

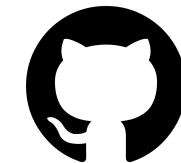
Compressing and indexing pangenomes with meta-colored compacted de Bruijn graphs

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The colored k-mer indexing problem

- A **k-mer** is a sub-string of length k of some string R .
- We are given a collection $\mathcal{R} = \{R_1, \dots, R_N\}$ of reference sequences. Each R_i is a (long) sequence over the DNA alphabet $\{A, C, G, T\}$.
- **Problem.** We want to build an *index* for \mathcal{R} so that we can retrieve the set $\text{Color}(x) = \{i \mid x \in R_i\}$ efficiently for any k-mer x . Note that $\text{Color}(x) = \emptyset$ if $x \notin \mathcal{R}$.

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- A lot of hype in the indexing community for the case where \mathcal{R} is a **pangenome**, i.e., a collection of related genomes.
- **Applications.** This problem is relevant for applications where sequences are first matched against known references (i.e., mapping/alignment algorithms): single-cell RNA-seq, metagenomics, etc.

Modular indexing layout

- **Goal.** What we want is the **map** $x \rightarrow \text{Color}(x) = \{i \mid x \in R_i\}$.

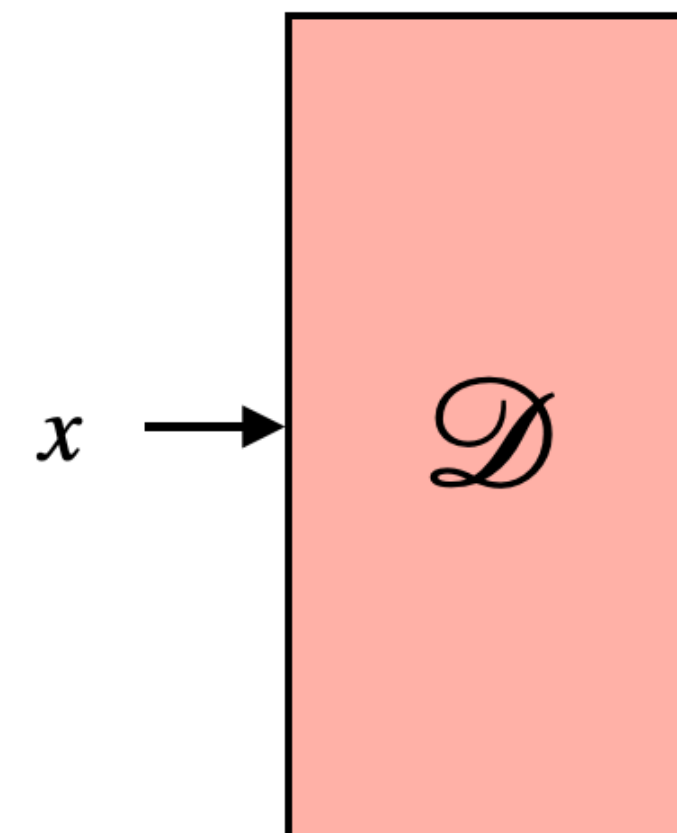
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Assume \mathcal{D} stores n distinct k-mers and supports a $\text{Lookup}(x)$ operation which, given a k-mer x , returns a unique integer $1 \leq h \leq n$ if $x \in \mathcal{D}$, and \perp otherwise.



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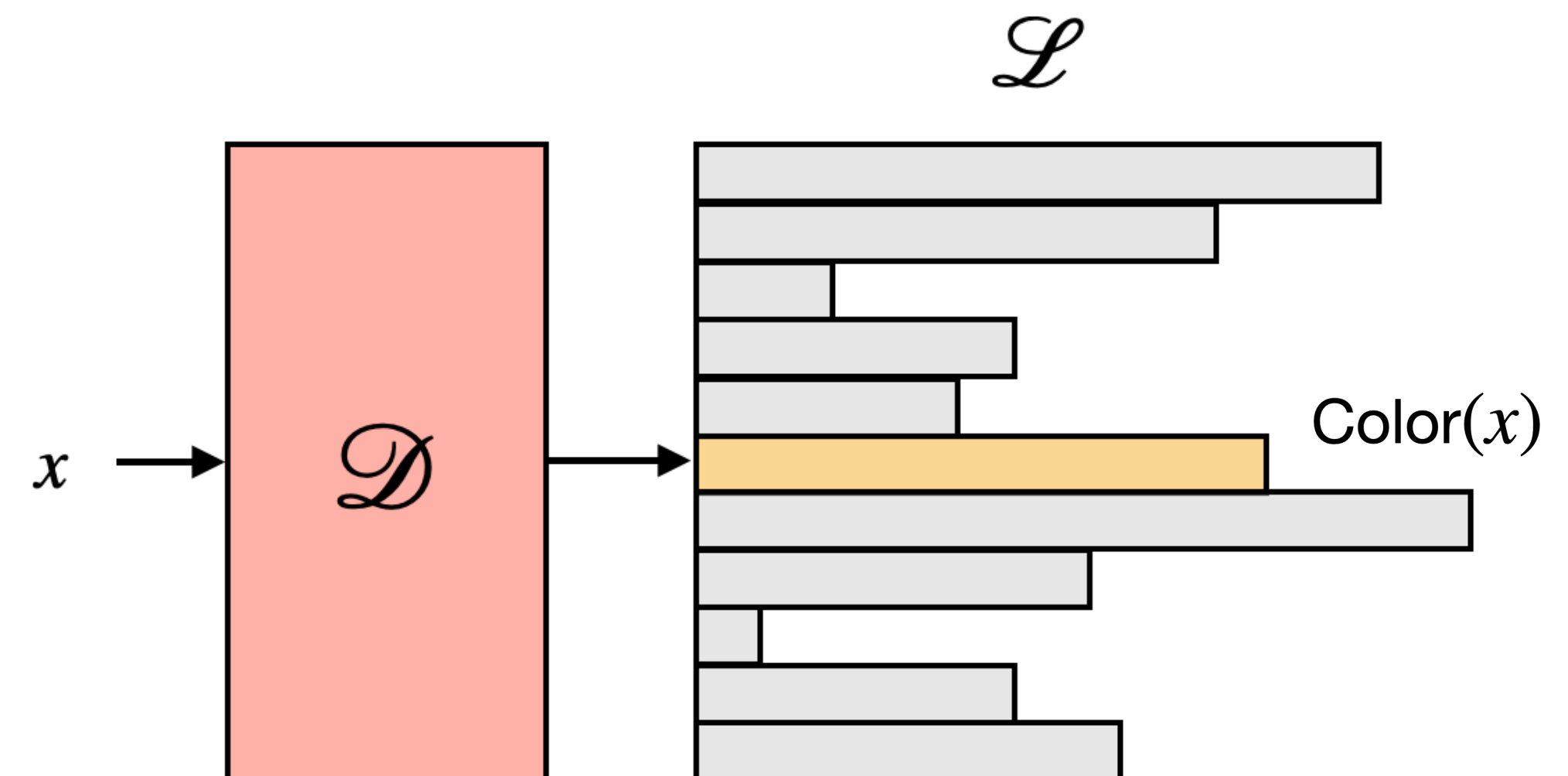
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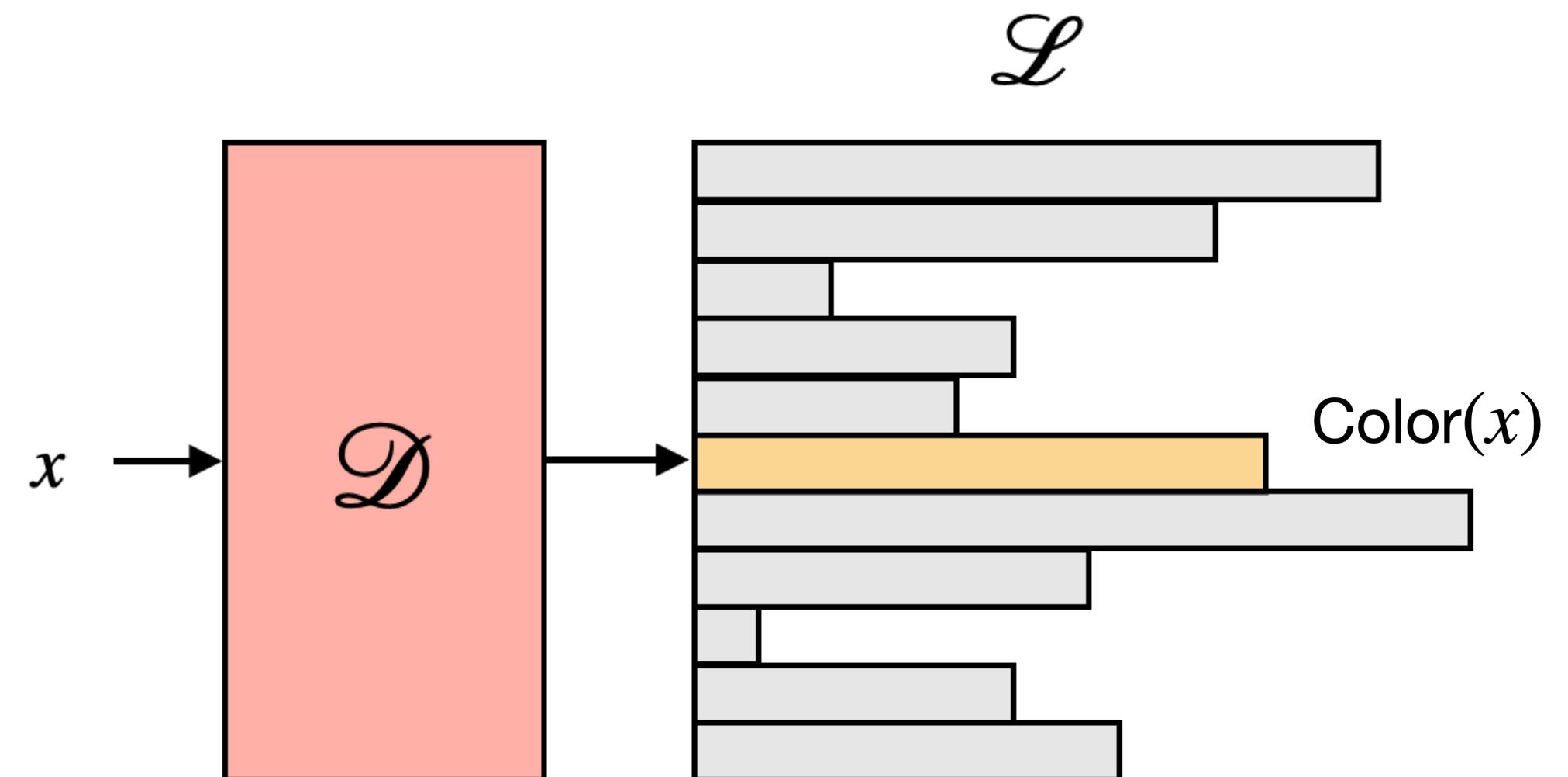
2. The sets $\{\text{Color}(x)\}_x$ are stored in order of $\text{Lookup}(x)$ in the **inverted index** \mathcal{L} .



