Indexing genomic sequences: suffix tree and suffix array

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Example

Let T = CAGAGA. $T_1 = \text{AGAGA}$ and $T_{\{3,5\}} = \{\text{AGA}, \text{A}\}$.

\$ A\$

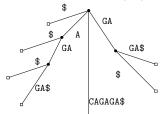
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AGA\$

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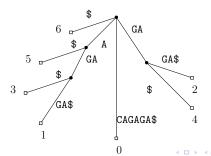
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The **suffix array** of T is a sorted array of $T_{[0..n]}$.

Example

Let T = CAGAGA\$. The suffix array of T is [6, 5, 3, 1, 0, 4, 2].

6: \$

5: A\$

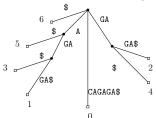
3: AGA\$

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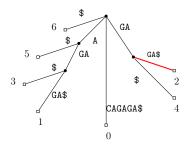
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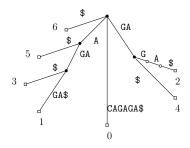
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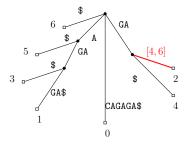
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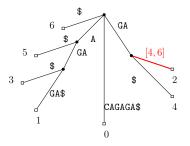
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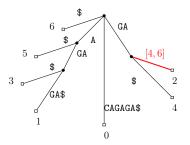


▶ Edge labels are substrings of *T*: represented by *T* intervals.

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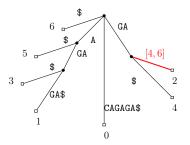


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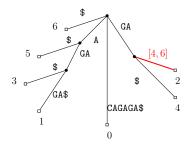
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- ► At most 2*n* edges.

Space linear in n: O(n).



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Let T be a string of length n over a linearly-sortable alphabet. The suffix tree of T can be constructed in O(n) time.

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In bioinformatics we usually have that $|\Sigma| = O(1)$.

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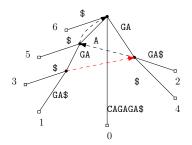
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Example

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QUERY: a pattern P; return all **occ** starting positions of P in T

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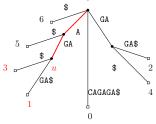
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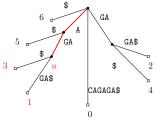
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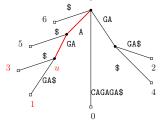
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Theorem

Exact string matching queries can be answered in O(|P| + occ) time after O(n) time preprocessing.



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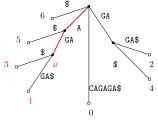
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Alternatively: binary search for P in the suffix array of T.

Theorem

Exact string matching queries can be answered in $O(|P| \log n + occ)$ time using the suffix array.



INPUT: a sequence T

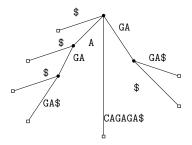
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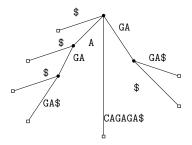


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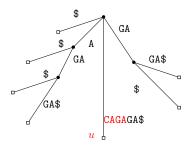
Every *locus* (node, depth) in the suffix tree represents a substring of the sequence and every substring is represented by some locus.

INPUT: a sequence T

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Example

Let T = CAGAGA\$. Locus (u, 4) represents CAGA.



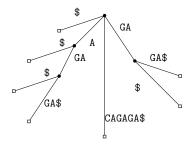
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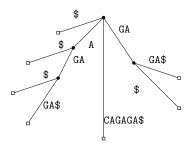


INPUT: a sequence T

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Example

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Count the number of distinct loci using a suffix tree traversal.

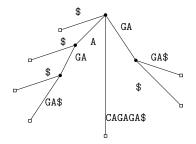


INPUT: a sequence T

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Example

Let T = CAGAGA\$.



Theorem

The number of distinct substrings can be computed in O(n) time.



