number is appropriate
(not appropriate for ISs or non autonomous transposable elements such as integron cassettes or MITEs)

Table 1

Types of transposable elements included in this proposed nomenclature system

Type of transposable element[a]	Definition
Composite transposons	Flanked by IS elements. The transposase of the IS element is responsible for the catalysis of insertion and excision.
Unit transposons	Typical unit elements encode an enzyme involved in excision and integration (DD(35)E or tyrosine) often a site specific recombinase or resolvase and one or several accessory (e.g. resistance) genes in one genetic unit.
Conjugative transposons (CTns) / Integrative conjugative elements (ICEs)	The conjugative transposons (CTns), also known as integrative conjugative elements (ICEs), carry genes for excision, conjugative transfer and for integration within the new host genome. They carry a wide range of accessory genes, including antibiotic resistance
Mobilisable transposons (MTns) / Integrative mobilisable elements (IMEs)	The mobilizable transposons (MTns), also known as integrative mobilizable elements (IMEs), can be mobilized between bacterial cells by other “helper”elements that encode proteins involved in the formation of the conjugation pore or mating bridge. The MTns exploit these conjugation pores and generally provide their own DNA processing functions for intercellular transfer and subsequent transposition.
Mobile genomic islands	Some chromosomally integrated genomic islands encode tyrosine or serine site-specific recombinases that catalyze their own excision and integration but do not harbor genes involved in transfer. They carry genes encoding for a range of phenotypes. The name of a genomic island reflects the phenotype it confers, e.g. pathogenicity islands encode virulence determinants (toxins, adhesins etc).
Integrated or transposable prophage	An integrated or transposable prophage is a phage genome inserted as part of the linear structure of the chromosome of a bacterium which is able to excise and insert from and into the genome.
Integrated satellite prophage	Bacteriophage genome inserted into that of the host which requires gene products from “helper” phages to complete its replication cycle
Group I intron	Small post-transcriptionally splicing (splicing occurs in the pre-mRNA), endonuclease encoding element. Will home to allelic site
Group II intron	Small post-transcriptionally splicing (splicing occurs in the pre-mRNA), restriction endonuclease encoding element
IStron intein	Chimeric ribozyme consisting of a group I intron linked to an IS*605* like transposase Small post-translational splicing (splicing occurs in the polypeptide), endonuclease encoding element. Will home to allelic site.

[a]; not all reported elements have been shown to be mobile

Table 2

Examples of transposable elements included in this nomenclature

Types of transposable element	Name	Enzyme[a]	Target site	Reference
Composite	Tn*5*	DD(35)E	Multiple	Reznikoff 1993
Unit	Tn*3*	DD(35)E transposase and a site-specific serine resolvase for co-integrate resolution	Preferential but variable	Kleckner, 1981, Grinsted *et al.*, 1990
	Tn*554*	Tyrosine	Specific	Murphy, 1983
	Tn*4430*	DD(35)E and Tyrosine recombinase for co-integrate resolution	Specific	Lereclus *et al.*, 1986
Mobilisable	Tn*4451*	Serine	Specific	Adams *et al.*, 2002
	SGI1	Tyrosine	Specific	Doublet *et al.*, 2005
	Tn*4555*	Tyrosine	Preferential but variable	Smith and Parker, 1993
Conjugative	Tn*916*	Tyrosine	Multiple	Franke and Clewell, 1981
	pSAM2	Tyrosine	Specific	Boccard *et al.*, 1988
	Tn*5397*	Serine	Preferential but variable	Mullany *et al.*, 1996
Mobile genomic island	HPI_{YPS}	Tyrosine	Specific	Buchrieser *et al.*, 1998
	SCCmec	Serine	Specific	Katayama *et al.*, 2000
Integrated or transposable prophage	Lambda	Tyrosine	Specific	Weil and Signer, 1968
	Mu	DDE	Multiple	Boram and Abelson, 1971
	phiC31	Serine	Specific	Thorpe and Smith, 1998
Integrated or transposable satellite prophage	P4	Tyrosine	Specific	Christie and Calendar, 1990
Mobile group I intron	unnamed group I intron inserted the *td* gene of *E. coli* phage T4.	Homing endonuclease	Specific	Edgell and Shub, 2001
Mobile group II intron	Ll.LtrB	Reverse transcriptase	Specific	Cousineau *et al.*, 1998
IStron	CdlSt1	Tyrosine	Multiple	Braun *et al.*, 2000
intein	unnamed intein inserted in the DNA helicase *DnaB* of *E. coli*	Homing endonuclease	Specific	Liu and Hu, 1997

[a] "Serine" or "tyrosine" refers to catalytic amino acid at the transposase (recombinase) active site