



# Suffix Trees and their applications

Amit Metodi and Tali Weinberger

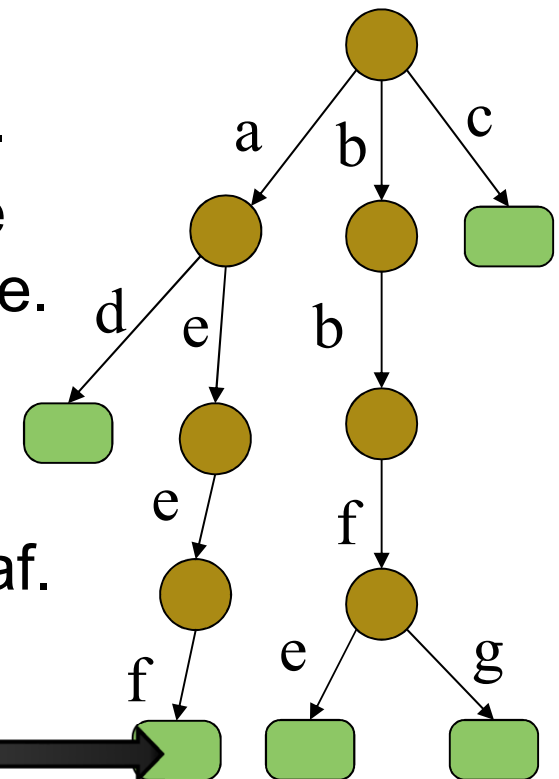


# Outline

- Introduction to Suffix Trees
  - Trie and Compressed Trie
  - Suffix Tree
  - Trivial Construction Algorithm  $O(N^2)$
  - Exact string matching
  - Generalized suffix tree
- Applications

# Trie

- A tree representing a set of strings.  
(Assume no string is a prefix of another)
- Each edge is labeled by a letter.
- No two edges outgoing from the same node are labeled the same.
- Each string corresponds to a leaf.



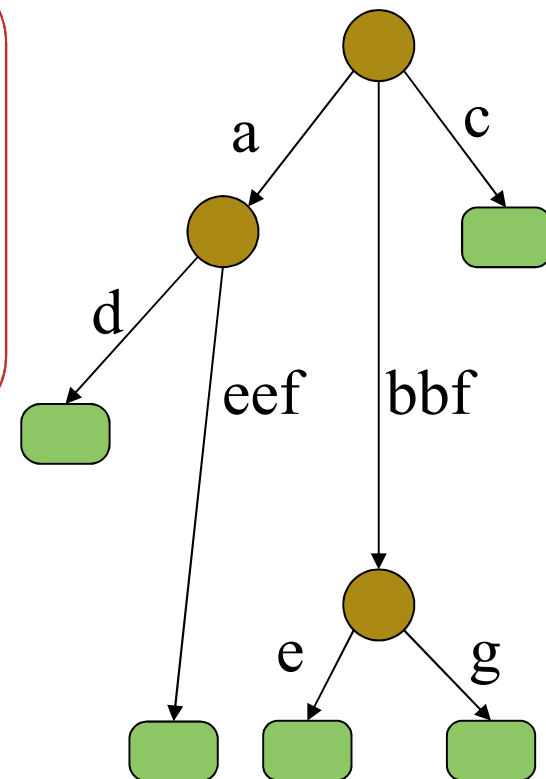
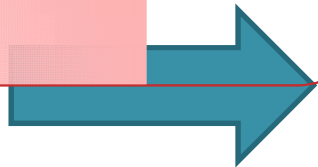
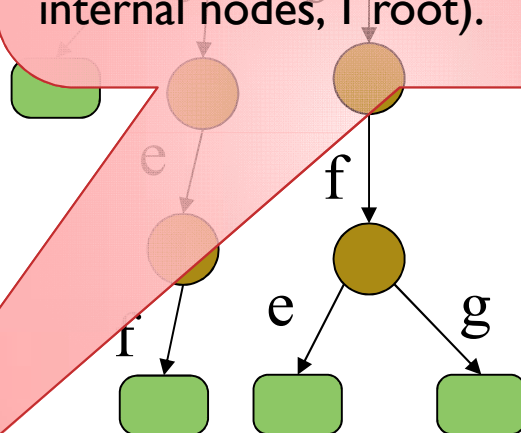
“aeef”

{ “aeef”, “ad”, “bbfe”, “bbfg”, “c” }

# Compressed Trie

- Compress unary nodes, label edges by strings.

All internal non-root nodes are branching, there can be at most  $n-1$  such nodes, and  $n+(n-1)+1=$   
 **$2n$  nodes in total** ( $n$  leaves,  $n-1$  internal nodes,  $1$  root).



{ "aeef", "ad", "bbfe", "bbfg", "c" }

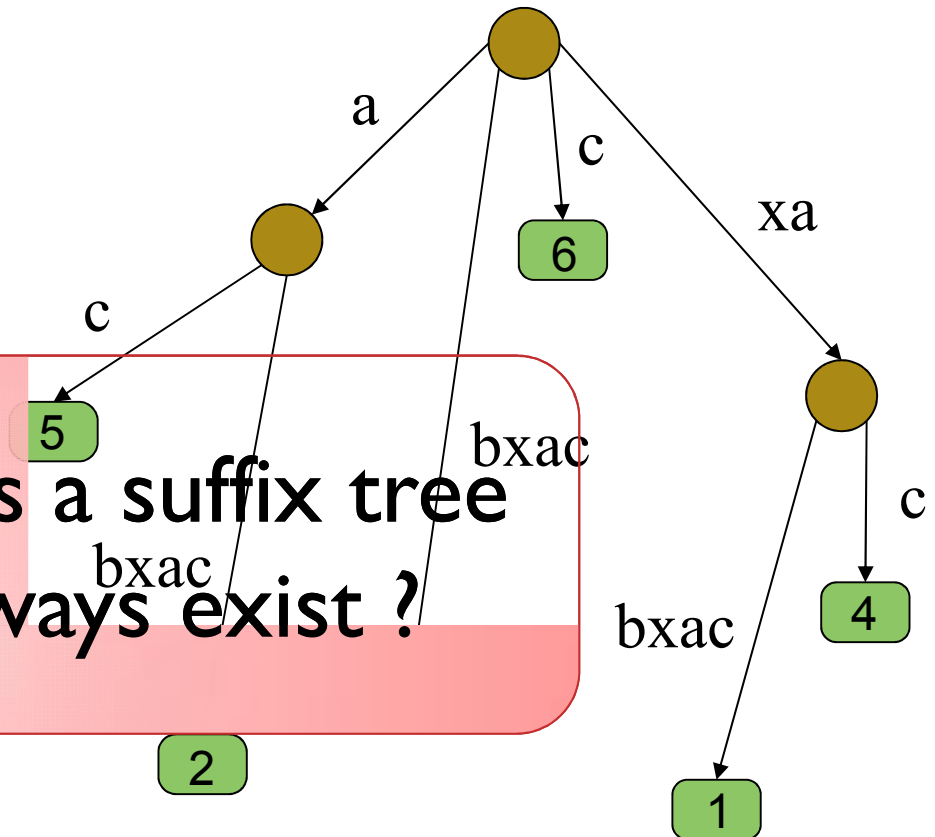
# Suffix Tree

- A suffix tree of string  $S[1..n]$  is a compressed trie of all suffixes of  $S$ .
- Denote  $S[i..n]$  by  $S_i$

$S = \text{"x a b x a c"}$   
 1 2 3 4 5 6

{  
 $S_6 = c$   
 $S_5 = ac$   
 $S_4 = xac$   
 $S_3 = bxac$   
 $S_2 = abxac$   
 $S_1 = abxac$   
 }

Does a suffix tree  
 always exist ?



# Suffix Tree

**S** = “x a b x a”  
      | 2 3 4 5

{

$S_5 = a$

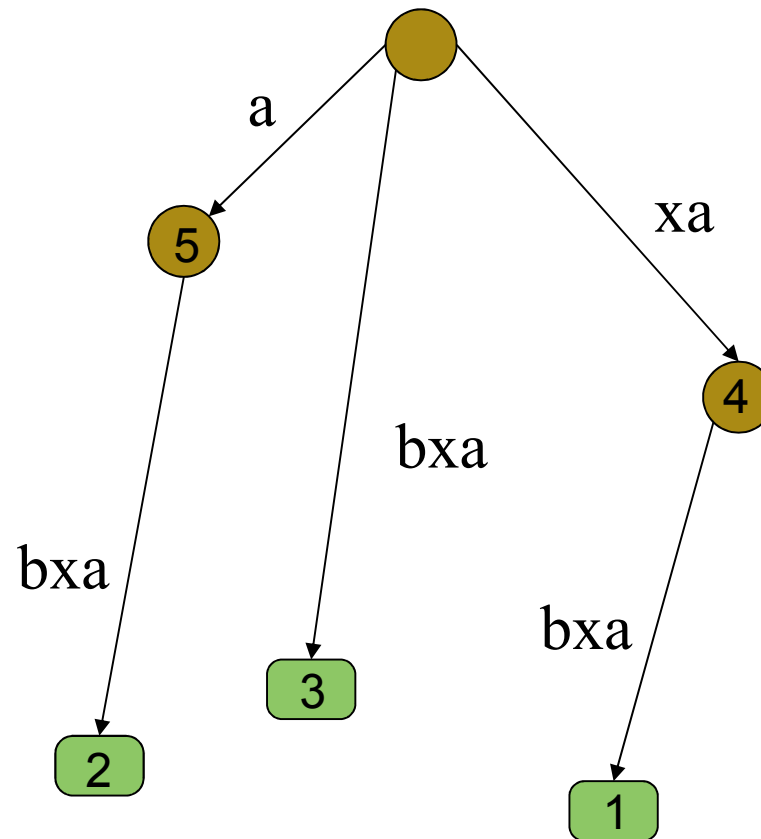
$S_4 = xa$

$S_3 = bxa$

$S_2 = abxa$

$S_1 = xabxa$

}



The fourth suffix *xa* or the fifth suffix *a* won't be represented by a leaf node.

# Suffix Tree

- Solution: insert a special terminal character at the end such as \$.
- Then, xa\$ will not be a prefix of the suffix xabxa\$.