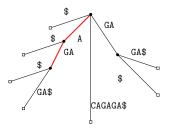
Application 3: Longest repeating substring

INPUT: a sequence T

OUTPUT: a longest string occurring at least twice in T

Example

Let T = CAGAGA\$. The answer is AGA.



Find a deepest internal node using a traversal of the suffix tree.

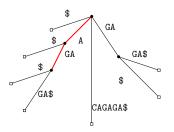
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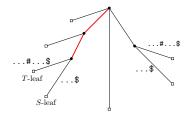
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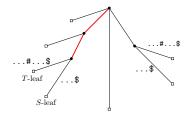
Suffix tree of T#S\$.



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Suffix tree of T#S\$.

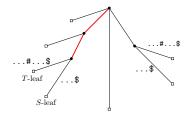


Find a deepest internal node containing both *T*- and *S*-leaves.

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Suffix tree of T#S\$.



Find a deepest internal node containing both T- and S-leaves.

Theorem

A longest common substring can be found in O(n + |S|) time.

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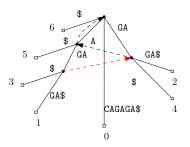
substring of T, for all $i \in [0, |S| - 1]$

PREPROCESS: a sequence T

QUERY: a sequence S; return the longest prefix of S_i that is a substring of T, for all $i \in [0, |S| - 1]$

Example

Let T = CAGAGA\$.



Scan S using the suffix tree of T.

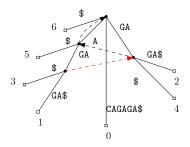


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Spell S_i as much as possible;

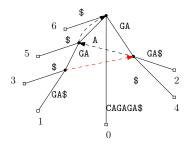


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Spell S_i as much as possible; say S[i..j-1].

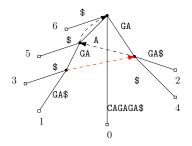


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Mismatch at S[i..j]?

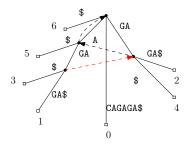


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Mismatch at S[i...j]? Use suffix link as the failure transition!

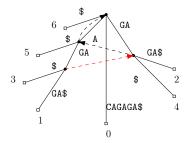


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This takes us at node u: str(u) = S[i+1...j].

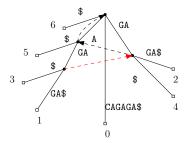


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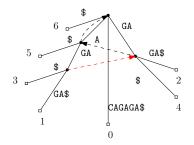


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Theorem

Matching statistics of S with respect to T can be computed in O(|S|) time after O(n) time preprocessing.

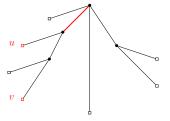
Application 6: Longest common prefix (LCP)

PREPROCESS: a sequence T

QUERY: a pair (i,j); return the length of the LCP of (T_i, T_j)

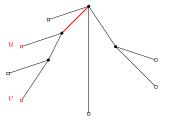
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Theorem (Bender and Farach-Colton, LATIN 2000)

Any tree of size O(N) can be preprocessed in O(N) time so that the LCA of any two nodes can be computed in O(1) time.



PREPROCESS: a sequence T

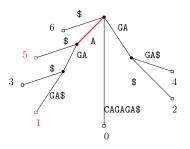
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Let T = CAGAGA. Let (1,5) be the query. The answer is 1 = |A|.

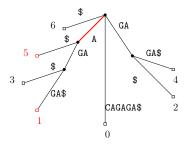


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Theorem

Longest common prefix queries can be answered in O(1) time after O(n) time preprocessing.

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OUTPUT: a longest palindromic substring of T

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Palindrome: $S = ATGTA = S^R = ATGTA$.

► Construct the suffix tree of $W = T \# T^R \$$.

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- Preprocess the suffix tree for LCA queries.

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- ► Construct the suffix tree of $W = T \# T^R \$$.
- Preprocess the suffix tree for LCA queries.
- Say we are interested in odd-length palindromes.

