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TnCentral: A Prokaryotic Transposable Element Database and Web Portal for Transposon
Analysis

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Importance

The ability of bacteria to undergo rapid evolution and adapt to changing environmental circumstances drives the public health crisis of multiple antibiotic resistance as well as outbreaks of disease in economically important agricultural crops and animal husbandry. Prokaryotic transposable elements (TE) play a critical role in this. Many carry "passenger genes" (not required for the transposition process) conferring resistance to antibiotics or heavy metals or causing disease in plants and animals. Passenger genes are spread by the normal TE transposition activities, by insertion into plasmids which then spread via conjugation within and across bacterial populations. Thus, an understanding of TE composition and transposition mechanisms is key to developing strategies to combat bacterial pathogenesis. Toward this end, we have developed TnCentral, a bioinformatics resource dedicated to describing and exploring the structural and functional features of prokaryotic TE and whose use is intuitive and accessible to users with or without bioinformatics expertise.

Abstract

We describe here the structure and organization of TnCentral (https://tncentral.proteininformationresource.org/), a web resource for prokaryotic transposable elements (TE). TnCentral currently contains ~400 carefully annotated TE, including transposons from the Tn*3,* Tn*7,* Tn*402* and Tn*554* families, compound transposons, integrons and associated insertion sequences (IS). These TE carry passenger genes, including genes conferring resistance to over 25 classes of antibiotics and nine types of heavy metal as well as genes responsible for pathogenesis in plants, toxin/antitoxin gene pairs, transcription factors and genes involved in metabolism. Each TE has its own entry page providing details about its transposition genes, passenger genes, and other sequence features required for transposition as well as a graphical map of all features. TnCentral content can be browsed and queried through text and sequence-based searches with a graphic output. We describe three use cases, which illustrate how the search interface, results tables, and entry pages can be used to explore and compare TEs.

TnCentral also includes downloadable software to facilitate user-driven identification, with manual annotation, of certain types of TE in genomic sequences.

Through the TnCentral homepage, users can also access TnPedia which provides
comprehensive reviews of the major TE families including an extensive general section, and
specialised sections with descriptions of insertion sequence and transposon families.
TnCentral and TnPedia are intuitive resources that can be used by clinicians and scientists to
assess TE diversity in clinical, veterinary and environmental samples.

Introduction

Transposable elements (TE) are key facilitators of bacterial evolution and adaptation
and central players in the emergence of antibiotic and heavy metal resistance and to the
transmission of virulence and pathogenic traits. Some TE can capture "passenger genes"
(genes not involved in the transposition process) encoding these traits and transmit them to
plasmids, where they accumulate and are then transferred within and between bacterial
populations by conjugation. TE also contribute significantly to the on-going reorganization of
bacterial genomes giving rise to new strains that are more adept at proliferating in clinical
and agricultural environments, as well as in natural ecosystems.

Understanding TE nature, distribution, and activity is therefore an indispensable part
of the struggle to cope with the public health crisis of multiple antibiotic resistance (ABR)
[1,2]. To understand the impact of TE on bacterial populations, it is essential to provide a
detailed description and catalog of TE structures and diversity. The simplest TE, known as
Insertion Sequences (IS), have a profound impact on genome organization and function (see
[3–7]) but do not themselves generally carry integrated passenger genes. There are a large
number of significantly more complex TE (Figure 1), arguably even more important in the
global emergence of ABR and other virulence and pathogenicity traits. These are generically
called transposons and may carry multiple passenger genes, including some of the most
clinically important antibiotic resistance genes. Like IS, these TE are grouped into a number
of distinct families with characteristic organizations [3]. Their transposition activities
facilitate the rapid spread of groups of antibiotic resistance genes and promote their
horizontal transfer. Yet another important aspect of their impact is their ability to assemble
passenger genes into resistance clusters [8,9]. While there appears to be a wide-spread
appreciation that mobile plasmids are responsible for the spread of antibiotic resistance, it

is less well-known that IS and transposons are the conduits that transfer this information

between chromosomes and plasmids.

There are a number of other bioinformatics resources that cover aspects of

prokaryotic TE biology. These include databases for TE passenger genes such as antibiotic

resistance (CARD [10], ARDB [11]) or toxin/antitoxin gene pairs (TADB [12], TASmania [13])

as well as the various classes of TE themselves such as insertion sequences (ISfinder [14]),

integrons (INTEGRALL [15]), integrative conjugative elements, ICE (ICEberg [16,17]),

plasmids (PlasmidFinder [18]) or more general databases which include a variety of these

genome components (ACLAME [19–21]). However, there is a need for a resource that

collects, compares and collates detailed information on the various different classes of TE

that are responsible for the transmission of medically and economically important

passenger genes in an intuitive and accessible way.

Here, we describe TnCentral (https://tncentral.proteininformationresource.org/), a

database of detailed structural and functional information on bacterial TE. Additionally,

TnCentral provides access to TnPedia (https://tnpedia.fcav.unesp.br/), a comprehensive

encyclopedia describing the current state of our knowledge of the biology of IS and

transposons. Together, TnCentral and TnPedia provide a detailed description of TE diversity

with easy-to-understand graphics outputs that are accessible to users without significant

bioinformatic knowledge. They allow users to rapidly analyse the landscape of TE in

genomes (chromosomes and plasmids) isolated from clinical, veterinary and environmental

samples.

Results

TnCentral Website Content

As of May 2021, TnCentral contains information on ~400 TE. About half of these TE are *Tn3*-

family transposons. The remainder are integrons, compound transposons, transposons from

the *Tn402*, *Tn554* and *Tn7* families, and IS that are associated with TE or are part of

compound transposons (Supplementary Table 1). They include TE with resistance to over 25

different classes of antibiotics and nine different heavy metals. The collection also contains

TE that carry a toxin/antitoxin system for bacterial plasmid maintenance [22–24] and TE

from xanthomonads carrying genes for plant pathogenicity.