Modular indexing layout

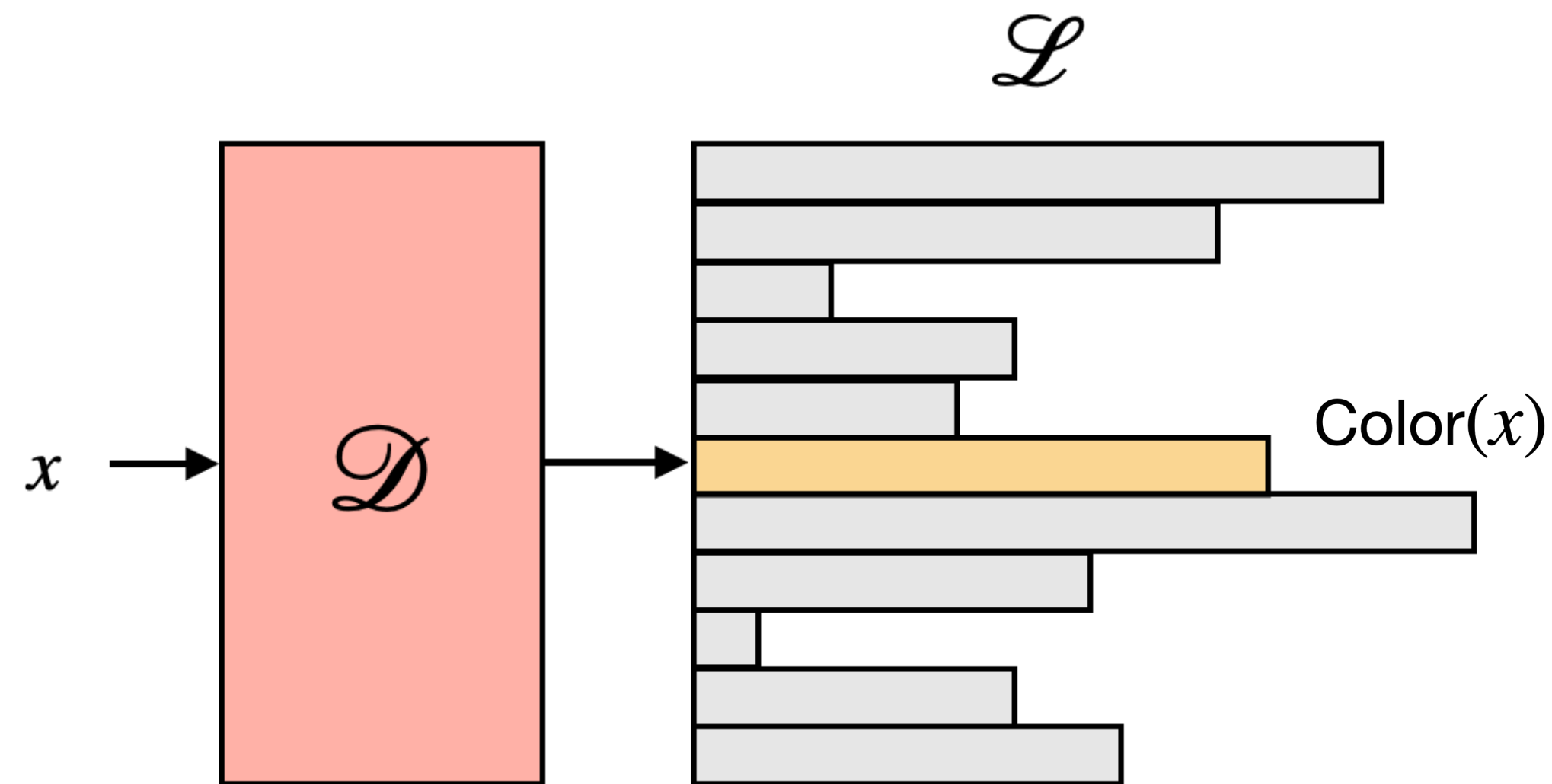
- Many k-mer based indexes (all of them?) are incarnations/adaptations of this **modular indexing layout**, $\mathcal{D} + \mathcal{L}$:

- deBGA [Liu et al. 2016]
- Kallisto [Bray et al. 2016]
- BIGSI [Bradley et al. 2017]
- Rainbowfish [Almodaresi et al. 2017]
- Mantis [Pandey et al. 2018]
- Pufferfish [Almodaresi et al. 2018]
- SeqOthello [Yu et al. 2018]
- COBS [Bingmann et al. 2019]
- Reindeer [Marchet et al. 2020]
- Raptor [Seiler et al. 2021]
- Metagraph [Karasikov et al. 2022]
- NIQKI [Agret et al. 2022]
- Pufferfish2 [Fan et al. 2022]
- Themisto [Alanko et al. 2023]
- Fulgor-v1 [Fan et al. 2023]
- Fulgor-v2 [P., Fan, Patro, 2023]



Modular indexing layout

- Our problem reduces to that of **representing two data structures**, \mathcal{D} and \mathcal{L} .
- To do so at best, we **must understand/exploit** the **properties** of our problem.
- **Q.** What are these properties?



What is special about k-mers?

- Since we take *all* the distinct k-mers (i.e., consecutive) from our references, **they share (k-1)-symbol overlaps**.

```
ACGGTAGAACCGATTCAAATTCGACGTAGC...
ACGGTAGAACCGA
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GGTAGAACCGATT
GTAGAACCGATTC
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AGAACCGATTCAA
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```

← Example for $k = 13$.

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- **Two** important consequences:
 1. It is very likely that, given x in a query sequence Q and its answer returned from the index, $next(x)$ has a very similar answer (if not identical) → **Compression for satellite data**.
 2. **Faster query time**: given the answer to x , the answer to $next(x)$ can be computed faster than the answer for another arbitrary k-mer $y \neq next(x)$.