**S** = “x a b x a \$”  
          1 2 3 4 5 6

{

$S_6 = \$$

$S_5 = a\$$

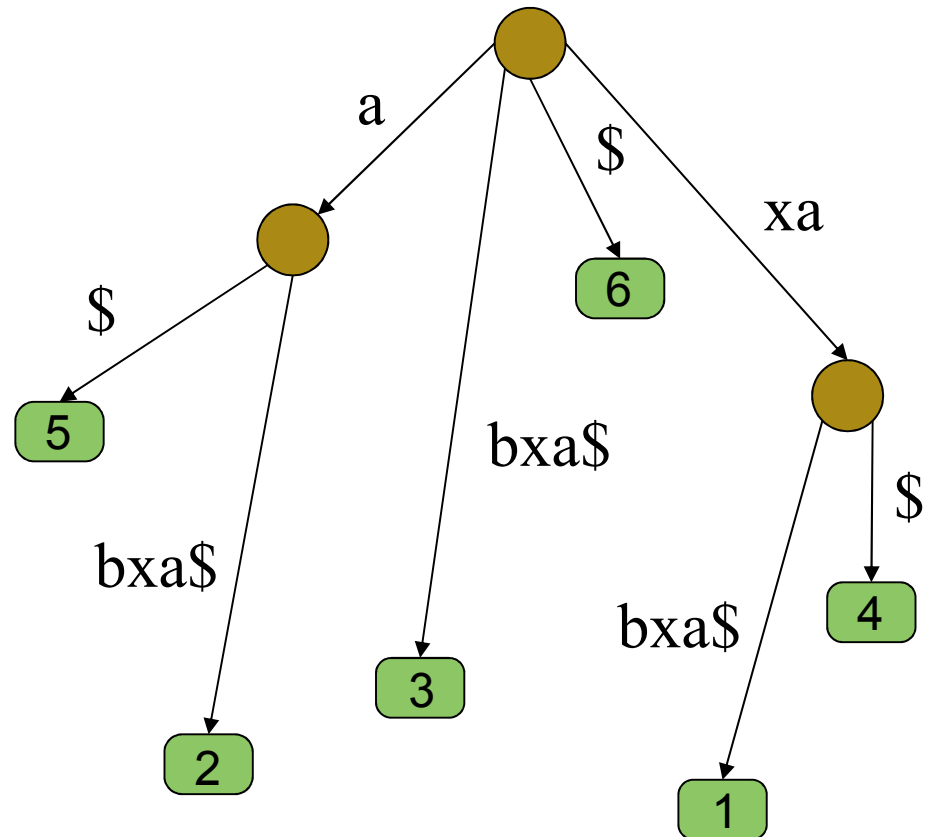
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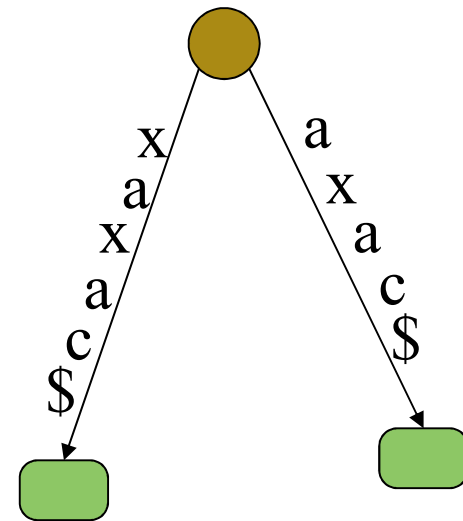




# Trivial algorithm to build Suffix tree

Build suffix tree  $S = \text{xaxac}$  ( $S' = \text{xaxac\$}$ )

- Put the largest suffix **xaxac\$**
- Put the suffix **axac\$**
- Put the suffix **xac\$**

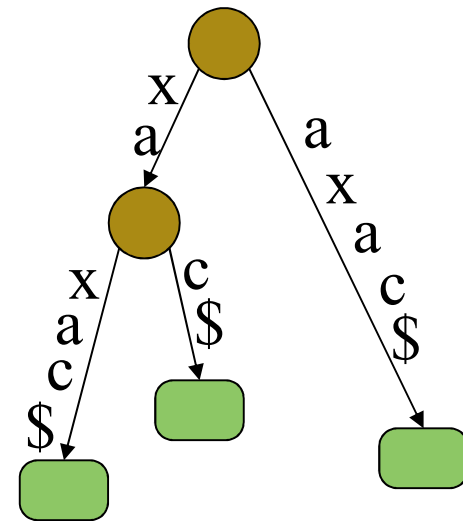




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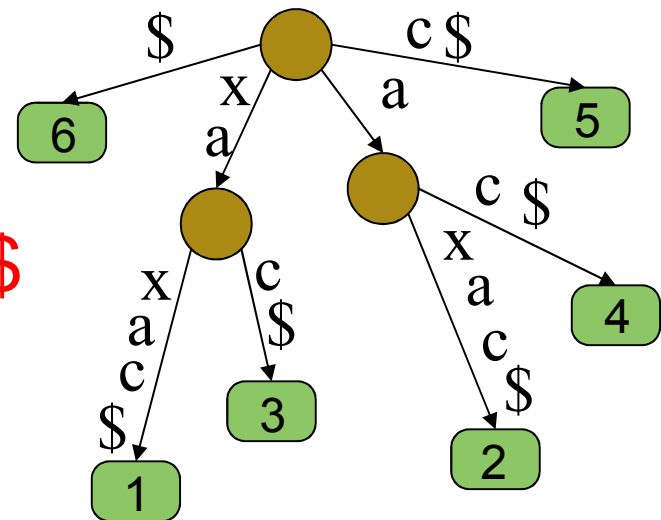
- Put the largest suffix **xaxac\$**
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- Put the suffix **ac\$**



# Trivial algorithm to build Suffix tree

Build suffix tree  $S = \text{xaxac}$  ( $S' = \text{xaxac\$}$ )

- Put the largest suffix **xaxac\$**
- Put the suffix **axac\$**
- Put the suffix **xac\$**
- Put the suffix **ac\$**
- Put the suffix **c\$**
- Put the smallest suffix **\$**
- Label each leaf with the starting point.



# Complexity – Run Time

- We need  $O(n-i+1)$  time for the  $i^{\text{th}}$  suffix. Therefore the total running time is:

$$\sum_{i=1}^n O(i) = O(n^2)$$

- Ukkonen in 1995 provided the first online-construction of suffix trees with the running time that matched the then fastest algorithms. These algorithms are all linear-time for a constant-size alphabet, and have worst-case running time of  $O(n \log n)$  in general.
- Martin Farach in 1997 gave the first suffix tree construction algorithm that is optimal for all alphabets  $O(n)$



# Complexity - Space

- Will also take  $O(n^2)$  if we would store every suffix in the tree separately.
- Note that, we should not store the actual substrings  $S[i \dots j]$  of  $S$  in the edges, but only their start and end indices  $(i, j)$ .
- Nevertheless we keep thinking of the edge labels as substrings of  $S$ .
- This will reduce the space complexity to  $O(n)$

# Exact string matching

- Given  $S$  and  $P$  strings where  $|S|=n$  and  $|P|=m$ . Find all occurrences of  $P$  in  $S$ .

$S=$	m	i	s	s	i	s	s	i	p	p	i
	1	2	3	4	5	6	7	8	9	10	11
$P=$	i	i	i	i	i	s	s	i	s	s	i

- Naïve algorithm =  $O(n*m)$

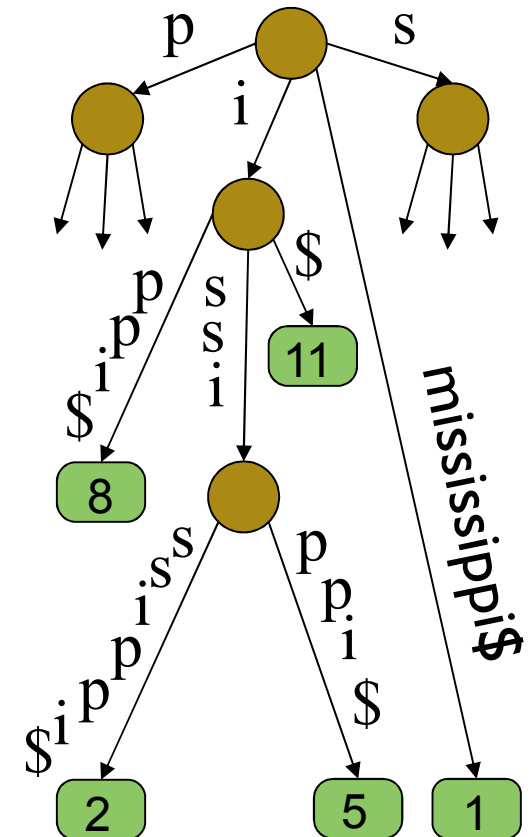
# Exact string matching

- Given  $S$  and  $P$  strings where  $|S|=n$  and  $|P|=m$ . Find all occurrences of  $P$  in  $S$ .

### Using suffix tree:

1. Build suffix tree  $\mathbf{O(n)}$
2. Try to match P on a path. Three cases:
  - a. No match  $\rightarrow$  P does not occur in T.
  - b. The match of P ends in a node u. Set  $x = u$ .
  - c. The match ends inside an edge (v,w). Set  $x=w$ . $\mathbf{O(m)}$
3. All leaves below x represent occurrences of P.  
 $\mathbf{O(k)}$  (where k = number of occurrences of P in S)

**Total time:  $O(n+m+k) \approx O(n)$**





# Generalized suffix tree

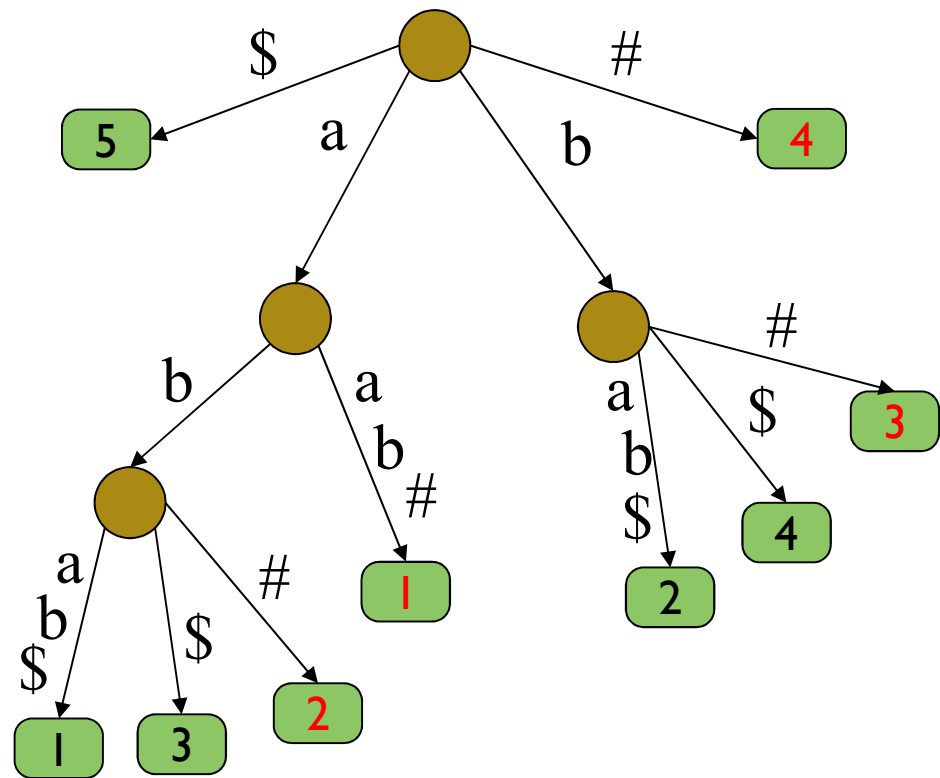
- Given a set of strings  $T$  a generalized suffix tree of  $T$  is a compressed trie of all suffixes of  $S \in T$ .
- To make these suffixes prefix-free we add a special char at the end of  $S$ .
- To associate each suffix with a unique string in  $T$ , add a different special char to each  $S \in T$ .



