Plasmid 60 (2008) 167–173

Contents lists available at ScienceDirect

Plasmid

journal homepage: www.elsevier.com/locate/yplas

Review

Revised nomenclature for transposable genetic elements

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ARTICLE INFO

Article history:
Received 11 August 2008
Available online 26 September 2008

Communicated by Manuel Espinosa

Keywords:
Transposable genetic element
Transposon
Conjugative transposon
Integrative conjugative element
Mobilizable transposon
Integrative mobilizable element

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, as 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 any future need 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.

1. 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

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0147-619X/$ - see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.plasmid.2008.08.001

strains of *Clostridium difficile* and *Enterococcus faecalis*, respectively (Sebaihia et al., 2006; Paulsen et al., 2003). Recently analysis of 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,b), 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.

2. 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,b). 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. For 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,b). We are not including non-autonomous elements such as integron cassettes and miniature inverted-repeat transposable elements (MITEs) in this scheme but stress there is a need for such nomenclature schemes to be worked out for these elements.

3. 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,b) 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 catalyze 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 and de la Cruz, 1989; 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*,