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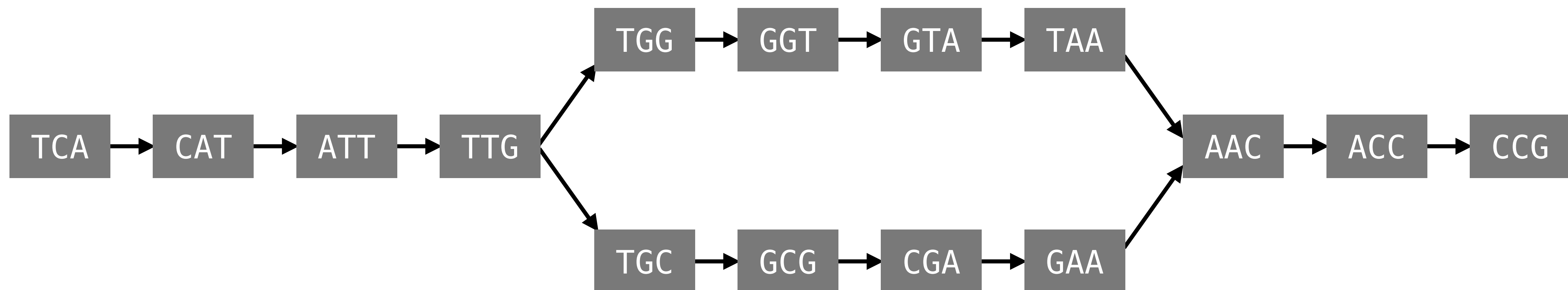
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← Example for $k = 13$.

- As simple as this might sound, indexes usually **overlook** this property to achieve better space and query time. Only few of them actually exploit it.
- Examples:
 - findere [\[Robidou and Peterlongo, 2021/22\]](#)
 - SSHash [\[P., 2022\]](#)
 - LPHash [\[P., Shibuya, Limasset 2022\]](#)

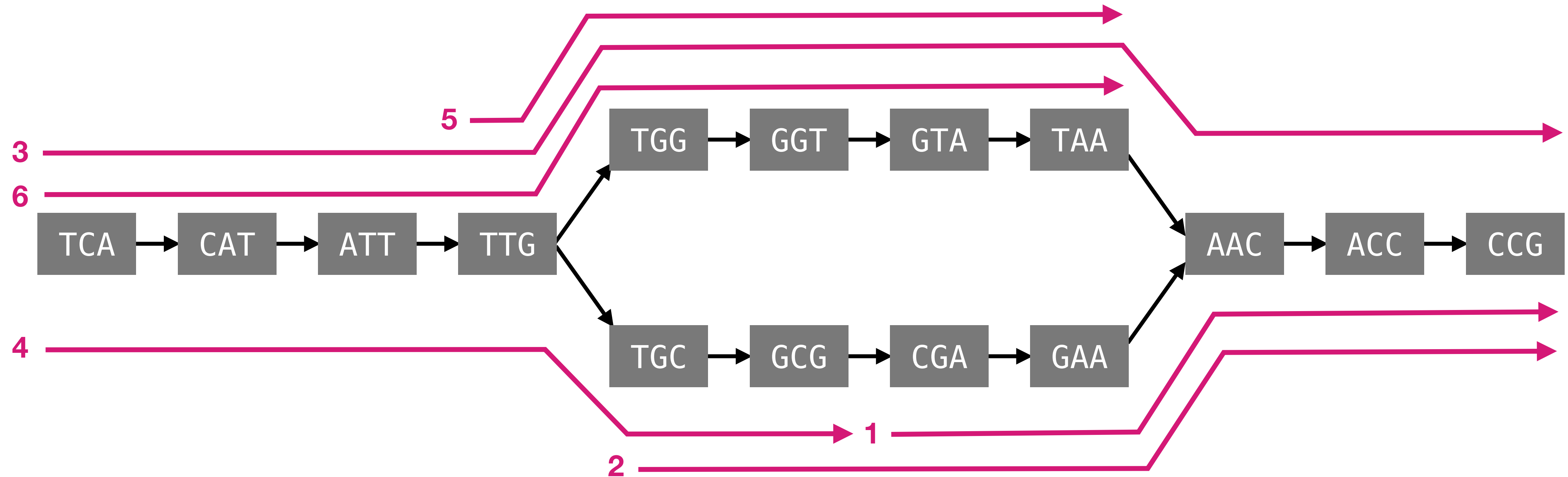
de Bruijn graphs

- The dictionary \mathcal{D} is a set of k -mers with $(k-1)$ -symbol overlaps.
- One-to-one correspondence between \mathcal{D} and a *de Bruijn* graph (dBG).
- Example for $k = 3$.