TnCentral Web Portal

The TnCentral home page is designed to give the user easy access to the contents of
TnCentral with a number of options (Figure 2A), including:

TnCentral Search *(search of the TnCentral database),*

Sequence Search *(BLAST-like search for sequence similarities in the database),*

Browse Tn list *(view all TE in TnCentral),*

Tnfinder Software *(access to downloadable scripts for identifying potential TE in*

sequence databases),

Documentation *(downloadable documentation for TnCentral),*

For Curators *(detailed curation guidelines),*

TnPedia *(TE Encyclopedia),*

Related links, *and*

Feedback.

TnCentral Search. The interface provides a variety of search functions divided into two
search types: ***Transposon search*** and ***Gene search*** (Figure 2B).

Transposon search. The transposon collection can be searched using the transposon
name, **synonyms** which may have been used in the literature, the **type** of mobile genetic
element (e.g., insertion sequence, transposon or integron), the **family** and **subgroup** to
which it belongs, the **host organism**, **country** of identification and **date** of identification. The
latter three search terms are intended for use in epidemiological tracking. These search
terms result in a table that can be sorted, customized and downloaded (See Use Case #1,
below).

Gene search. It is also possible to search for TE-associated genes by name, by class
(Transposase, Accessory Gene or Passenger Gene) or by function (Antibiotic Resistance,
Heavy Metal Resistance) and to retrieve information on the transposons in which they are
found (see Use Case #2, below).

Sequence Search. Sequence Search allows users to perform sequence similarity

searches using BLAST [26,27] (see Use Case #3, below). By default, the search database is

the TnCentral database, but the page also provides links to BLAST against the ISfinder

(https://isfinder.biotoul.fr/blast.php),   NCBI   https://blast.ncbi.nlm.nih.gov/Blast.cgi),

Comprehensive   Antibiotic   Resistance   Database   (CARD;

https://card.mcmaster.ca/analyze/blast) and the Toxin-Anitoxin (TADB;

https://bioinfo-mml.sjtu.edu.cn/TADB2/)   databases.   The   BLAST   tool   automatically

distinguishes between DNA and protein query sequences.

Browse Tn list. This option allows the user to browse the entire TnCentral database.

The Transposon entry page. All of the search and browse options provide links to entry

pages for each TE (Figure 3), which provide detailed information about TE features and

origins. The page includes: 1) host information: host species, strain, and

plasmid/chromosome in which the transposon was found as well as the date and geographic

location of the isolate; 2) a graphic representation of the annotated sequence with color-

coded features; 3) Terminal Inverted Repeats (IR); 4) DNA sequence; 5) internal

recombination sites (e.g. *res* sites) including their coordinates, length and DNA sequence; 6)

ORF summary, which includes all protein coding genes in the order in which they appear, 5'-

3', in the TE sequence, the element with which they are associated (important for nested TE

in which one TE is inserted into another), their coordinates, their class (e.g., Transposase,

Accessory Gene, Passenger Gene) and subclass (e.g., Antibiotic Resistance, Heavy Metal

Resistance) and their relative orientation within the TE; 7) a detailed ORF description

including the amino acid sequence; 8) if applicable, a table of Internal Transposable

Elements (TE inserted in the main element) including the name, type location and length; 9)

if applicable, a table of Internal Repeats (repeat elements, other than the terminal inverted

repeats, that are found within the TE), including the associated TE, coordinates and DNA

sequence; 10) Bibliographic references with direct links to PubMed [25]. Each section can be

collapsed using a button on the right-hand side of the section heading. Sections can be

viewed either by scrolling down on the page or by clicking on the section name in the menu

located on the left side of the page. Sequence files in FASTA and GenBank format can be

downloaded using the links on the left side of the page under the menu.

Tnfinder Software. This section provides three user-downloadable scripts written in-house

for identifying transposons. They provide users with local control over analyses and help

them screen datasets containing large numbers of genomic sequences using their own

servers for identifying potential candidates and which are then manually curated.

Tn3 Transposon Finder (Tn3_finder) performs the automatic prediction of

transposable elements of the Tn*3* family in bacteria and archaea. It compares user-provided

bacterial and archaeal genome sequences to custom Tn*3* transposase and resolvase

databases by BLAST alignments. The criteria for identifying potential transposon regions

according to similarity, coverage and distance values can be adjusted by the user. Additional

ORFs that might be related to passenger genes are also predicted, and flanking regions can

also be retrieved and analyzed. The automatic prediction results are written in report files

and pre-annotated GenBank files to help in subsequent manual curation. Tn*3*_finder allows

for the concurrent analysis of multiple genomes by multithreading.

Composite Transposon Finder (TnComp_finder) predicts the putative composite

transposons in bacterial and archaeal genomes based on insertion sequence replicas in a

relatively short span. It works by comparing nucleotide sequences from bacterial and

archaeal genomes to a custom transposon database and identifying duplicated transposons

in user-defined genomic regions from BLAST alignments. Similar to Tn3_finder,

multithreaded analyses of multiple genomes are available and parameters for similarity,

coverage, distance and flanking regions can be adjusted by the user. Results are written in

report files and pre-annotated GenBank files to help in subsequent manual curation.

Antibiotic Resistance Gene-associated IS Finder (ISAbR_finder) is an experimental

program for the automatic prediction of antibiotic resistance genes associated with known

IS elements derived from the ISfinder database and has yet to be tested extensively. It

works by comparing IS nucleotide sequences from bacterial and archaeal genomes to a

custom antibiotic resistance database based on the parsing of BLAST alignment results,

using a number of parameters that can be customized by the user for stricter or more

relaxed criteria and allowing multithreaded alignments of multiple genomes. ISAbR_finder

also produces report files and pre-annotated GenBank files on which the recommended
manual curation should be performed.

Documentation. This section, which can be downloaded as a pdf file, provides a short
background description of transposons and TnCentral together with a short description of
the **curation workflow** and of planned future developments.

For Curators. This section provides a detailed description of the curation workflow used in
generating the annotated TnCentral data.