# Generalized suffix tree

- Let  $S_1 = abab$  and  $S_2 = aab$  here is a generalized suffix tree for  $S_1$  and  $S_2$

{  
 \$            #  
 b\$        b#  
 ab\$      ab#  
 bab\$    aab#  
 abab\$  
 }





# Applications of suffix trees

- Longest Common Substring
  - DNA Contamination Problem
- Maximal Repetitive Structures
- Longest common extension
- Finding maximal palindromes
- The k-mismatch problem

# Longest Common Substring

- Given strings A and B find the longest substring common to both strings.

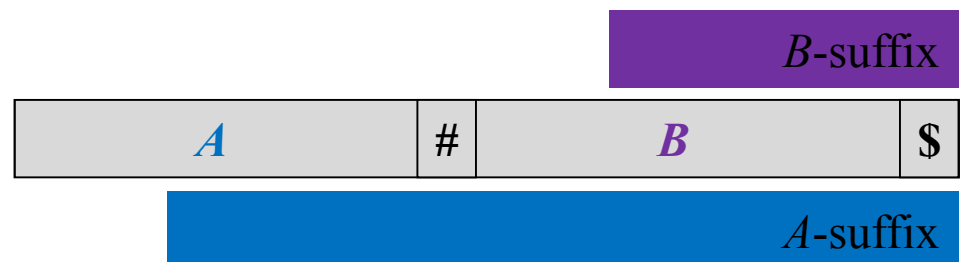
- String A = lambada
- String B = abady
- Longest Common Substring = bad

**Donald E. Kn**  
conjectured in  
1970 that

It is impossible  
Longest Comm  
problem in  $O(|$

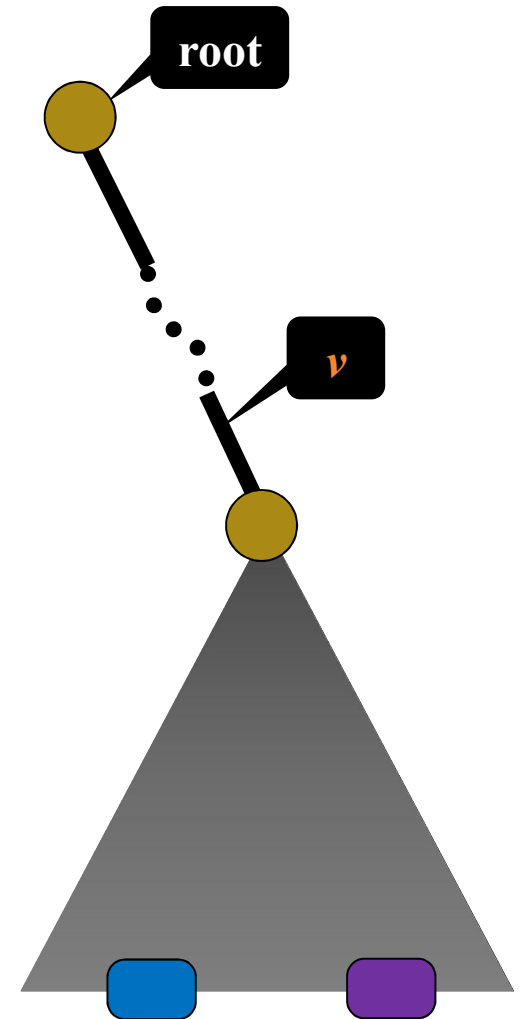
# LCS<sub>substring</sub> - Idea

- Construct a suffix tree  $T$  for  $A\#B\$$ , where  $\#$  and  $\$$  are two characters not in  $A$  and  $B$ .
- There are exactly  $|A|+|B|+2$  leaves in  $T$ , each leaf corresponds to a suffix of  $A\#B\$$ .
  - $A$ -leaf: with label in  $\{1, 2, \dots, |A|\}$ 
    - corresponds to an  $A$ -suffix.
  - $B$ -leaf: with label in  $\{|A|+2, \dots, |A|+|B|+1\}$ 
    - corresponds to a  $B$ -suffix.



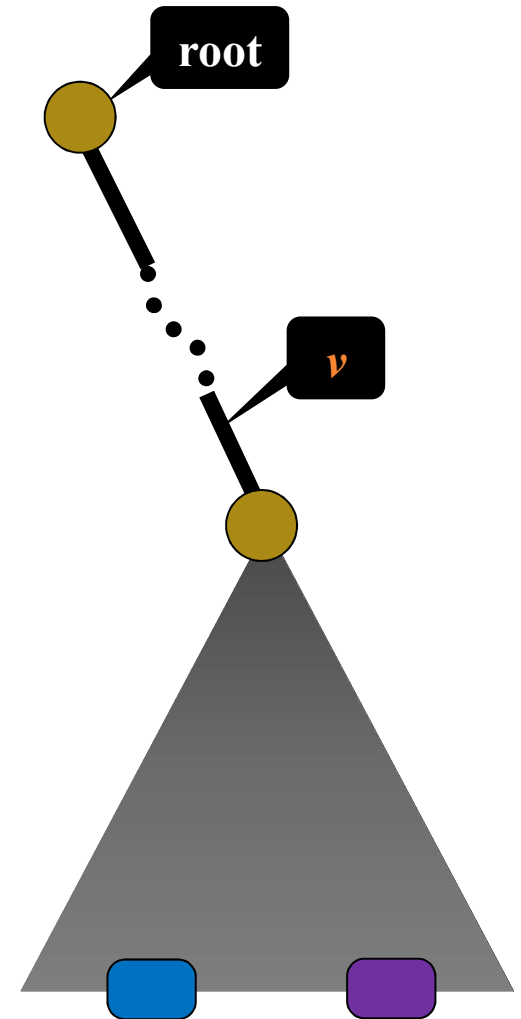
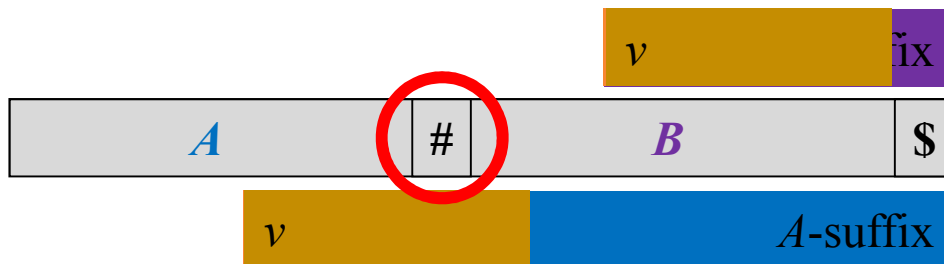
# LCS<sub>substring</sub> - Observation

- Let  $v$  be an arbitrary position of  $T$  (i.e.,  $v$  is not necessarily a node of  $T$ )
  - $v$  has a descendant  $A$ -leaf if and only if  $v$  corresponds to a prefix of an  $A$ -suffix of  $A\#B\$$ .
  - $v$  has a descendant  $B$ -leaf if and only if  $v$  corresponds to a prefix of a  $B$ -suffix of  $A\#B\$$ .



# LCS<sub>substring</sub> - Lemma

- Let  $v$  be a position of  $T$ .  
 $v$  has descendant  $A$ -leaf and  $B$ -leaf  
 if and only if  $v$   
 corresponds to a  
 common substring of  
 $A$  and  $B$ .