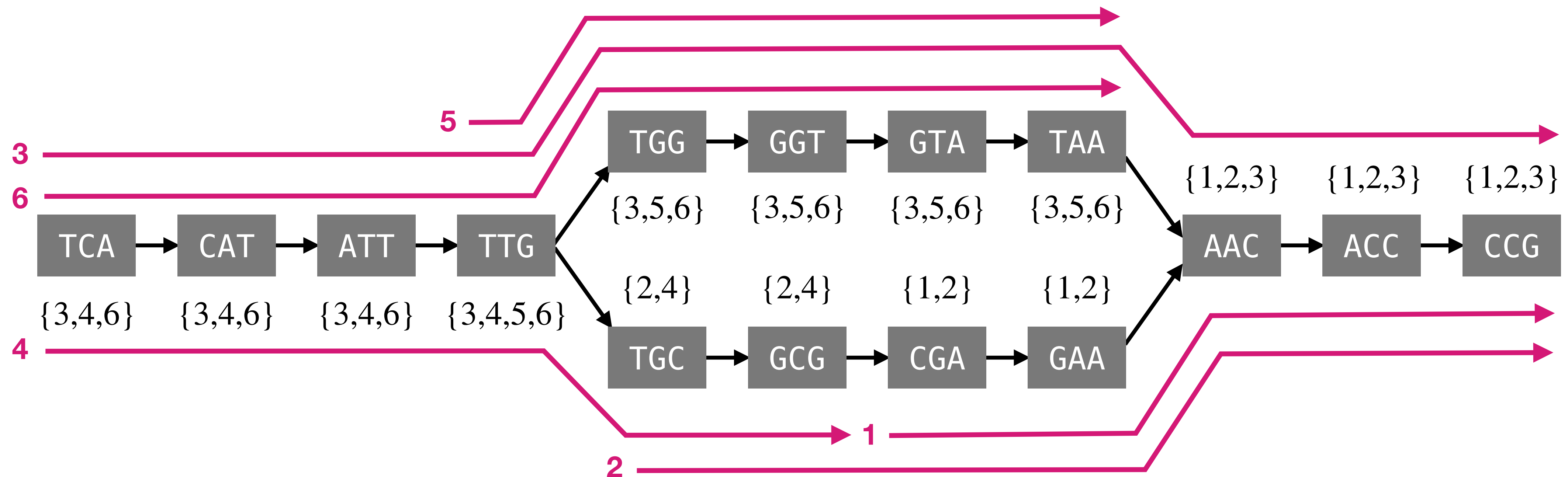
Colored de Bruijn graphs

- Example for $k = 3$ and $N = 6$ references. References in \mathcal{R} are spelled by **paths** in the graph.



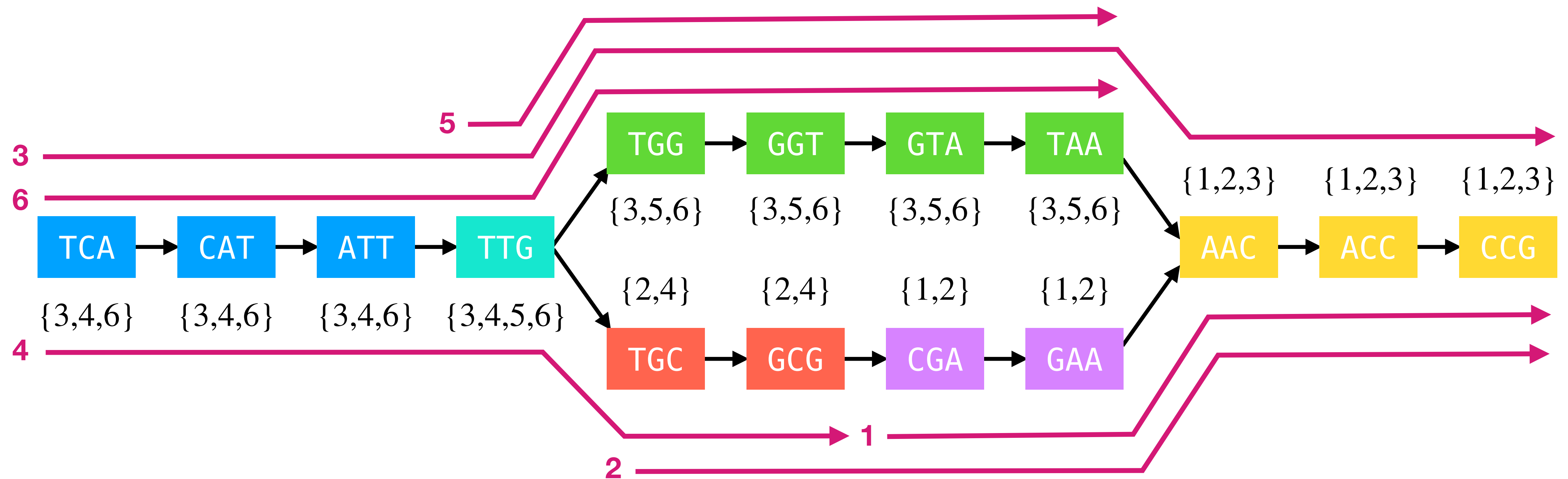
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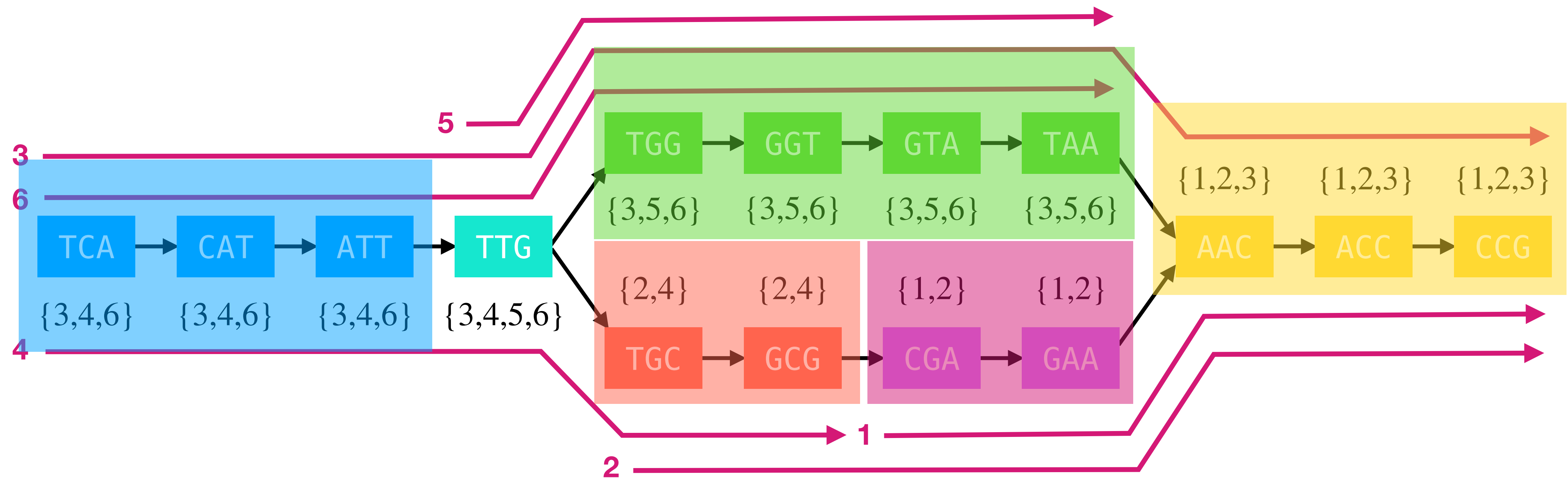
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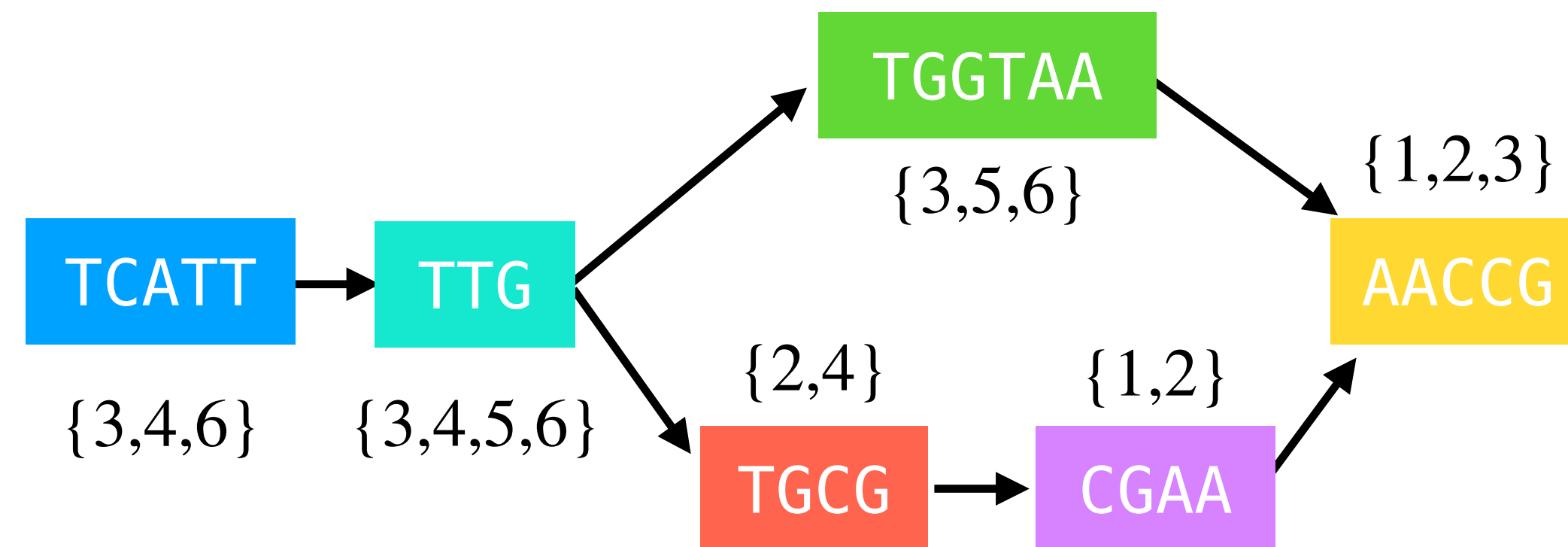
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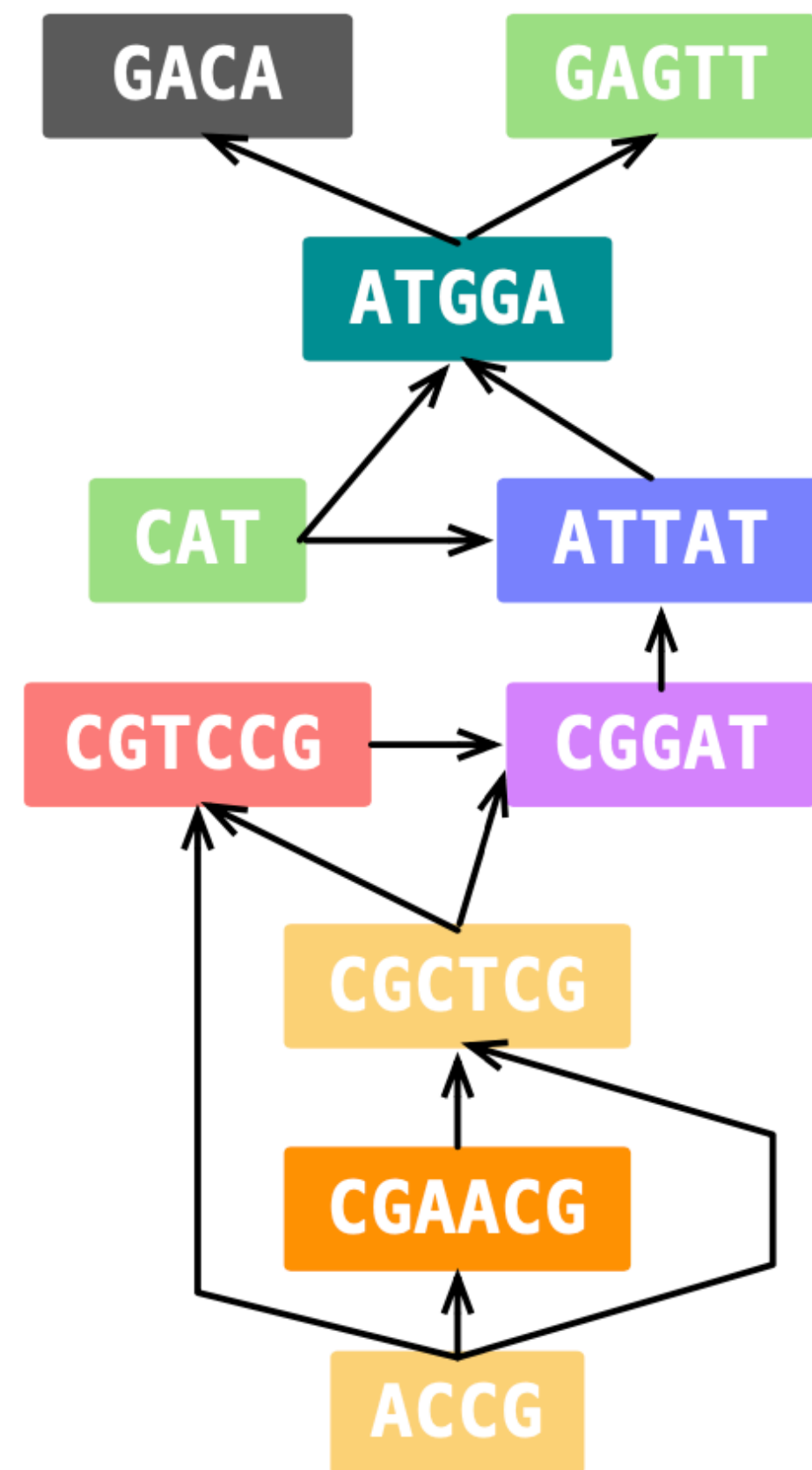
Colored compacted de Bruijn graphs

- Example for $k = 3$ and $N = 6$ references.
- Nodes having the **same color along non-branching paths** are collapsed into **unitigs**.



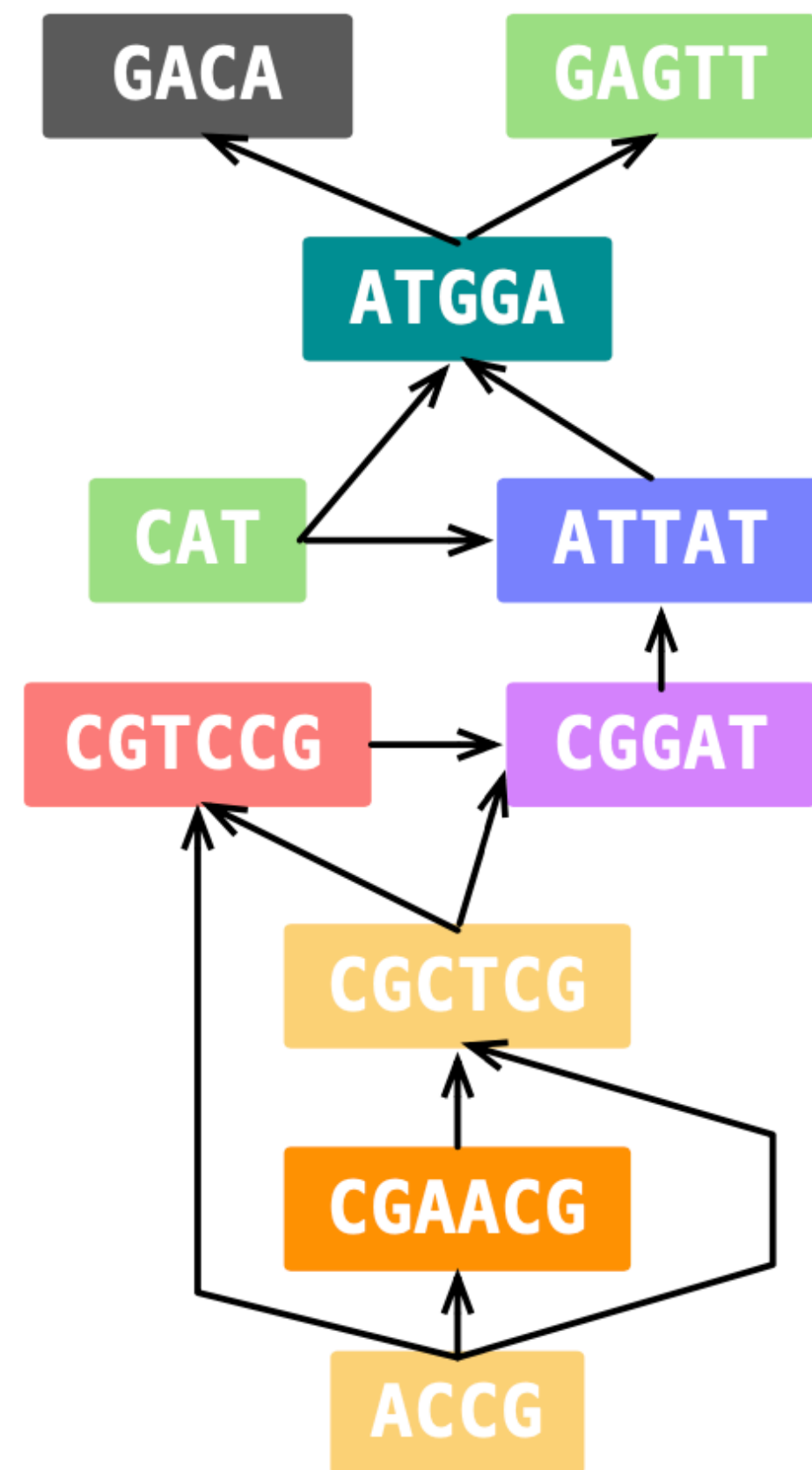
Colored compacted de Bruijn graphs