TnPedia. TnCentral provides access from the homepage to TnPedia, an online knowledge
base which contains information concerning transposition in prokaryotes. TnPedia is
developed using MediaWiki (https://www.mediawiki.org) and can also be accessed directly
(https://tnpedia.fcav.unesp.br/). It is structured into three main sections: **General**
Information, IS Families and Transposon Families (Figure 4).

The **General Information** section provides a series of clickable sections with an
extensive bibliography and direct links to the articles in PubMed. It includes a historical
perspective, definitions and descriptions of a variety of prokaryotic TE, the basic
mechanisms involved in their movement and the enzymes involved in these processes. It
also contains information describing their impact on their host genomes and how their
activities are controlled.

The **IS Families** section consists of individual chapters describing each of the ~25 IS
families in detail and covers, where possible, the identification of the founding members,
their organisation, distribution, variability and phylogenetic relationships, regulation of their
transposition, impact on their host genomes, and their transposition mechanisms including
genetic, biochemical and structural studies.

The **Transposon Families** section describes each transposon family with similar
information to that included in the IS family descriptions but, in addition, including a
detailed description of their structures and the passenger genes which they may carry.

Examples of TnCentral Use

Use Case #1: Comparing Protein Coding Genes in Tn*554* Family Members

The Tn*554* family is a small family restricted to the Firmicutes. Members encode three genes, *tnpA*, *tnpB* and *tnpC*, involved in transposition [28,29] (https://tnpedia.fcav.unesp.br/index.php/Transposons_families/Tn554_family). TnpA and TnpB both exhibit a C-terminal motif which shares all the important catalytic residues of a typical tyrosine site-specific recombinase [28,29]. They insert in a sequence-specific way into the DNA repair gene *radC* [30,31] and can also be found in a circular form [32–36]. To compare the protein coding genes in Tn*554* family members side by side, we searched for Tn*554* in the TE family field of the Transposon Search interface (Figure 5A). Fourteen Tn*554* family members were found (of which only 10 are shown in Figure 5B). In order to perform a side-by-side comparison of the protein-coding genes in these TE, we used the Customize Display option on the search results page, to add the "All Gene Fields" columns, which provide information about the protein coding genes, to the display and to remove several columns (e.g., Host Organism, Country) (Figure 5B). Results for two of the Tn*554* transposons (Tn*558.3* and Tn*559*) are shown in Figure 5C. Both transposons have the three-part transposition module (*tnpA*, *tnpB*, *tnpC*) characteristic of the family. However, the two transposons are quite diverse in their passenger genes. Tn*558.3* has gene called *fla*, which contains a flavodoxin-like domain, and the ABR gene *fexA*, which confers resistance to phenicol antibiotics. Tn*559* has just a single passenger gene, the ABR gene, *dfrK*, which confers resistance to diaminopyrimidine antibiotics. As shown by this example, the flexible search results page makes it easy to compare features across multiple transposons.

Use Case #2: Type II Toxin/Antitoxin Systems in Tn*3* Transposons

Toxin/Antitoxin (TA) systems are implicated in plasmid maintenance in bacterial populations [37]. These systems are characterized by a stable toxin and an unstable antitoxin that binds to the toxin and inhibits its lethal effect. Loss of a plasmid carrying a TA system will lead to rapid depletion of the antitoxin, allowing the persistent toxin to kill the cell. Thus, only members of a population that retain the plasmid will survive. Recently, a set of Tn*3*-family transposons carrying TA systems were characterized and included in the TnCentral database [22]. To explore these Tn, we used the TnCentral Gene Search function, selecting "Passenger Gene" from the Gene Class pull-down menu and "Toxin" from the Gene Sub-Class pull-down

menu (Figure 6A, red box). The search results included eight different toxin genes (Gp49,

HEPN, PIN, PIN_3, *abiEii*, *higB*, *parE*, and zeta) found in 43 different transposons. Similarly,

transposons carrying antitoxin genes were identified using the Gene Search function with

the Gene Sub-Class menu set to "Antitoxin" (Figure 6B, red box). There were 44 transposons

carrying 11 different antitoxin genes. Combinations of toxin and antitoxin genes in individual

transposons were examined by going to the ORF Summary section of the entry pages for the

TA transposons. For example, Tn*Sku1* (Figure 6B, yellow box; Figure 6C) has a Gp49 toxin

gene and an antitoxin gene containing an HTH domain (referred to as HTH). Most

transposons have a single toxin/antitoxin gene pair except for Tn*Xca1*, which has two TA

pairs, and Tn*5501.5*, which has a *parD* antitoxin gene and no toxin gene. The majority of

Tn*5501* derivatives in TnCentral have a *parE* toxin gene as well as the *parD* antitoxin,

suggesting that Tn*5501.5* may have undergone a deletion in the region containing *parE*

(Supplementary Figure 1).

Use Case #3: Tn*21* and its Relatives

Tn*21* is the canonical member of a subfamily of Tn*3* transposons that confers a variety of

antibiotic resistances [38–40] and several analyses have proposed mechanisms to explain

how *Tn21* arose from simpler ancestor transposons (e.g., [40,41]). Tn*21* has a mercury

resistance operon at the 5'- (left) end, a *tnpA*/*tnpR* transposition module at the 3'-(right)

end, and a transposition-deficient integron (In2) carrying several ABR genes (a GCN5-related

N-acetyltransferase (GNAT_fam), *sul1*, *qacEdelta1*, and *aadA*) in the middle (Supplementary

Figure 2). These ABR genes confer resistance to aminoglycosides, sulfones, sulfonamides,

quaternary ammonium salts, and acridine dye. More recently, a transposon that lacks the

integron insertion but is otherwise identical to Tn*21* (the hypothetical Tn*21* backbone Tn21Δ

in [40]) was discovered [42]. This transposon, Tn*5060*, was proposed to be the ancestor of

Tn*21* [42]. Tn*21* also has numerous relatives that carry different combinations of antibiotic

resistance genes within and outside the integron. To explore the Tn*21* subfamily, we

performed a TnCentral Sequence Search (BLAST) using the putative ancestral Tn*5060*

sequence (Figure 7A). In addition to Tn*5060* itself, we identified ten transposons in the

database (Tn*20*, Tn*21*, Tn*21.1*, Tn*21.2,* Tn*5086,* Tn*2411,* Tn*2424,* Tn*4*, Tn*1935*, and Tn*As3*;

Supplementary Figure 2) that contain all (or nearly all) of the Tn*5060* sequence. With the

exception of Tn*20*, which is almost identical to Tn*5060* (99.5%), these transposons have two

or more discontinuous sub-regions that align to Tn*5060*. For example, Tn*21* has two sub-

regions, one of which is a close match to the left half of Tn*5060* and the other of which is a

close match to the right half of Tn*5060* (red bars in Figure 7B). This suggests that these

transposons arose from Tn*5060* via the insertion of other sequences.