# $\text{LCS}_{\text{substring}}$ – Algorithm

Single  
DFS

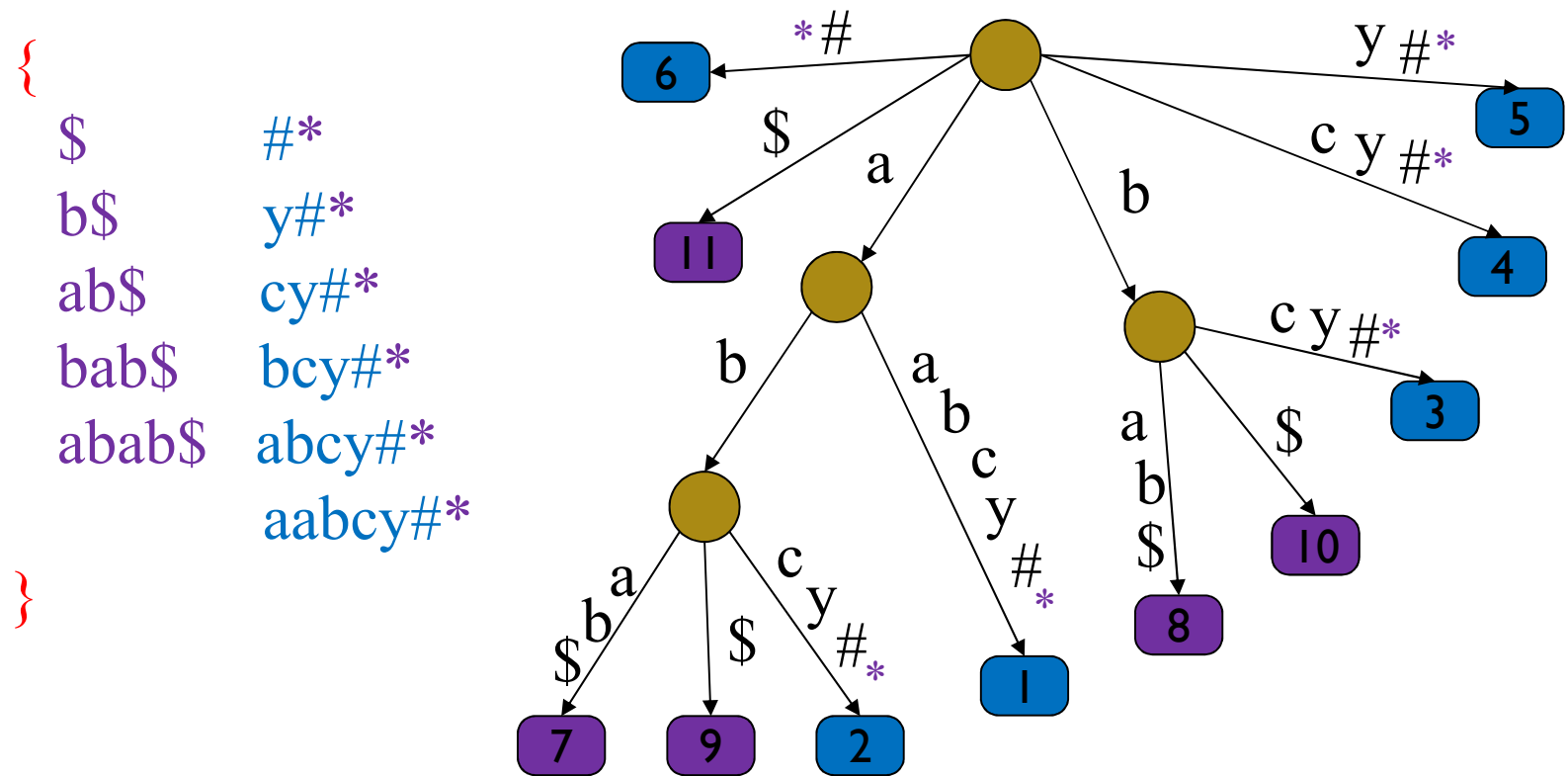
- Construct a suffix tree  $T$  for  $A\#B\$$ .  $\mathbf{O(|A|+|B|)}$
- Marking the colors of each node, including each leaf and each internal nodes.  $\mathbf{O(|A|+|B|)}$
- Computing the depths of all nodes.  $\mathbf{O(|A|+|B|)}$
- Find a deepest internal node with both colors.  $\mathbf{O(|A|+|B|)}$
- Output the string corresponding to the deepest internal node  $v$  such that the subtree of  $T$  rooted at  $v$  contains both  $A$ -leaf and  $B$ -leaf.
- **Time:**  $\mathbf{O(|A|+|B|)}$
- **Space:**  $\mathbf{O(|A|+|B|)}$

**Space** can be reduced to  
 $\mathbf{O(|A|)}$



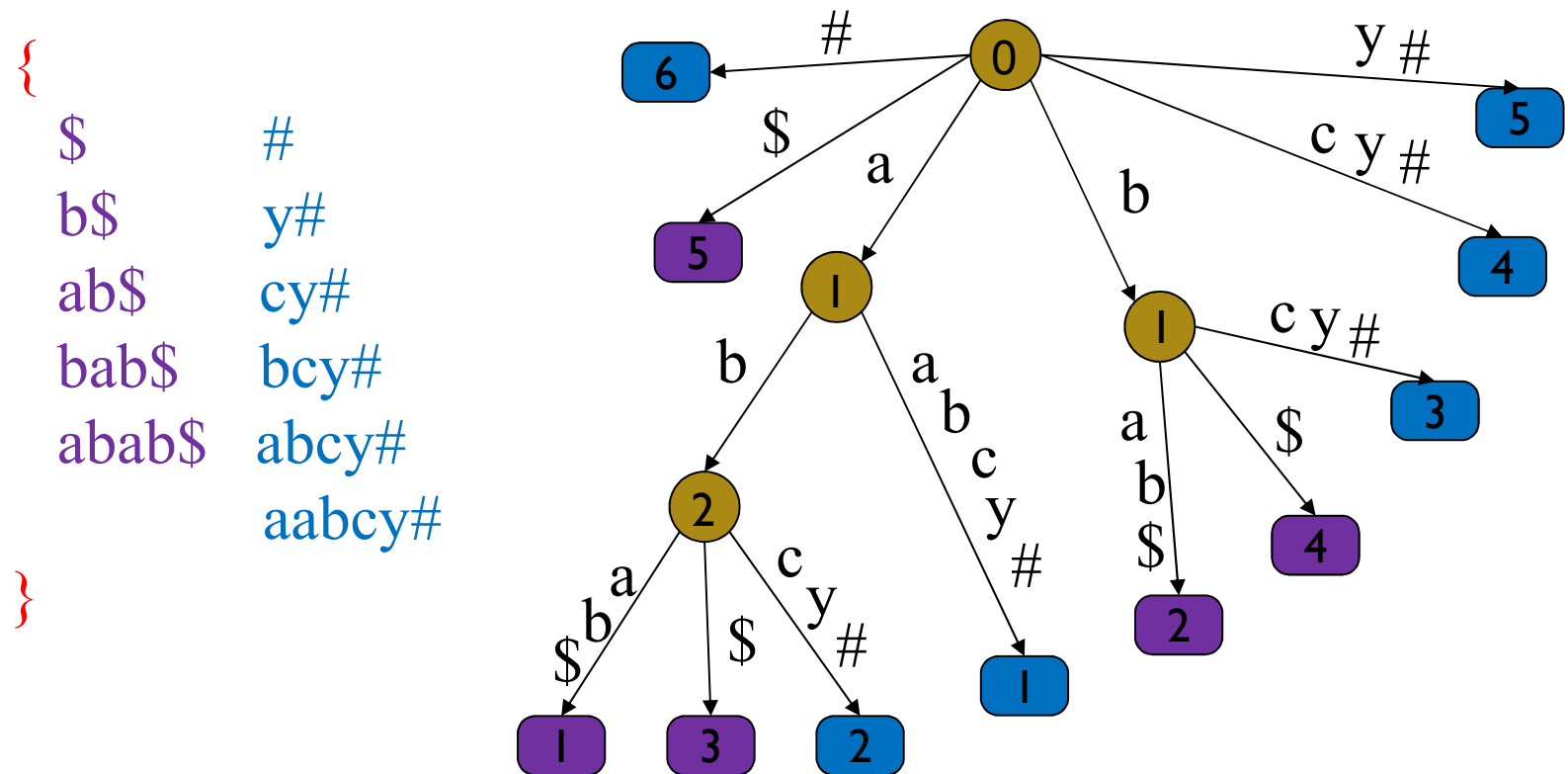
# LCS<sub>ubstring</sub> - Example

- Let  $A=aabcy$  and  $B=abab$ , here is a generalized suffix tree for  $A$  and  $B$ .



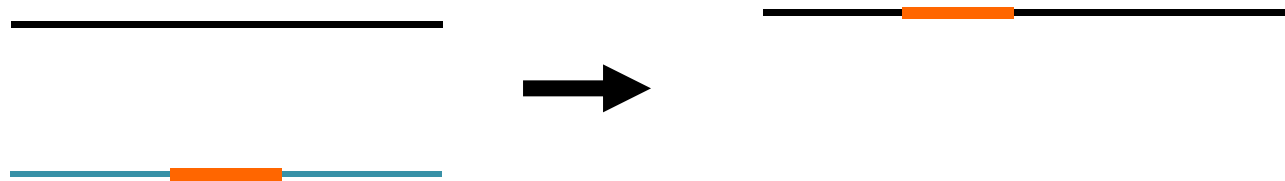
# LCS<sub>substring</sub> - Example

- Let  $A=aabcy$  and  $B=abab$ , here is a generalized suffix tree for  $A$  and  $B$ .



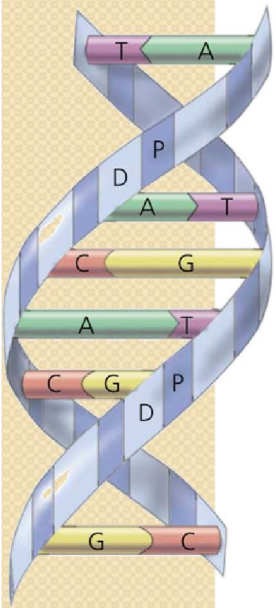
# DNA Contamination Problem

DNA contamination: During laboratory processes, unwanted DNA inserted into the DNA of interest.



Contamination sources: Human, bacteria,...

DNA from Dinosaur bone: More similar to human DNA than to bird and crockodilian DNA





# DNA Contamination Problem

S: DNA of interest

P: DNA of possible contamination source

If S and P share a common substring longer than  $l$ , then S has been contaminated by P.

To find all common substrings of S and P that are longer than  $l$ .

In general, P is set of DNA that are potential contamination sources.



# Applications of suffix trees

- Longest Common Substring
  - DNA Contamination Problem
- Maximal Repetitive Structures
- Longest common extension
- Finding maximal palindromes
- The k-mismatch problem



# Maximal Repetitive Structures

## Maximal Pair

- A maximal pair in string S:

A pair of identical substrings  $\alpha$  and  $\beta$  in S s.t. the characters to the immediate left and right of  $\alpha$  is different from the characters to the immediate left and right of  $\beta$ , respectively.

- That is, Extending  $\alpha$  and  $\beta$  in either direction would destroy the equality of the two strings.
- Example: S = xabcyiii~~z~~abcqabcyrxar



## Maximal Pair (continued)

- Overlap is allowed:

$S = \text{cxxaxxxb}$

  cxxaxxa

    axxxb

- To allow a prefix or suffix of  $S$  to be part of a maximal pair:

$S \rightarrow \#S\$$  ( $\#$ ,  $\$$  don't appear in  $S$ ).

Example: #abcxabc\$

# Maximal Repeat

- A maximal repeat in string S:

A substring of S that occurs in a maximal pair in S.

- Example: S = xabcyiii~~z~~abcqabcyrxar

maximal repeats: abc, abcy, ...