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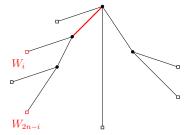
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- Preprocess the suffix tree for LCA queries.
- Say we are interested in odd-length palindromes.
- ▶ Answer LCP queries for W_i and W_{2n-i} , for all i.

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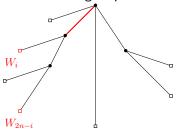
$$T = \mathbf{C} \underline{\mathbf{A}} \underline{\mathbf{T}} \underline{\mathbf{T}} \underline{\mathbf{T}} \mathbf{T} \\ T^R = \underline{\mathbf{T}} \underline{\mathbf{T}} \underline{\mathbf{T}} \underline{\mathbf{T}} \underline{\mathbf{C}} \mathbf{C}$$

$$W = T \# T^R \$ = \mathtt{CAT} \underbrace{^3}_{\mathbf{X}} \mathtt{TT} \# \mathtt{TTAT} \underbrace{^{13}}_{\mathbf{X}} \mathtt{C} \$$$



INPUT: a sequence T

OUTPUT: a longest palindromic substring of T



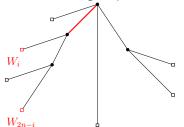
$$T = \mathtt{CATGTA}\mathtt{TT}$$

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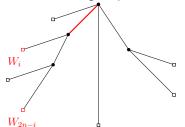
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► A longest LCP represents a longest odd-length palindrome.

INPUT: a sequence T

OUTPUT: a longest palindromic substring of T



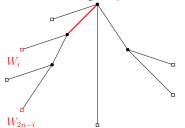
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- ▶ A longest LCP represents a longest odd-length palindrome.
- Even-length palindromes are handled analogously.

INPUT: a sequence T

OUTPUT: a longest palindromic substring of T



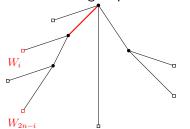
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- ▶ A longest LCP represents a longest odd-length palindrome.
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- ▶ Take the longer of the two as the globally longest.

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- ► A longest LCP represents a longest odd-length palindrome.
- Even-length palindromes are handled analogously.
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Theorem

A longest palindromic substring can be computed in O(n) time.



INPUT: a sequence T, a pattern P, and an integer k > 0 OUTPUT: all positions i in T: $d_H(T[i+|P|-1],P) \le k$

INPUT: a sequence T, a pattern P, and an integer k>0 OUTPUT: all positions i in T: $d_H(T[i+|P|-1],P) \le k$ Hamming distance d_H : $d_H(GCTA,GCAA) = 1$; $d_H(GCTA,ACAA) = 2$.

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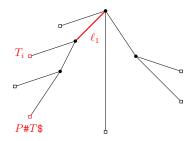
- Construct the suffix tree of P#T\$.
- ▶ Answer LCP query for T_i and P#T\$, for i = 0.

INPUT: a sequence T, a pattern P, and an integer k>0 OUTPUT: all positions i in T: $d_H(T[i+|P|-1],P) \le k$ Hamming distance d_H : $d_H(GCTA,GCAA) = 1$; $d_H(GCTA,ACAA) = 2$.

- ► Construct the suffix tree of *P*#*T*\$.
- ▶ Answer LCP query for T_i and P#T\$, for i = 0.
- ▶ Say this gives an LCP of length ℓ_1 .

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▶ "Jump" over the mismatch $T[i + \ell_1] \neq P[\ell_1]$.

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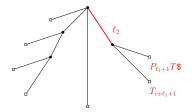
- ▶ "Jump" over the mismatch $T[i + \ell_1] \neq P[\ell_1]$.
- ▶ Via answering the LCP query for $T_{i+\ell_1+1}$ and P_{ℓ_1+1} .

INPUT: a sequence T, a pattern P, and an integer k > 0 OUTPUT: all positions i in T: $d_H(T[i+|P|-1], P) \le k$

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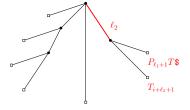
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- ▶ This gives an LCP of length ℓ_2 .