We compared the antibiotic resistance profiles of the ten transposons by inspecting their

TnCentral entry pages. Tn*20*, like Tn*5060*, carries no ABR genes. The other nine transposons

carry ABR genes targeting aminoglycosides, sulfones, sulfonamides, and quaternary

ammonium salts (Figure 7C). Other resistances found in a subset of the six include acridine

dye (Tn*1935*, Tn*21*, Tn*2411*, Tn*4*, Tn*As3,* Tn*2424,* Tn*5086*), carbapenams (Tn*1935* and Tn*4*),

cephalosporins (Tn*1935* and Tn*4*), carbapenems (Tn*4*), monobactams (Tn*4*), phenicols

(Tn*As3*, Tn*2424*, Tn*21.1*, Tn*21.2*), diaminopyrimidines (Tn*5086*, Tn*21.1*, *Tn21.2*), and

tetracyclines (Tn*21.2*)**.** Interestingly, in some cases where the transposons have resistances

in common, they are conferred by different genes (Figure 7C). For example, phenicol

resistance is conferred by *CAT* in Tn*As3, catB2 in* Tn*2424*, and *cmlA6* in Tn*21.1* and Tn*21.2*.

Similarly, sulfonamide and sulfone resistance is conferred by *sul1* in all of the antibiotic-

resistant family members except for Tn*21.1* and Tn*21.2*, where those resistances are

conferred by *sul3*. Thus, even this closely related subfamily of transposons shows diversity in

its antibiotic resistance genes. This is partially due to the flexibility of the integron to

incorporate new antibiotic resistance gene cassettes but also to insertion of ABR-gene

containing elements outside of the integron region (e.g., Tn*3.1* in Tn*4*, Supplementary Figure

2).

Discussion

Here, we have described TnCentral, a user-friendly resource for exploration of prokaryotic

TE. TnCentral provides a flexible search interface, TE-specific entry pages with intuitive

graphics and detailed information about TE features, and a BLAST interface that allows users

to identify TE that carry features of interest or to identify TE that are present in sequences

of interest (e.g., plasmids). As shown in the use cases, the flexible search results page makes

it easy to compare features across multiple transposons, the detailed entry pages allow

exploration of TE passenger genes, such as ABR genes, and the Sequence Search enables

retrieval of TE with related sequences that could be used as a starting point for evolutionary

analyses. Moreover, TnCentral provides access to Tnfinder software for locating candidate

TE in sequence data and to TnPedia, a comprehensive review of the biology of selected TE

families.

As discussed in the Introduction, a variety of resources dedicated to aspects of prokaryotic

TE biology currently exist. TnCentral's unique contribution to this universe of resources lies

in its coverage of a variety of TE (e.g. different transposon families and compound

transposons with their associated IS and integrons) and its detailed focus on both core

transposition genes and passenger genes of clinical, environmental, and economic

importance. It has the additional feature of providing a clear graphic output for visualizing

the often complex structures of TE.

The next step beyond annotation of individual TE is to annotate and visualize the TE content

of prokaryotic chromosomes and plasmids. These studies are critical for understanding the

propagation of high impact passenger genes, such as those that confer antibiotic resistance.

Several tools that address this problem are available. For example, ISsaga [43], which is

integrated into ISfinder, annotates IS present in user-provided sequences. Other software

suites have been designed specifically to annotate IS in short read raw data (e.g. ISQuest

[44], Transposon Insertion Finder [45], ISMapper [46] and panISa [47]) using preassembled

libraries of TE and their components, while yet other approaches are based on *ab initio*

prediction (e.g., OASIS [48], ISseeker [49] ISEscan [50], or provide a comparative view of IS

mobilisation events (e.g. ISCompare [51]). These annotation tools are only as good as their

underlying TE databases. ISfinder, which includes nearly 6000 individual examples of IS

classified in distinct families and subfamilies according to their transposition mechanism and

structural organization, provides such a rigorous framework for IS and has been

incorporated into a number of annotation pipelines (e.g., ISsaga [43], MobileElementFinder

[52]). However, IS represent only a fraction of prokaryotic TE, and unlike transposons and

integrons, they rarely carry passenger genes. We hope that TnCentral will become a

benchmark for more complex TE as ISfinder is for IS.

TnCentral is an ongoing project, and we will continue to expand and update the content. In
addition to the exporting annotated TE in GenBank format, we plan to make all files
available in a SnapGene file format which will allow users to use SnapGene
(https://www.snapgene.com/), a commercial software tool (with a free viewer version) for
visualizing and documenting nucleotide sequences and their features, to analyze and
explore them. We also intend to enhance the visualization of TnCentral Sequence Search
(i.e., BLAST) results to better support the analysis of plasmid sequences that may carry a
complex complement of TE although it should be noted that the Sequence Search tool can
already accommodate analysis of large plasmids. Ultimately, we envision that TnCentral
could be used to analyze the TE content of a collection of sequences, such as patient,
veterinary and environmental samples from an antibiotic resistance outbreak, to
understand TE-driven evolution of the prokaryotic mobilome.