## Finding All Maximal Repeats In Linear Time

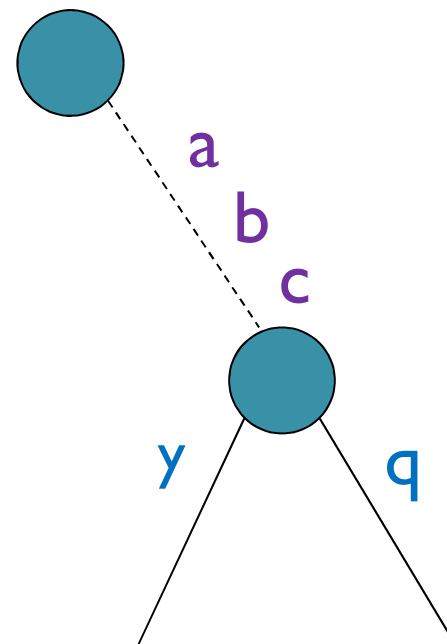
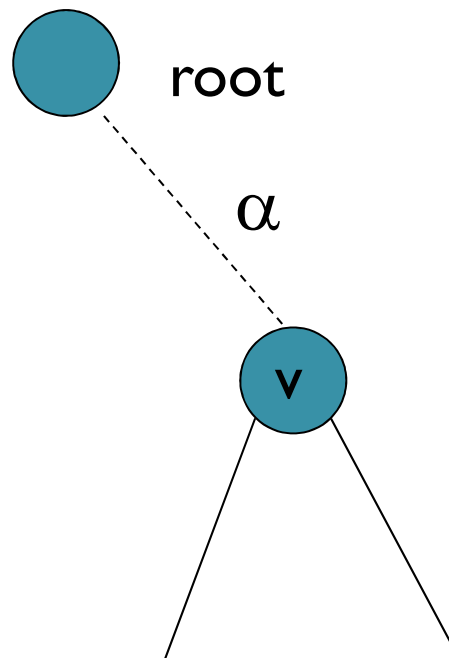
- Given: String  $S$  of length  $n$ .
- Goal: Find all maximal repeats in  $O(n)$  time.
- Lemma:

Let  $T$  be a suffix tree for  $S$ .

If string  $\alpha$  is a maximal repeat in  $S$ ,  
then  $\alpha$  is the path-label of an internal node  $v$  in  $T$ .

## Proof – by def. of maximal repeat

$S = \text{xabcyiiiizabcqabcyrxar}$



A maximal repeat in string  $S$ :

A substring of  $S$  that occurs in a maximal pair in  $S$ .



## Observation

- T has at most  $n$  internal nodes.
- Why?

Since T has  $n$  leaves (one for each index), and each internal node other than the root must have at least two children, T can have at most  $n$  internal nodes.




## Conclusion

- There can be at most  $n$  maximal repeats in any string of length  $n$ .

- Proof:

by the lemma, since  $T$  has at most  $n$  internal nodes.



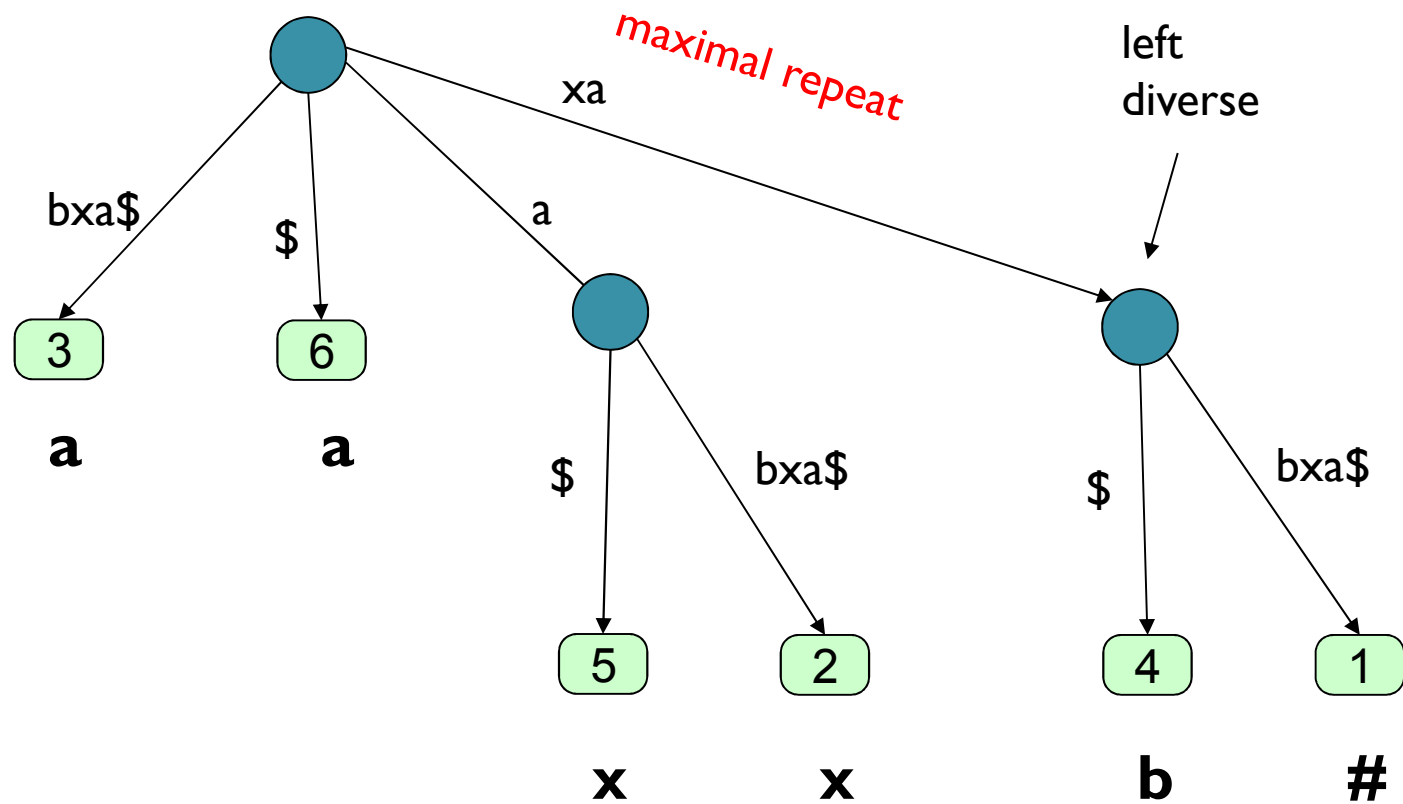
## Which internal nodes correspond to maximal repeats?

- The left character of leaf  $i$  in  $T$  is  $S(i-1)$ .
- Node  $v$  of  $T$  is called left diverse if at least 2 leaves in  $v$ 's subtree have different left characters.
- A leaf can't be left diverse.
- Left diversity propagates upward.



Example:  $S = \#xabxa\$$

1 2 3 4 5 6



## Theorem

The string  $\alpha$  labeling the path to an internal node  $v$  of  $T$  is a maximal repeat



$v$  is left diverse.

## Proof of $\Rightarrow$

- Suppose  $\alpha$  is a maximal repeat  $\rightarrow$
- It participates in a maximal pair  $\rightarrow$
- It has at least two occurrences with distinct left characters:  $x\alpha, y\alpha, x \neq y \rightarrow$
- Let  $i$  and  $j$  be the two starting positions of  $\alpha$ .  
Then leaves  $i$  and  $j$  are in  $v$ 's subtree and have different left characters  $x, y$ .  $\rightarrow$
- $v$  is left diverse.

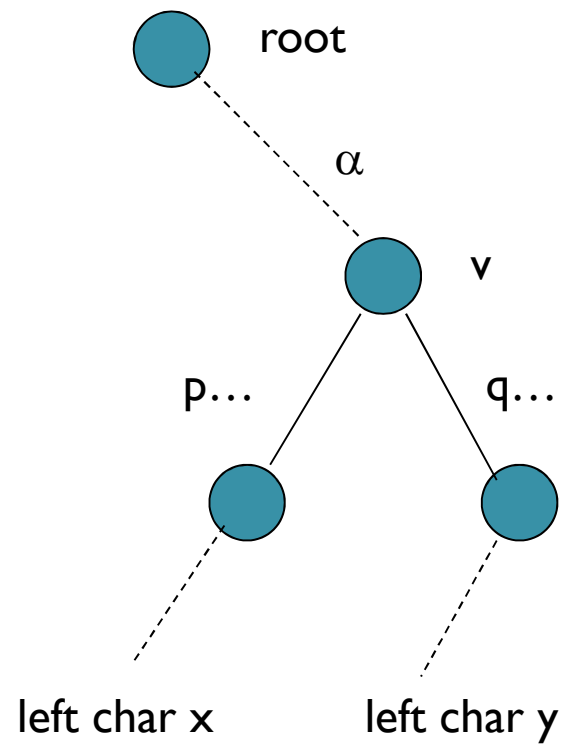
## Proof of $\Leftarrow$

- Suppose  $v$  is left diverse  $\rightarrow$  there are substrings  $x\alpha p$  and  $y\alpha q$  in  $S$ ,  $x \neq y$ .
- If  $p \neq q \rightarrow \alpha$ 's occurrences in  $x\alpha p$  and  $y\alpha q$  form a maximal pair  $\rightarrow \alpha$  is a maximal repeat.
- If  $p = q \rightarrow$  since  $v$  is a branching node, there is a substring  $z\alpha r$  in  $S$ ,  $r \neq p$ .  
If  $z \neq x \rightarrow$  It forms a maximal pair with  $x\alpha p$ .  
If  $z \neq y \rightarrow$  It forms a maximal pair with  $y\alpha p$ .  
In either case,  $\alpha$  is a maximal repeat.

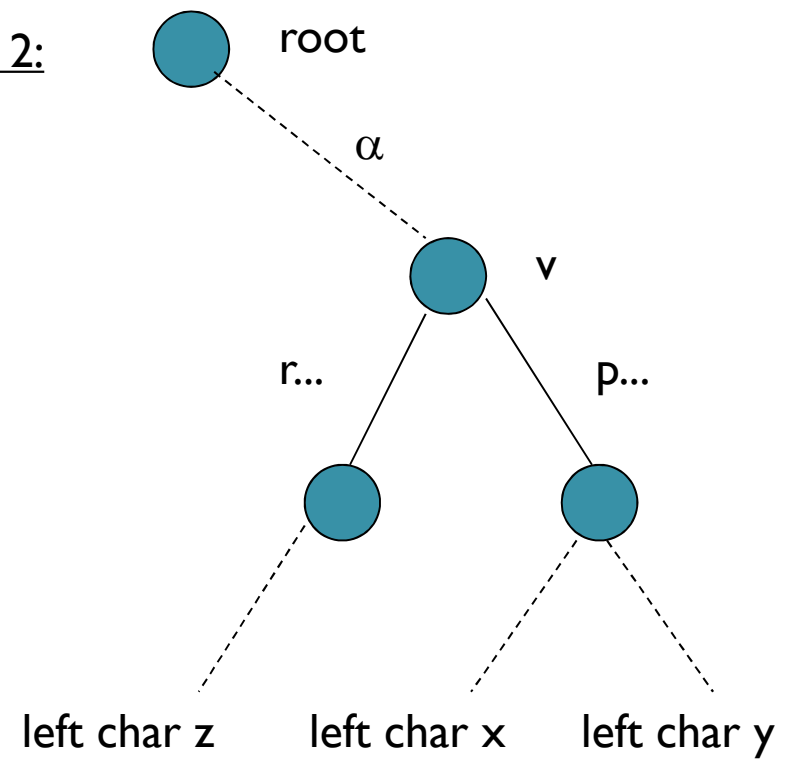
These cases cover all the cases, since  $x \neq y$ .