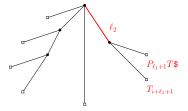


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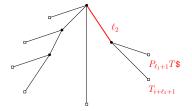


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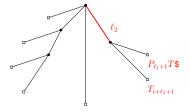
Answer (at most) k + 1 LCP queries per i.

INPUT: a sequence T, a pattern P, and an integer k > 0 OUTPUT: all positions i in T: $d_H(T[i+|P|-1],P) \le k$



- Answer (at most) k + 1 LCP queries per i.
- ▶ Report *i* if the total length $\ell_1 + 1 + \ell_2 + 1 + \cdots$ is at least |P|.

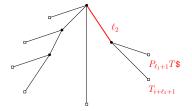
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- ▶ Repeat for all $i \in [1, n]$.



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Theorem (Landau and Vishkin, TCS 1986)

Approximate string matching can be solved in O(kn) time.



Application 9: Shortest unique substring

INPUT: a sequence T

OUTPUT: a shortest unique substring of T

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► Construct the suffix tree of *T*.

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OUTPUT: a shortest unique substring of T

- Construct the suffix tree of T.
- For each leaf node labeled i, for all $i \in [0, n]$, pick up the closest ancestor v using a depth-first traversal.

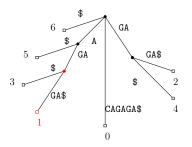
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Example

Let T = CAGAGA\$.



INPUT: a sequence T

OUTPUT: a shortest unique substring of T

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ightharpoonup str(v) concatenated with the succeeding letter is the shortest unique substring starting at i.

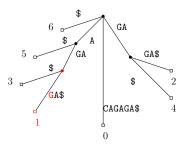
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ightharpoonup str(v) concatenated with the succeeding letter is the shortest unique substring starting at i.

Example

Let T = CAGAGA\$. The shortest unique substring starting at 1 is AGAG.



INPUT: a sequence T

OUTPUT: a shortest unique substring of T

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OUTPUT: a shortest unique substring of T

► Take a shortest substring among all *i*.

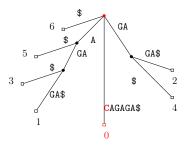
INPUT: a sequence T

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► Take a shortest substring among all *i*.

Example

Let T = CAGAGA\$. The shortest unique substring is C.



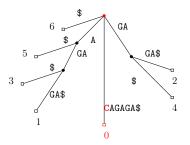
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OUTPUT: a shortest unique substring of T

► Take a shortest substring among all i.

Example

Let T = CAGAGA\$. The shortest unique substring is C.



Theorem

A shortest unique substring can be computed in O(n) time.

INPUT: a sequence T

OUTPUT: LZ factorization of T

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$$T = F_0 \cdot F_1 \cdots F_k;$$

INPUT: a sequence T

OUTPUT: LZ factorization of T

- $ightharpoonup T = F_0 \cdot F_1 \cdots F_k;$
- ▶ F_i : longest prefix of $F_i \cdots F_k$ with some occurrence to the left.

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- (or a single letter in case this prefix is empty.)

INPUT: a sequence T

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LZ factorization of T:

- $ightharpoonup T = F_0 \cdot F_1 \cdot \cdot \cdot F_k;$
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- (or a single letter in case this prefix is empty.)

Example

Let T = abbaabbbaaabab.

INPUT: a sequence T

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LZ factorization of T:

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Example

Let T = abbaabbbaaabab. The LZ factorization of T is

 $a \cdot b \cdot b \cdot a \cdot abb \cdot baa \cdot ab \cdot ab$.



INPUT: a sequence T

OUTPUT: LZ factorization of T

LZ factorization of T:

- $ightharpoonup T = F_0 \cdot F_1 \cdots F_k;$
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Let T = abbaabbbaaabab. The LZ factorization of T is

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Why do we care?



INPUT: a sequence T

OUTPUT: LZ factorization of T

LZ factorization of T:

- $ightharpoonup T = F_0 \cdot F_1 \cdot \cdot \cdot F_k;$
- ▶ F_i : longest prefix of $F_i \cdots F_k$ with some occurrence to the left.
- (or a single letter in case this prefix is empty.)