Methods

Curation Workflow

The TnCentral curation workflow is depicted in Figure 8. Curation is performed by members
of the TnCentral development team as well as by graduate students in bioinformatics
courses at Georgetown University Medical Center. TnFinder scripts are run against RefSeq
and other sequence databases and GenBank files potentially containing TE are retrieved. TE
sequences are isolated and annotated using SnapGene (https://www.snapgene.com).
Features of interest (i.e., protein coding genes, TE, repeat elements, and recombination
sites) are annotated according to detailed curation guidelines (provided in the "For
Curators" of TnCentral). Fully annotated features are saved in a SnapGene Custom Library.
New transposon sequences can be searched against this library, enabling detection of
features previously identified in other TEs. All annotated TE files are checked by a second
curator. An enhanced GenBank file containing all annotations is exported from SnapGene
and checked for common curation formatting errors using a custom Perl script. Detected
errors are manually corrected in the SnapGene file, which is then exported as a revised
enhanced GenBank file. Information from this GenBank file is used to populate the
TnCentral database, which, in turn, serves as the backend for the TnCentral web portal. An

image file showing a color-coded map of TE features is also exported from SnapGene and

displayed on the TE entry page.

Although we have adhered to the standard nomenclature for transposons extracted from

the literature, for the many transposons newly identified during TnCentral database-

building, we have temporarily used names indicating their source. In all cases, the

Transposon Registry [53] accession number is provided as a synonym. There is some

ambiguity in the literature concerning class 1 integrons and members of the Tn*402*

transposon family. Class 1 integrons appear to be derivatives of this transposon family and

include members with a range of Tn*402* transposition genes with varying degrees of

completeness. We have therefore elected to include all Class 1 integrons as members of the

Tn*402* family (Supplementary Table S1). ISfinder classification is used for the individual IS

and in the case of compound transposons, the group to which they are belong is defined by

the flanking IS.

Properties of protein coding genes are annotated with cross-references to database or

ontology identifiers whenever possible. Antibiotic resistance gene properties, including gene

name, sequence family, antibiotic resistance mechanism, and target drug classes are

annotated according to the Antibiotic Resistance Ontology (ARO) as presented in

Comprehensive Antibiotic Resistance Database (CARD) [10]. The Pfam [54] and InterPro

resources [55] are used to define sequence family information.

TnCentral Website implementation

TE features and sequence information are extracted from the enhanced GenBank files. TE

feature information is used for the search and the entry pages, and the TE DNA and protein

sequence information are used for the Sequence Search and display. The extracted data is

loaded into the TnCentral database, implemented using MySQL. The website is built on a

Linux server with Apache, and the web application is built on Perl CGI. Apache Lucene is

used to index the data for flexible and fast search and retrieval. JavaScript is used for the

interactive web-interface and display. BLAST is used for similarity search.

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Figure Legends

Figure 1. Structural arrangement of prokaryotic Transposable Elements. The TE is indicated by a pale-yellow horizontal bar at the top of each section. Open reading frames are shown as horizontal arrows with the arrowheads indicating the direction of expression: purple, transposition-associated genes; red, antibiotic resistance genes; green, other passenger genes. The inverted terminal repeats found at the ends of the majority of TE are shown as grey arrows and the direct target repeats generally produced by insertion are indicated by small black arrows. **A.** Insertion Sequence (IS), a short DNA segment encoding only the mobilization protein (Transposase, TnpA), flanked by two imperfect Inverted Repeats (IRs), and generally containing a short flanking directly repeated duplication (DR) on the target of insertion. **B.** tIS (transporter IS) are structurally similar to an IS, but contain passenger genes. They are presently restricted to the IS*1595* and IS*66* families. **C.** Compound transposons are formed by two IS in either direct or inverted orientation, flanking a variety of passenger genes including those for antibiotic resistance. **D.** Transposons are more heterogeneous structures and include different sets of transposition-related genes which are specific to each Tn family and multiple antibiotic resistances, virulence and other passenger genes. This is an example of a Tn*3* family transposon with transposon, *tnpA*, and resolvase genes, *tnpR*.

Figure 2. A) TnCentral homepage showing clickable links to various TnCentral sections in the box on the left. B) TnCentral search interface showing search choices for TE on the left and for transposition-related and passenger genes on the left.

Figure 3. TnCentral TE Entry Page. #1-10: Sections of the entry page (see text for details).

Figure 4. The main sections of TnPedia, a TnCentral-related wiki compiling information on prokaryotic transposable elements. Only three of the four sections (General Information, IS families and Transposon families) are illustrated. The fourth section is a Transposition Glossary, which is under construction.

Figure 5. Comparing Protein Coding Genes in Tn*554* Family Members. A) TnCentral
Transposon Search interface, showing a search for Tn*554* in the TE family field. B) Interface
for customizing the columns in the search results display. Clicking on "Customize Display"
(red box) opens the interface. C) Partial Tn*554* family search results after customization to
show information on protein coding genes (All Gene Fields).

Figure 6. Exploring Toxin/Antitoxin Genes in TnCentral. A) Partial results of searching
TnCentral for toxin genes. The settings used to obtain these results are shown in the red
box. Links to entry pages for the TE carrying the indicated genes are provided in the MGE
Accession column (e.g., Tn*Sku1*-CP002358.1, yellow box). B) Partial search results for
antitoxin genes in TnCentral. Settings are shown in the red box. C) ORF Summary section of
the entry page for Tn*Sku1*-CP002358.1, showing the presence of a toxin/antitoxin gene pair
(Gp49 toxin/HTH antitoxin).

Figure 7. Analysis of ABR in Tn*21* Relatives. A) TnCentral Sequence Search using the
sequence of Tn*5060*, the proposed ancestor of Tn*21*, as a query. B) Sequence Search results.
The query sequence is represented by the width of the Alignment column. The red bars
represent regions of the matched transposons that are highly similar to regions of Tn*5060*.
C) ABR genes and targeted antibiotic classes in Tn*21* relatives. Red shading in the table cells
indicates that the transposon carries at least one gene targeting the antibiotic class; blue
shading indicates that it does not. The ABR genes found in each transposon are indicated in
the table cells.

Figure 8. TnCentral Curation Workflow (see text for description).