- Another, larger, example for **N = 16** references that we will use in the following.



Colored compacted de Bruijn graphs

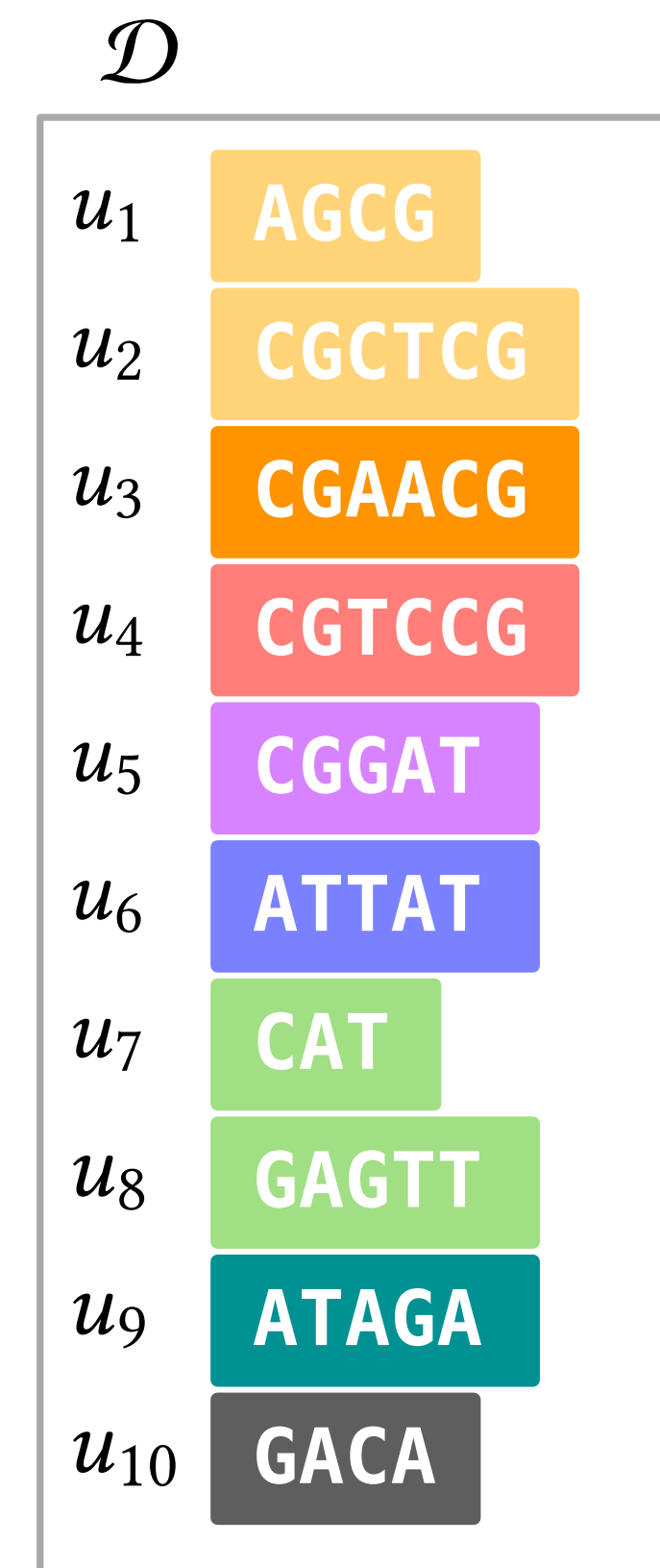
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- Let's now consider the properties of colored compacted dBGs and **how** we can exploit them for efficient indexing.

Properties of colored compacted dBGs

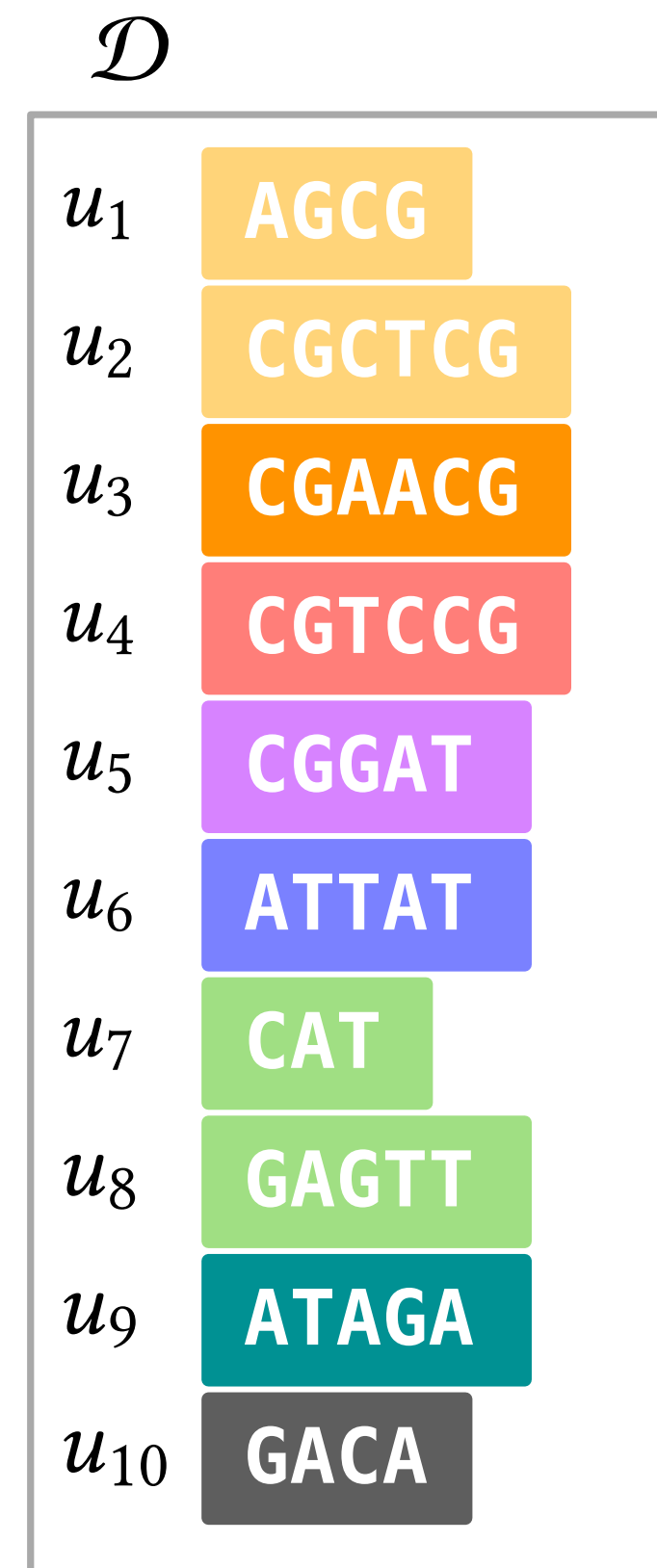
1. **Unitigs spell references in \mathcal{R} .** \rightarrow We can represent the set of unitigs instead of the set of k-mers. Better space effectiveness and cache locality.



Properties of colored compacted dBGs

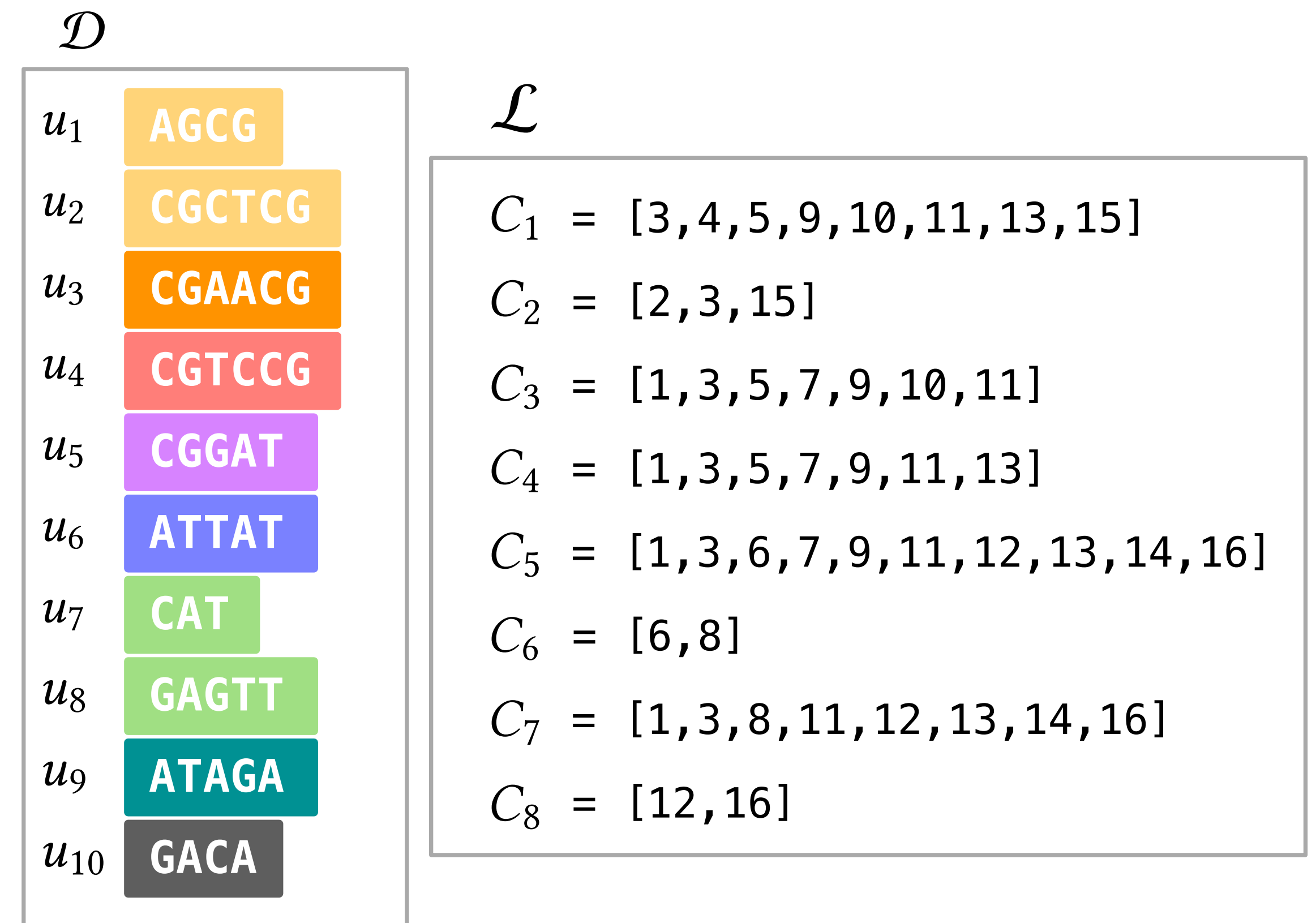
1. **Unitigs spell references in \mathcal{R} .** \rightarrow We can represent the set of unitigs instead of the set of k-mers. Better space effectiveness and cache locality.