## Proof of $\Leftarrow$ (continued)

Case 1:



Case 2:



# Compact Representation

- Node  $v$  in  $T$  is a frontier node if:
  - $v$  is left diverse.
  - none of  $v$ 's children are left diverse.
- Each node at or above the frontier is left diverse.
- The subtree of  $T$  from the root down to the frontier nodes is the compact representation of the set of all maximal repeats of  $S$ .
- Representation in  $O(n)$  though total length of all maximal repeats may be larger.



## Linear time algorithm

- Build suffix tree  $T$ .
- Find all left diverse nodes in linear time.
- Delete all nodes that aren't left diverse, to achieve the compact representation.



## finding all left diverse nodes in linear time

- Traverse  $T$  bottom-up, recording for each node:
  - either that it is left diverse
  - or the left character common to all leaves in its subtree.
- For each leaf: record its left character.
- For each internal node  $v$ :
  - If any child is left diverse  $\rightarrow v$  is left diverse.
  - Else If all children have a common character  $x \rightarrow$  record  $x$  for  $v$ .
    - Else record that  $v$  is left diverse.



## Time Analysis

- Suffix tree construction  $\rightarrow O(n)$ .
- Bottom-up traversal  $\rightarrow O(n)$ .
- Total  $O(n)$ .



# Applications of suffix trees

- Longest Common Substring
  - DNA Contamination Problem
- Maximal Repetitive Structures
- Longest common extension
- Finding maximal palindromes
- The k-mismatch problem



# Longest common extension

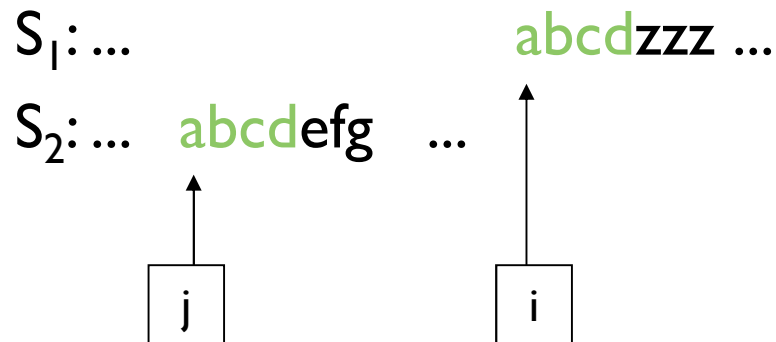
Longest common extension:

a bridge to inexact matching

# Longest common extension problem

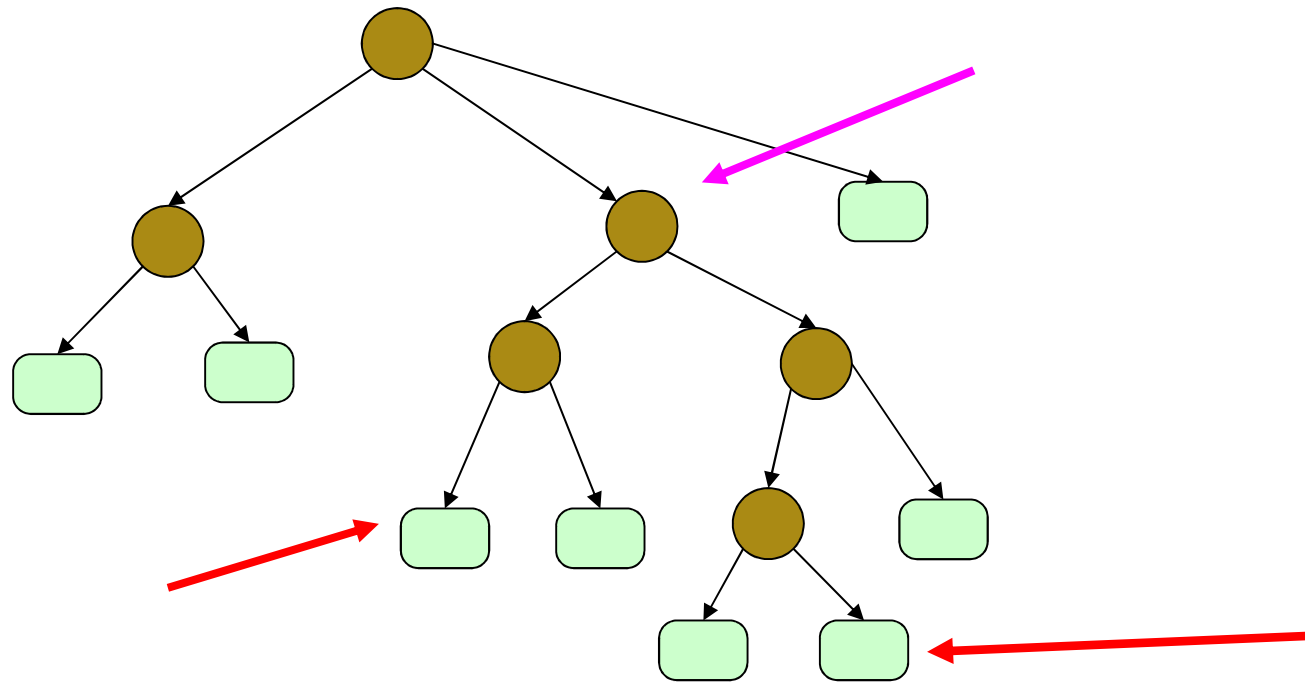
Preprocess strings  $S_1$  and  $S_2$  s.t. the following queries can be computed in  $O(1)$  time each:

- Given index pair  $(i, j)$ , find the length of the longest substring of  $S_1$  starting at position  $i$  that matches a substring of  $S_2$  starting at position  $j$ .



# Lowest common ancestors

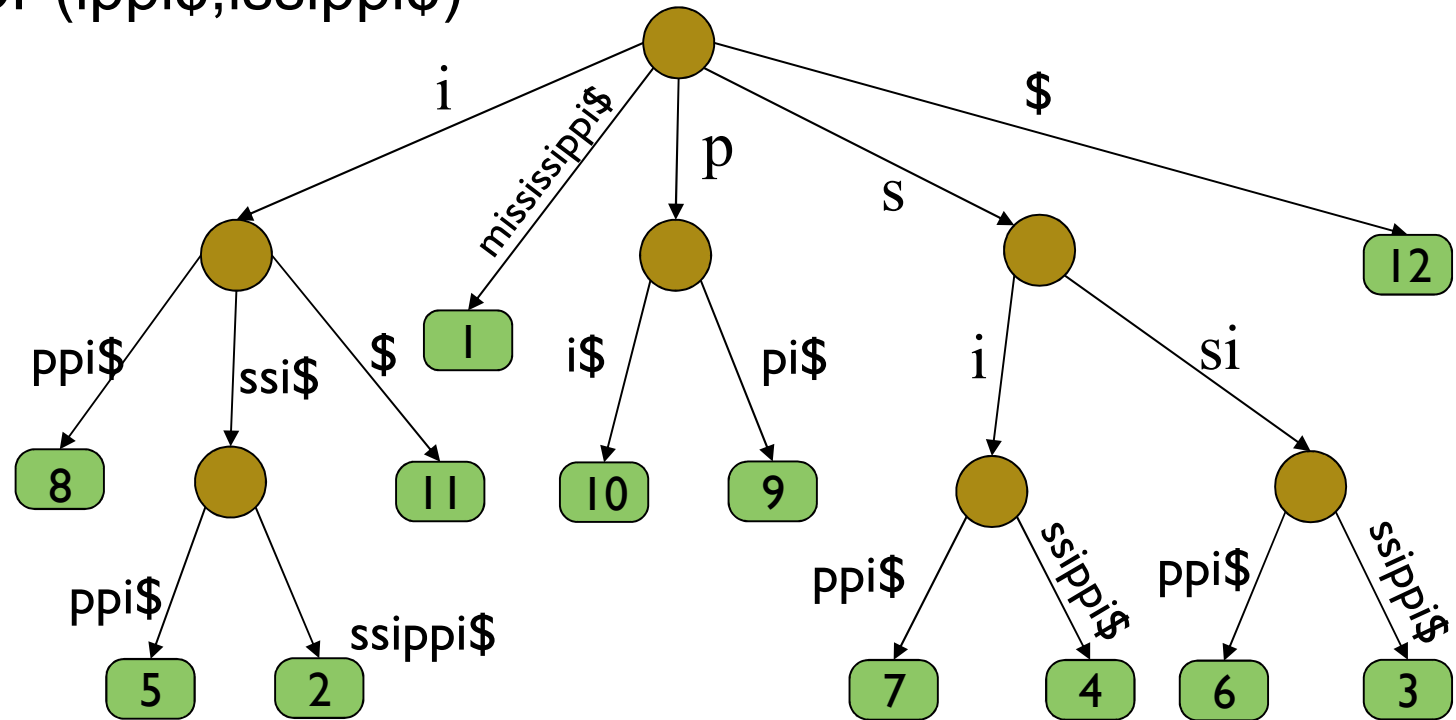
A lot more can be gained from a suffix tree if we preprocess it so that we can answer LCA queries on it



# Why to find LCA?

For two suffixes of  $S$ , we can compute their **Longest Common Prefix** by finding the LCA of the corresponding leaves in the suffix tree.