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501

Supplementary Figures
Supplementary Figure 1. Maps of Tn*5501* and Tn*5501.5* showing the loss of *parE* toxin gene
in Tn*5501.5*. Feature color code: yellow--TE; purple--transposition genes; dark orange--
toxin/anti-toxin genes; light orange--other open reading frames; grey--repeat elements;
green--recombination sites. Maps were created with SnapGene.

Supplementary Figure 2. Maps of Tn*21* and its relatives. The feature color code is the same

as in Supplementary Figure 1. Maps were created with SnapGene. Note that the different

transposon derivatives are not to scale but their individual lengths are included.

Supplementary Table S1. The table displays the entire collection of TE at present in the

database (May 2021) with columns indicating their **TnCentral accession numbers**, their

names, **synonyms** from the literature and/or the Transposon Registry [53], TE **Type, Family**

Group), **Host Organism** and **Molecular Source** (e.g., plasmid or chromosome). If no

information is provided in the Molecular Source column, the source is chromosomal or

unknown.

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A

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TnPedia (TE Encyclopedia)
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TnCentral

An annotated prokaryotic transposon database

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B

TnCentral Search

Transposon Search

Any field: [_____________]

TE Name [contains ▾] [__________]

TE Synonym: [contains ▾] [__________]

TE type: [All ▾]

TE family: [contains ▾] [__________]

TE group: [contains ▾] [__________]

TnCentral accession: [contains ▾] [__________]

Host organism: [contains ▾] [__________]

Country: [__________]

Date of Isolation: [__________]

[Submit] [Reset]

Gene Search

By Gene Name:
[__________]
[Submit]

By Gene Class:
[-- Select one ---------------- ▾]
[Submit]

By Gene Function:
[-- Select one ---------------- ▾]
[Submit]

1

Transposon

Name: Tn5501

Family: Tn3 **Group:** Tn3000

Evidence of Transposition: Yes

Host

Host Organism: Delftia sp. KV29 **Molecular Source:** plasmid pKV29

Date of Isolation: 1998

Map

2

Tn5501–JN648090.1
7928 bp

Terminal Inverted Repeats (IR)

3

IRL (Length: 38 bp) → GGGGTTCTTAAGCCGGAACCGCCGAAAATTCCGTCAGCC

IRR (Length: 38 bp) → GGGGTTCTTAAGCCAGAACCGCCGAAATTTCCGTCATCC

Sequence

4

DNA Sequence Length 7928

```
----------10--------20--------30--------40--------50--------60--------70--------80--------90-------100
GGGGTTCTAA GCCGGAACCG CCGAAAATTC CGTCAGCCGA TCAACGTGGC TTGTCCCGAG CCCGGTCGAT GGGGTAGACC CAACAGTCGT GTCACTAGCC 100
GCCATTTCGA TCACGGCAAT GCCAGCCGGA CGTCACGTCC AGATTGTTCC TGCTGGATG AGACGCGGTGG CATACAACTG GGAA 200
CTGTGAGTCC TGCAGGGGGG CAGCTGCTG ACCGGACGGC GAGCATCGAC CCATCTCATG TATTAGTCAT GTCAGCTTTG ACACTGCGCA CGCGACGGCA 300
CCCGACCCGT TGCAGACCCC CAGACATATG GAAAGCTGAC CACAATG GAGTTAGCCG GCGCGGCGCG GCTTCATCGC GCAGCGTCCG TGTTGATGGA 400
```

Recombination Sites

5

Name	Coordinates	Length	Sequence
res	4139-4269	131	GCCTGTCGGA AAACATTTGT TTTTCGACAG GCCTTCAACG GTCCTCTGCA CCAACCTCCG AGTGGCCGCA AAATTGTGCG GAAAACTCTG TCGCCAGACG CTACCATACG GAAACCTCGT CTTAATGGTT T

ORFs

6

ORF Summary

Gene Name	Associated TE	Coordinates	Class	Sub Class	Orientation
tnp	ISDIsp1	462-1436	Transposase		+
cupin2	Tn5501	1626-2111	Passenger Gene	Other	-
tnpA	ISGNB1-1	2150-3097	Transposase		-

ORF Details

7

Gene Name	Protein Name	Associated TE	Length	Coordinates	Strand
tnp	Tnp	ISDIsp1	975	462-1436	+

Class: Transposase

Transpoase Chemistry: DDE

Protein Sequence:
```
MLTGMKQSSL ELNLSTRKTR KQELLAQMDR VVPWAALVEL IAPYYPEGKN GRPPFALEAM LRVHCMQQWF TLSDLAMEEA FFDTPIYREF AGLDAHGRMP
DESTILRFRH RLEKHRLAEQ ILATVNDLLA ARGLLLKAGT AVDATLIAAP SSTKNKDRKR DPEMHSSQKG NEWHFGMKAH IGVDADSGLV HTVIGTSGNV
ADVTEGNSLL HGEETDAFGD AGYQGAHKRP DARKDVTWHV AMRPGKRKEL DKENNPVDAL IDQVEKIKAS IRAKVEHPFR VIKRQFGYTK VRYRGLKKNT
LQLKTLFALS NLWMVRHQLL GAQG
```

Internal Transposable Elements (TE)

8

TnCentral Accession	TE Name	Type	Coordinates	Length
ISDIsp1-JN648090.1	ISDIsp1	Insertion Sequence	409-1592	1184
ISGNB1-1-EF628291	ISGNB1	Insertion Sequence	2097-3143	1047

Internal Repeat Elements

9

Name	Associated Mobile Element	Coordinates	Sequence (Top Strand)
IRL	ISDIsp1	409-428	GGAAATCCTG CAAAACCTCG
IRR	ISDIsp1	1574-1592	GCTCAACAAG TCCTGTAGG

References

10

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General Information

Main Page

Welcome to TnPedia, the TnCentral Wiki

This Tnpedia has been written in an attempt to assemble a body of information (including many of the historical articles) generally dispersed in the literature as an aid to understanding how knowledge has been built up to our present view of the key role played by transposable elements (TE) in prokaryotes – both in influencing gene expression, in driving genome evolution and in facilitating horizontal gene transfer (HGT). It is divided into four sections:

General Information on Prokaryotic Elements

A section providing general information about Transposition and **T**ransposable **E**lements (TE) with emphasis on prokaryotic elements. It was originally written for ISfinder (https://www-is.biotoul.fr/index.php) with contributions from P. Siguier and E. Gourbeyre. It contains historical, mechanistic and genetic information.