Example

Let T = abbaabbbaaabab. The LZ factorization of T is

$$a \cdot b \cdot b \cdot a \cdot abb \cdot baa \cdot ab \cdot ab$$
.

Why do we care? LZ factorization is a basic and powerful technique for text compression (and string algorithms)!



INPUT: a sequence T

OUTPUT: Lempel-Ziv factorization of ${\it T}$

INPUT: a sequence T

OUTPUT: Lempel-Ziv factorization of T

Construct the suffix tree of T.

INPUT: a sequence T

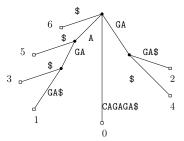
OUTPUT: Lempel-Ziv factorization of T

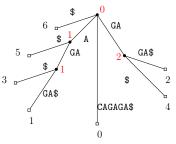
- Construct the suffix tree of T.
- Decorate each internal node with the leftmost starting position the string it represents occurs.

INPUT: a sequence T

OUTPUT: Lempel-Ziv factorization of T

- Construct the suffix tree of T.
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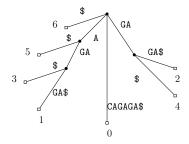
► How?

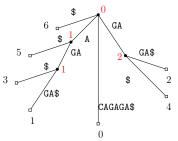


INPUT: a sequence T

OUTPUT: Lempel-Ziv factorization of T

- Construct the suffix tree of T.
- Decorate each internal node with the leftmost starting position the string it represents occurs.





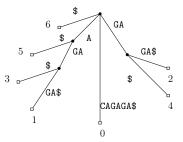
► How? Use a depth-first traversal, propagate the starting positions upwards, and keep the minimum value.

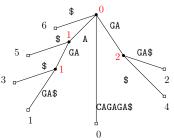


INPUT: a sequence T

OUTPUT: Lempel-Ziv factorization of T

- ► Construct the suffix tree of *T*.
- ▶ Decorate each internal node with the leftmost starting position the string it represents occurs.





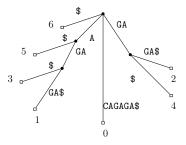
▶ Spell *T*, from left to right, in the suffix tree of *T*.

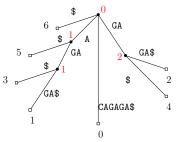


INPUT: a sequence T

OUTPUT: Lempel-Ziv factorization of T

- Construct the suffix tree of T.
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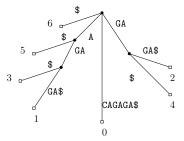


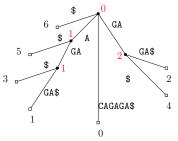
- ▶ Spell *T*, from left to right, in the suffix tree of *T*.
- ▶ For each match T[i..j] check the leftmost starting position p.

INPUT: a sequence T

OUTPUT: Lempel-Ziv factorization of T

- Construct the suffix tree of T.
- Decorate each internal node with the leftmost starting position the string it represents occurs.





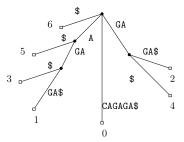
▶ If $p \ge i$, we have not seen T[i..j] previously, increment i.

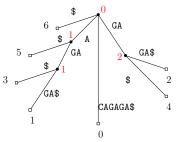


INPUT: a sequence T

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- ► Construct the suffix tree of *T*.
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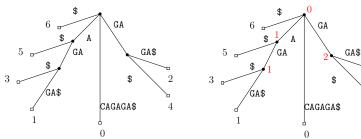
- ▶ If $p \ge i$, we have not seen T[i..j] previously, increment i.
- ▶ If p < i, we have seen T[i..j] previously, increment j.



INPUT: a sequence T

OUTPUT: Lempel-Ziv factorization of T

- Construct the suffix tree of T.
- Decorate each internal node with the leftmost starting position the string it represents occurs.



Theorem

The Lempel-Ziv factorization can be computed in O(n) time.