$\text{LCP}(\text{ippi}\$, \text{issippi}\$) =$

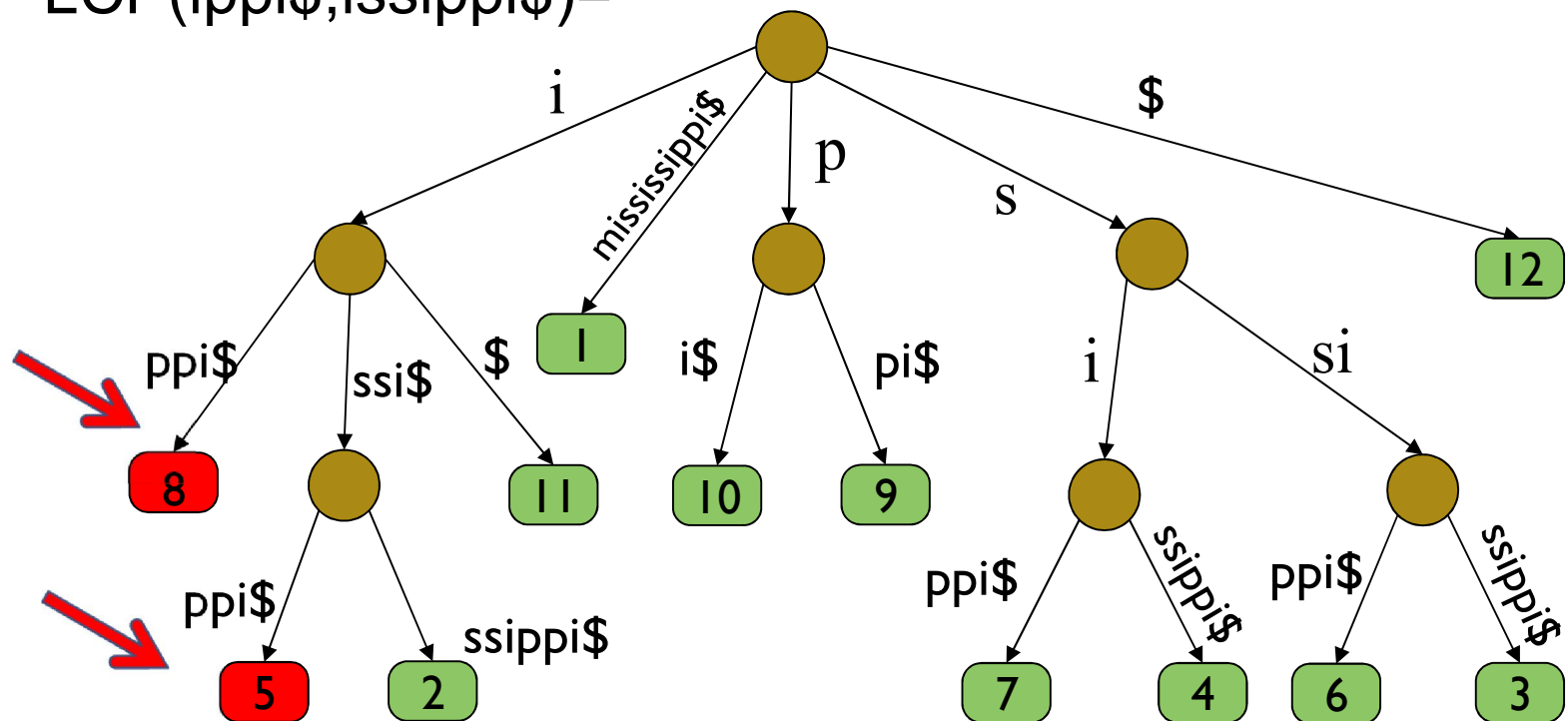




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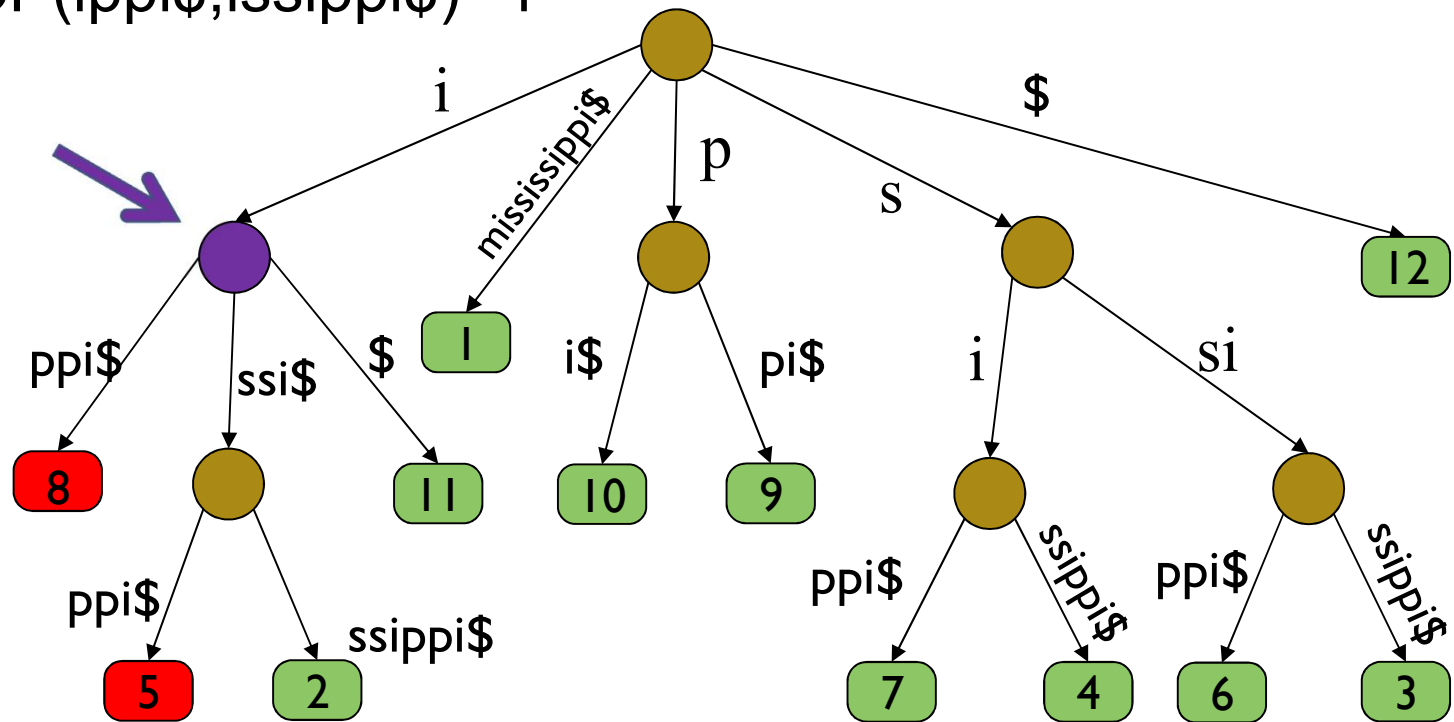
$\text{LCP}(\text{ippi}\$, \text{issippi}\$) =$



# Why to find LCA?

For two suffixes of  $S$ , we can compute their **Longest Common Prefix** by finding the LCA of the corresponding leaves in the suffix tree.

$\text{LCP}(\text{ippi}\$, \text{issippi}\$) = \text{i}$



# Lowest common ancestors

after a linear amount of preprocessing of a rooted tree, for any two specified nodes, their lowest common ancestor can be found in a constant time, independent of  $n$ .

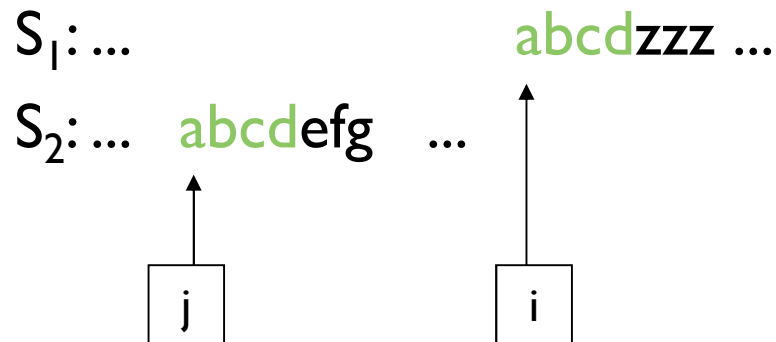
The lca result was first obtained by Harel and Tarjan:  
Harel, Dov; [Tarjan, Robert E.](#) (1984), "Fast algorithms for finding nearest common ancestors", *SIAM Journal on Computing* **13**.

and later simplified by Schieber and Vishkin:  
Schieber, Baruch; [Vishkin, Uzi](#) (1988), "On finding lowest common ancestors: simplification and parallelization", *SIAM Journal on Computing* **17**.

# Longest common extension problem

Preprocess strings  $S_1$  and  $S_2$  s.t. the following queries can be computed in  $O(1)$  time each:

- Given index pair  $(i, j)$ , find the length of the longest substring of  $S_1$  starting at position  $i$  that matches a substring of  $S_2$  starting at position  $j$ .



# Longest common extension - Solution

Preprocess:  $O(|S_1| + |S_2|)$

- Build generalized suffix tree  $T$  for  $S_1$  and  $S_2$ .
- Preprocess  $T$  for constant-time LCA queries.
- Compute string-depth of every node.

To answer query  $(i,j)$ :  $O(1)$

- Find LCA node  $v$  of leaves corresponding to suffix  $i$  of  $S_1$  and suffix  $j$  of  $S_2$ .
- Return  $\text{string-depth}(v)$ .