Insertion Sequence (IS) Families

A second section describing each **I**nsertion **S**equence (IS) family in some detail. This section has been entirely updated compared to that which was included in a previous ISfinder version. It contains information from a number of reviews and from the primary literature together with analyses undertaken in the framework of ISfinder and TnCentral. P. Siguier and E. Gourbeyre provided a large proportion of these analyses.

Transposon families [In progress]

A third section presenting detailed descriptions of transposon and transposon families written in the framework of TnCentral.

IS Families

Transposon families

A — Transposon Search

Any field: ___
TE Name: [contains ▾] ___
TE Synonym: [contains ▾] ___
TE type: [All ▾]
TE family: [contains ▾] Tn554
TE group: [contains ▾] ___
TnCentral accession: [contains ▾] ___
Host organism: [contains ▾] ___
Country: ___
Date of Isolation: ___
[Submit] [Reset]

B — Transposon Search

Transposon Search Output Page

search ▸ [MGE Family ▾] [AND ▾] [Any Field ▾] + add input box
Tn554 — del input box

Page Size [10 items/page ▾]

Fields Not in Display: Country, Date of Isolation, Evidence of Transposition, First Isolate
Fields In Display: All Gene Fields, MGE Family, MGE Name
[apply ✓] [cancel ✗]

14 entries | 2 pages | 10 / page | [1] 2

[Select]

 Customize Display Save Result As: ⌄TABLE | ⌄FASTA

TnCentral Accession	MGE Name	MGE Synonyms	MGE Type	MGE Family	MGE Group	Host Organism	Country	Date of Isolation
Tn5406-AF186237	Tn5406		transposon	Tn554		Staphylococcus aureus MRSA	Spain	January 2011
Tn554-X03216.1.1	Tn554		transposon	Tn554		Staphylococcus aureus	USA	1979
Tn554Cad-AB037671.1	Tn554Cad		transposon	Tn554		Staphylococcus aureus 85_2082	New Zealand	2001
Tn558-AJ715531.1	Tn558		transposon	Tn554		Staphylococcus lentus	USA	2004
Tn558.1-AM408573.1	Tn558.1		transposon	Tn554		Staphylococcus warneri	Denmark	2006
Tn558.2-MH018573	Tn558.2		transposon	Tn554		Enterococcus Enterococcus avium strain C674	China	2018
Tn558.3-CP025122	Tn558.3		transposon	Tn554		Bacillus sp. HBCD-sjtu	China	2017
Tn559-FN677369	Tn559		transposon	Tn554		Staphylococcus aureus ST398	Germany	2010
Tn6133-FR772051.1	Tn6133		transposon	Tn554		Staphylococcus aureus subsp. aureus ST398	Switzerland	2011
Tn6188-HF565366	Tn6188		transposon	Tn554		Listeria monocytogenes 6179	Austria	2013

C

TnCentral Accession	MGE Name	MGE Family	Gene Name	Gene Class	Gene Function	ORF Target	Gene Length (bp)	Protein Length (aa)	Protein Molecular Function	Sequence Family
Tn558.3-CP025122	Tn558.3	Tn554	tnpA	Transposase			1086	361		
			tnpB	Transposase			1920	639		
			tnpC	Accessory Gene	Helper		366	121		Tn554_family
			fla	Passenger Gene	Other		417	138		flavodoxin
			fexA (ARO:3002704)	Passenger Gene	Antibiotic Resistance	phenicol antibiotic (ARO:3000387)	1428	475	antibiotic efflux (ARO:0010000)	major facilitator superfamily (MFS) antibiotic efflux pump (ARO:0010002)
Tn559-FN677369	Tn559	Tn554	tnpA	Transposase			1086	361		
			tnpB	Transposase			1893	630		
			tnpC	Accessory Gene	Helper		378	125		Tn554_family
			dfrK (ARO:3002869)	Passenger Gene	Antibiotic Resistance	diaminopyrimidine antibiotic (ARO:3000171)	492	163	antibiotic target replacement (ARO:0001002)	trimethoprim resistant dihydrofolate reductase dfr (ARO:3001218)

Gene Search

Gene Search Output Page

8 items | 1 page | 10 / page |

↓ Select   ↘Customize Display   Save As ↘TABLE

☐ Gene Name	Gene Class	Gene Function	ORF Target	MGE Accession	MGE Name	Host Organism	Country
☐ Gp49	Passenger Gene	Toxin	ribosome associated mRNA	TnpPGH1-Y09450.1	TnpPGH1	Pseudomonas putida	
				TnSku1-CP002358.1	TnSku1	Sulfuricurvum kujiense DSM 16994	Japan
				Tn4662a.1-AY831462.1	Tn4662a.1	Pseudomonas putida GJ31	
				Tn4662a-NC_014124.1	Tn4662a	Pseudomonas putida HS	U.S.A
				Tn5501.12-CP017294.1	Tn5501.12	Pseudomonas aeruginosa PA83	Germany
☐ HEPN	Passenger Gene	Toxin	RNA	TnSod9-NC_004349	TnSod9	Shewanella oneidensis MR-1	
☐ PIN	Passenger Gene	Toxin	single stranded RNA	TnXca1-NC_007507	TnXca1	Xanthomonas campestris pv. vesicatoria	
				TnPsy42-KX009060.1	TnPsy42	Pseudomonas syringae pv. actinidiae RT594	Japan
				TnXax1.1-NC_016053	TnXax1.1	Xanthomonas arboricola pv. pruni CFBP 55306	