# Applications of suffix trees

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- The k-mismatch problem

# Finding maximal palindromes

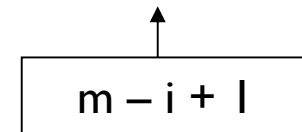
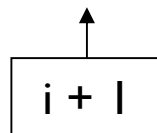
- A palindrome: caabaac, cbaabc
- Want to find all maximal palindromes in a string **S**

Let **S = cbaaba**

$S^r$  - the reverse of string S

The maximal palindrome with center between  $i$  and  $i + 1$  is the LCP of the suffix at position  $i + 1$  of S and the suffix at position  $m - i + 1$  of  $S^r$

Example: **S = cbaaba\$** and  **$S^r = abaabc\#$**





# Maximal palindromes algorithm

Prepare a generalized suffix tree for

$S = cbaaba\$$  and  $S^r = abaabc\#$

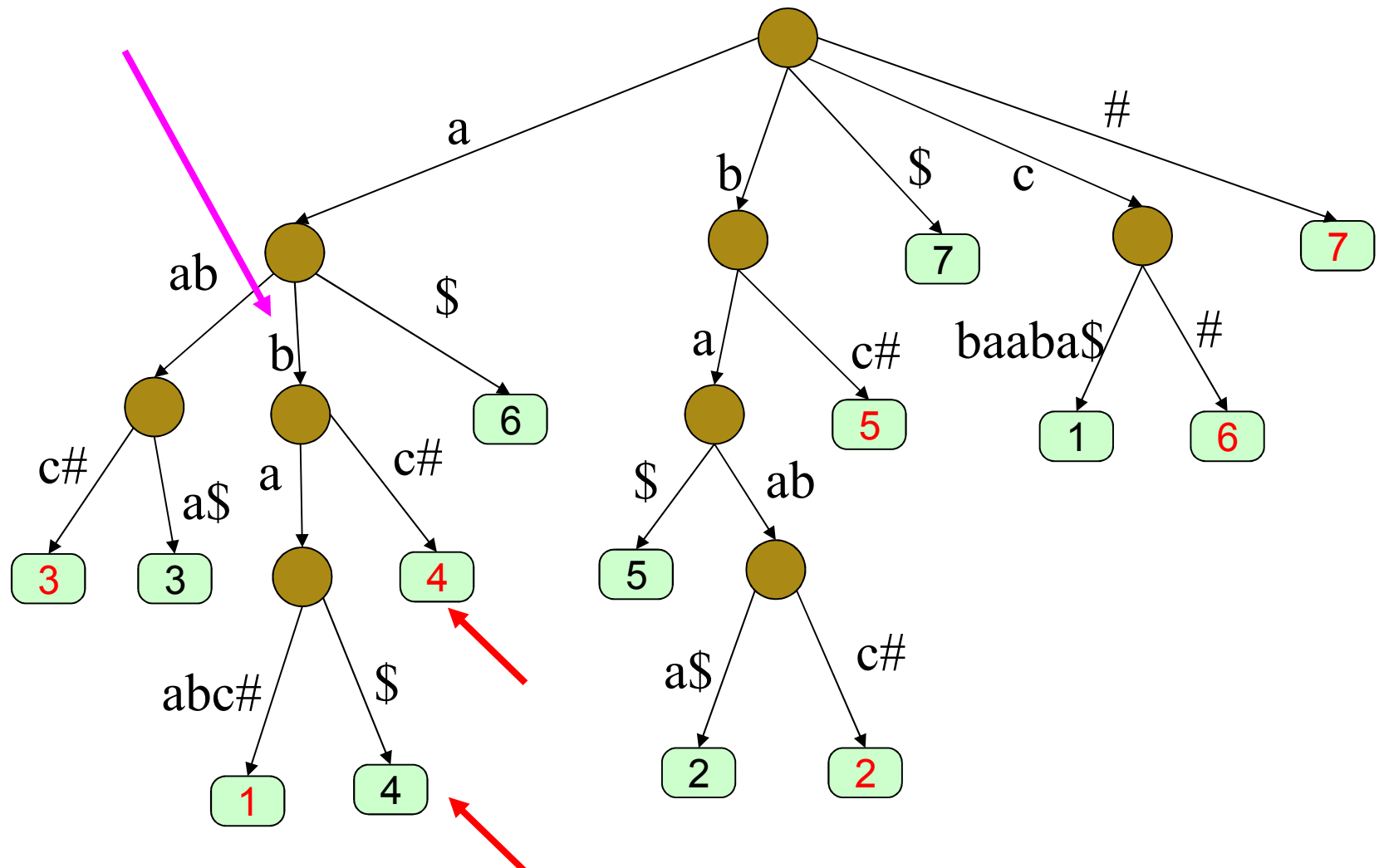
Preprocess:  $O(n)$

Build generalized suffix tree  $T$  for  $S$  and  $S^r$ .

Preprocess  $T$  for constant-time longest common extension.

For every  $i$  find the LCA of suffix  $i$  of  $S$  and suffix  $m-i+1$  of  $S^r \rightarrow$  solve the longest common extension for  $(i+1, m-i+1)$

If the extension has nonzero length  $k$ , then there is a maximal palindrom of radius  $k$  center at  $i$





# Applications of suffix trees

- Longest Common Substring
  - DNA Contamination Problem
- Maximal Repetitive Structures
- Longest common extension
- Finding maximal palindromes
- The k-mismatch problem

# The k-mismatch problem

- Given: pattern  $P$ , text  $T$ , fixed number  $k$ .
- k-mismatch of  $P$ : a  $|P|$ -length substring of  $T$  that matches at least  $|P|-k$  characters of  $P$  (i.e. it matches  $P$  with at most  $k$  mismatches).
- The k-mismatch problem:  
Find all k-mismatches of  $P$  in  $T$ .

## Example

P = bend

T = abentbananaend

k = 2

⇒ T contains three 2-mismatches of P:

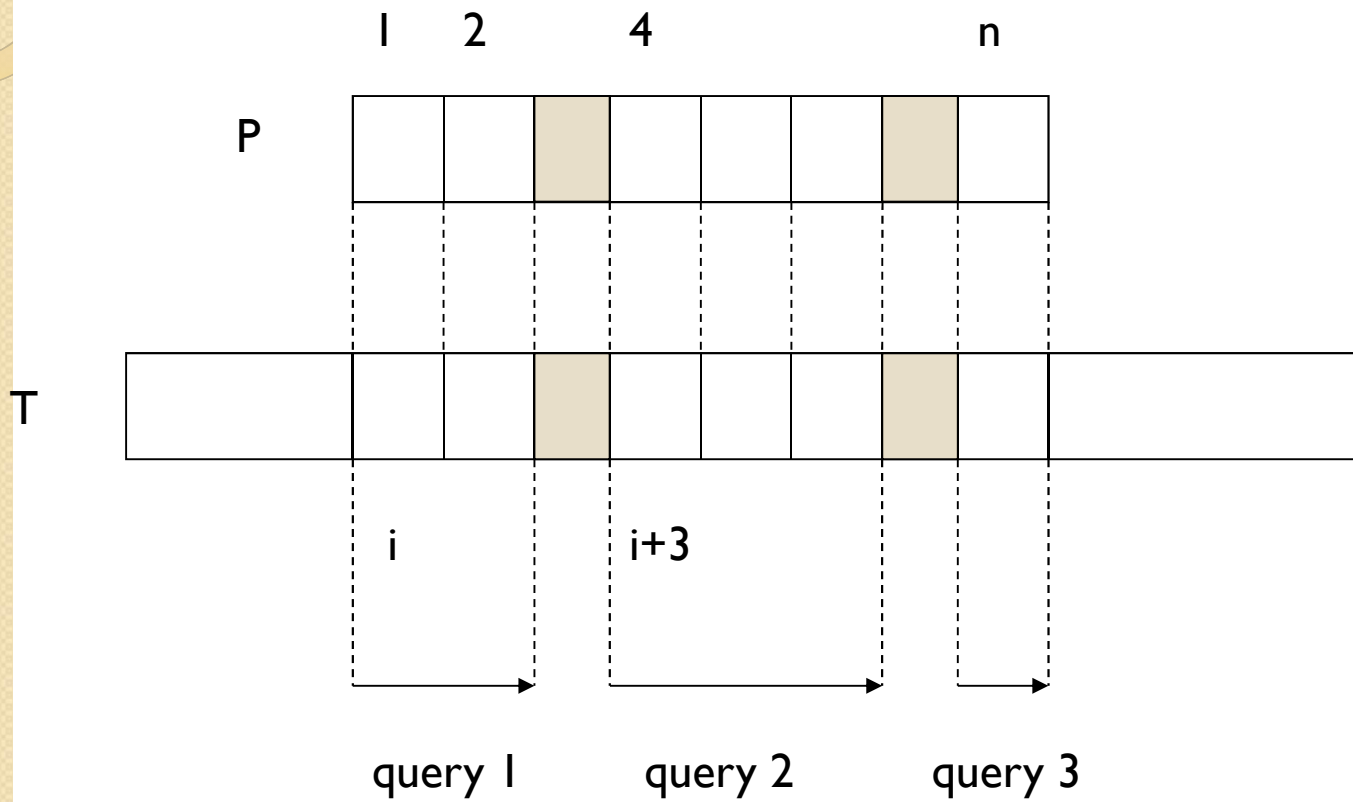
a	<u>b</u>	<u>e</u>	<u>n</u>	<u>t</u>	<u>b</u>	<u>a</u>	<u>n</u>	<u>a</u>	<u>n</u>	<u>a</u>	<u>e</u>	<u>n</u>	<u>d</u>
	b	e	n	d	b	e	n	d		b	e	n	d

1-mismatch   2-mismatch   1-mismatch

# Solution

- Notation:  $|P|=m$ ,  $|T|=n$ ,  $k$  independent of  $n$  and  $m$  ( $k \ll m$ ).
- General idea:
  - For each position  $i$  in  $T$ , determine whether a  $k$ -mismatch of  $P$  begins at position  $i$ .
  - To do this efficiently: successively execute up to  $k+1$  longest common extension queries.
  - A  $k$ -mismatch of  $P$  begins at position  $i$  if these extensions reach the end of  $P$ .

## solution (continued)





## Algorithm for index $i$

1.  $j \leftarrow 1$   
 $i' \leftarrow i$   
 $\text{count} \leftarrow 0$
2. Compute the length  $l$  of the longest common extension starting at positions  $j$  of  $P$  and  $i'$  of  $T$ .
3. if  $j+l=m+1$   
then a  $k$ -mismatch of  $P$  occurs in  $T$  starting at  $i$ ; stop.
4. if  $\text{count} < k$   
then  $\text{count} \leftarrow \text{count} + 1$   
 $j \leftarrow j + l + 1$   
 $i' \leftarrow i' + l + 1$   
go to step 2.  
else, a  $k$ -mismatch of  $P$  does not occur in  $T$  starting at  $i$ ; stop.



## Example

$P = abcaabaccc$

$T = cabcdabbcccd$

## Example

$P =$  *abcaabaccc*

$T =$  *cabcdabbcccd*

$j_1 = 3$

## Example

$P =$  *abcaabccc*

$T =$  *cabcdabbcccd*

$j_1 = 3, j_2 = 2$

## Example

$P =$  *abcaabccc*

$T =$  *cab cdabbcccd*

$$j_1 = 3, j_2 = 2, j_3 = 3$$

## Time Analysis

- Preprocessing of  $T$  and  $P$  for longest common extension queries  $\rightarrow O(n)$ .
- For each index  $i=1, \dots, n-m+1$  of  $T$ , up to  $k+1$  longest common extension queries  $\rightarrow O(k)$  per index  $\rightarrow O(kn)$  total.
- Total  $O(kn)$  time.