11 items | 2 pages | 10 / page | 1 | 2

↓ Select   ↘Customize Display   Save As ↘TABLE

☐ Gene Name	Gene Class	Gene Function	ORF Target	MGE Accession	MGE Name	Host Organism	Country
☐ HTH	Passenger Gene	Antitoxin		TnSku1-CP002358.1	TnSku1	Sulfuricurvum kujiense DSM 16994	Japan
☐ HTH_37	Passenger Gene	Antitoxin		Tn4662a.1-AY831462.1	Tn4662a.1	Pseudomonas putida GJ31	
				Tn4662a-NC_014124.1	Tn4662a	Pseudomonas putida HS	U.S.A
				Tn5501.12-CP017294.1	Tn5501.12	Pseudomonas aeruginosa PA83	Germany
				TnpPGH1-Y09450.1	TnpPGH1	Pseudomonas putida	
☐ PIN_12	Passenger Gene	Antitoxin		TnBth3-CP003766	TnBth3	Bacillus thuringiensis HD-789	

ORF Summary

Gene Name	Associated TE	Coordinates	Class	Sub Class	Orientation
HTH	TnSku1	126-416	Passenger Gene	Antitoxin	+
Gp49	TnSku1	419-712	Passenger Gene	Toxin	+
tnpR	TnSku1	713-1336	Accessory Gene	Resolvase	-
tnpA	TnSku1	1492-4410	Transposase		+

A

Sequence Search (BLAST)

Job Name: [   ]

Database

TnCentral

Other Sequence Search Services: iSfinder: ◯ CARD: ◯ Toxin/Antitoxin: ◯ NCBI: ◯

Query Sequence

Enter a sequence here:

```
>Tn5060
GGGGGCACCTCAGAAAACGGAAAATAAAGCACGCTAAGGCATAGCTGACCTTGCCAGGCCTGCTTCGCCCTGTAGTGACGCGATCAACGGGCAG
GAAACATTCCCCTTTCGTGCATGGCAGGCGCACACGAGTTCAGACAGCACGGTTTCCATGCGCGCCAAGTCGGCCATCTTCTCGCGCACGTCCT
TGAGCTTGTGTTCGGCCAGGCTGCTGGCCTCCTCGCAGTGGGTGCCATCGTCGAGCCGCAACAGCTCGGCAATCTCGTCCAGACTGAACCCCAG
CCGCTGTGCCGATTTCACGAATTTCACCCGAACCACGTCCCGCTCTCCCATAGCGGCGATGCTGCCGTAAGGCTTGTCCGGTTCCGGCAACAGG
CCCTTGCGCTGATAGAAGCGGATTGTCTCCACGCTGACCCCGGCCGCCTTGGCAAAAACGCCAATGGTCAGGTTTTCCAAATTATTTTCCATAT
CGCTTGACTCCGTACATGAGTACGGAAGTAAGGTTACGCTATCCAATCCAAATTCAAAAGGGCCAACGTATGTCTGAACCACAAAACGGGCGCG
GTGCGCTCTTCGCCGGCGGGCTGGCCGCCATTCTTGCATCGACCTGCTGCCTGGGGCCGCTAGTACTGGTCGCCCTGGGCTTCTCCGGTGCTTG
GATCGGCAACCTGACGGTGCTGGAACCCTATCGACCGTTGTTCATCGGCGCGGCGCTAGTGGCGCTGTTCTTCGCCTGGAAGCGGATTTACCGG
CCCGTGCAGGCATGCAAGCCAGGTGAGGTCTGCGCGATTCCGCAGGTGCGCGCCACCTACAAGCTGATTTTCTGGATCGTGGCCGTGCTGGTCC
```

Or, upload file (Fasta format) : [Choose File] No file chosen

B

TnCentral Accession	TE Name	TE Length	Host Organism	TE Family	Alignment (by score)
Tn5060-AJ551280.1	Tn5060	8667	Pseudomonas sp. A19-1	Tn3	
Tn20-AF457211.1	Tn20	8644	Escherichia coli	Tn3	
Tn21-AF071413	Tn21	19672	Shigella flexneri	Tn3	
TnAs3-CP000645.1	TnAs3	18735		Tn3	
Tn21.2-MH626558	Tn21.2	35400	Salmonella enterica subsp. enterica serovar Typhimurium	Tn3	
Tn2424-UGCJ01000005	Tn2424	26008	Escherichia coli NCTC11186	Tn3	
Tn5086-CP054343	Tn5086	15341	Escherichia coli SCU-164	Tn3	
Tn1935-MK797990	Tn1935	23364	Salmonella enterica subsp. enterica serovar Wien ZM3	Tn3	
Tn21.1-MH257753	Tn21.1	21668	Salmonella enterica subsp. enterica serovar Typhimurium	Tn3	
Tn2411-FN554766	Tn2411	18055	Escherichia coli 042	Tn3	
Tn4-KY749247.1	Tn4	23009	Salmonella enterica subsp. enterica serovar Paratyphi B	Tn3	

C

	Tn1935	Tn21	Tn2411	Tn4	TnAs3	Tn2424	Tn5086	Tn21.1	Tn21.2
aminoglycosides	GNAT_fam, aadA, aph3'-Ia	GNAT_fam, aadA				GNAT_fam, AAC(6')-Ia, aadA3	GNAT_fam	aadA, aadA2	
sulfonamides	sul1							sul3	
sulfones	sul1							sul3	
quaternary ammonium salts	qacEdelta1								qacL
acridine dye	qacEdelta1								
phenicols					CAT	catB2		cmlA6	
diaminopyrimidines							dfrA7	dfrA12	
tetracyclines									tetR, tet(B), tetC_p
penams	bla-OXA-1			bla-TEM-1					
cephalosporins	bla-OXA-1			bla-TEM-1					
penems				bla-TEM-1					
monobactams				bla-TEM-1					

TnFinder Scripts, Literature

GenBank File

SnapGene® 5.2.4

- New DNA File...
- New Protein File...
- Open
- Open Recent File
- Import

Transposon Feature Map (Image file)

Curation Guidelines

Enhanced GenBank File

QC: Validation by Second Curator Automated Format Checking (Perl Script)

TnCentral Database

TnCentral
An annotated prokaryotic transposon database

TnCentral Website