- Represent \mathcal{D} with **SSHash** [P., 2022].
- SSSHash stores a set of unitigs **in any wanted order** (*order-preserving*).



Properties of colored compacted dBGs

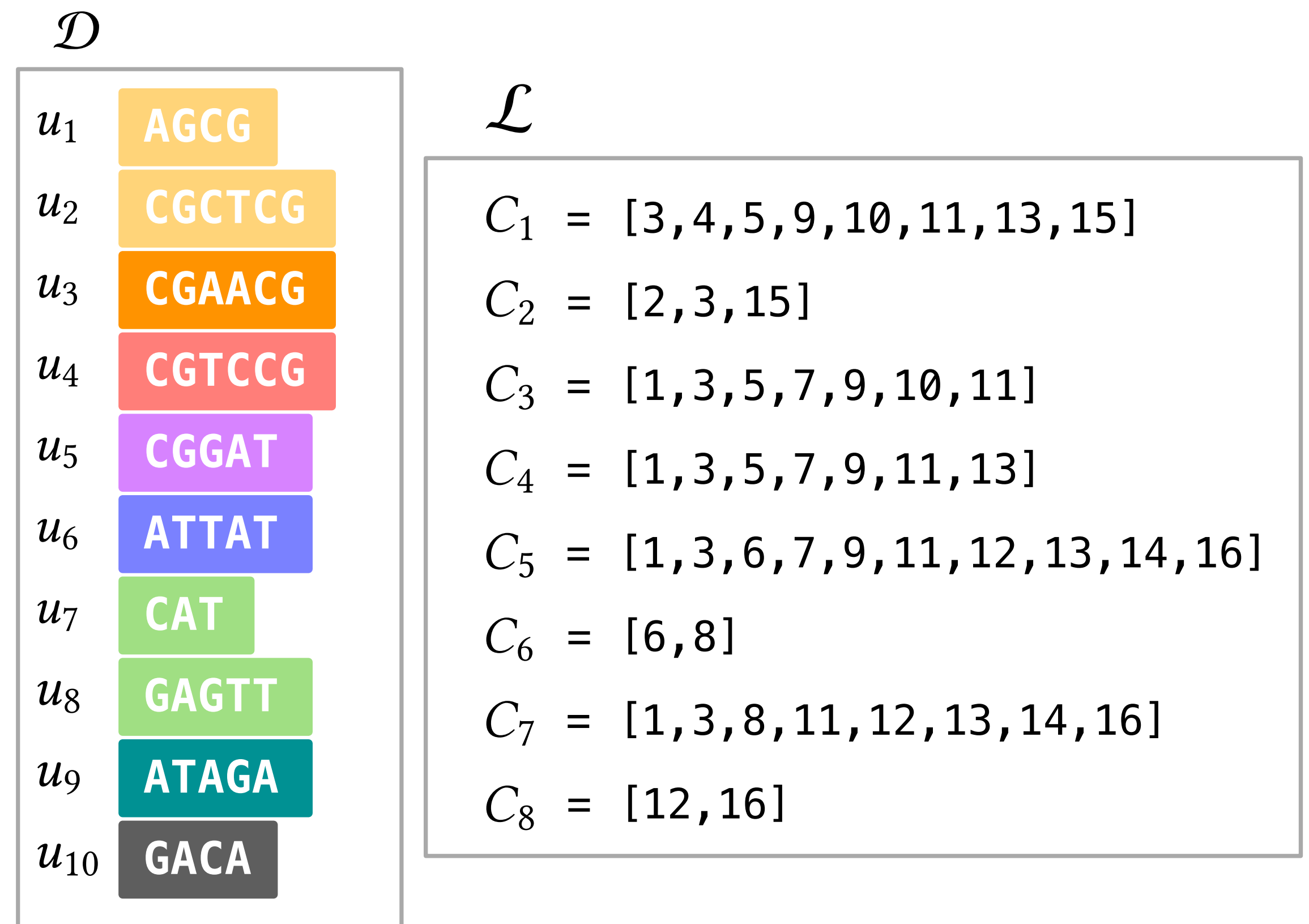
2. **Unitigs are monochromatic.** \rightarrow We store a color set for each unitig, rather than for each k-mer because $\text{Color}(x) = \text{Color}(y)$ if k-mers x and y are part of the same unitig. Thus, we need an efficient **map from k-mers to unitigs**, $x \rightarrow \text{unitig}(x)$.



Properties of colored compacted dBGs

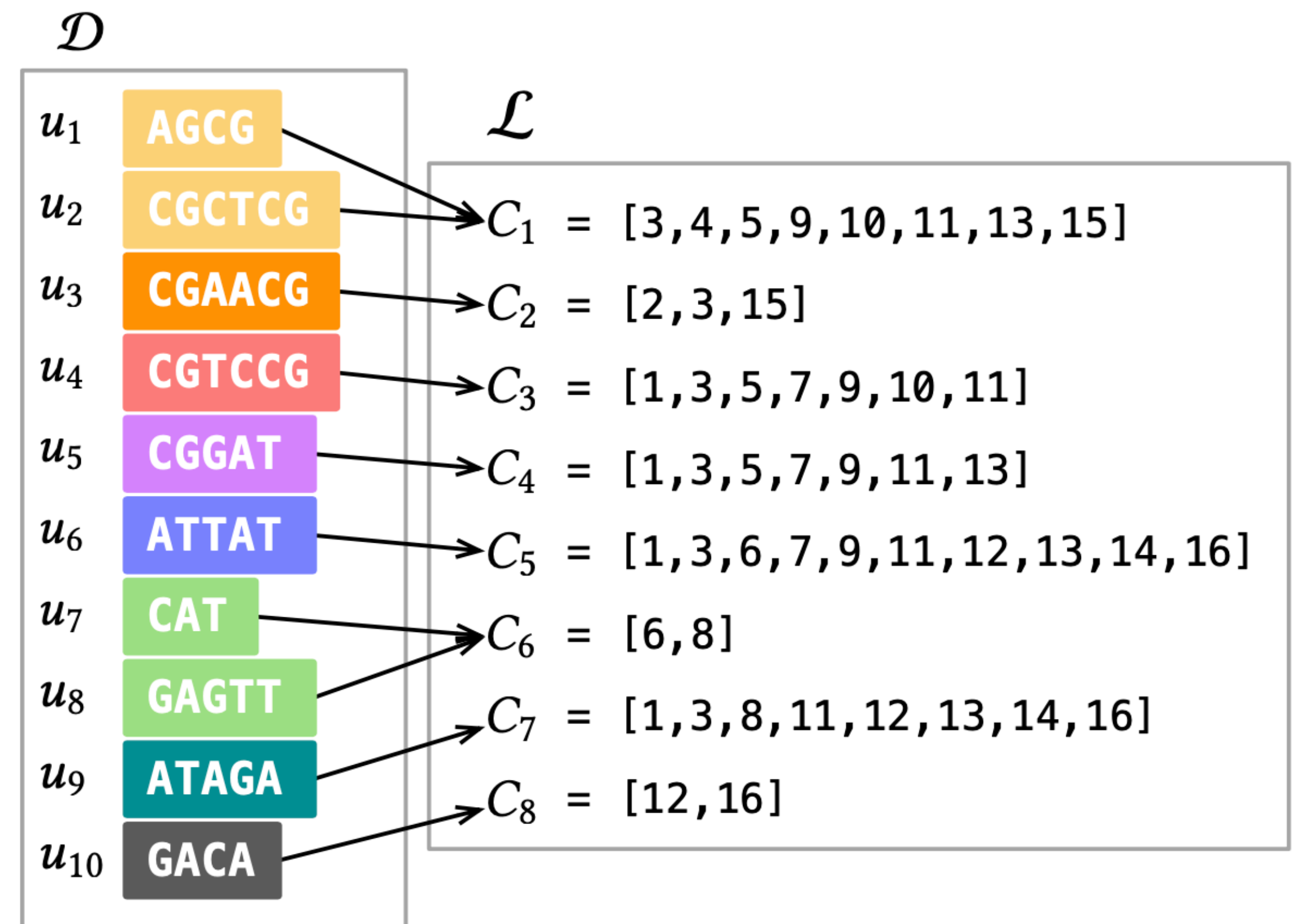
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- Represent \mathcal{D} with **SSHash** [P., 2022].
- SSSHash stores a set of unitigs in any wanted order, so it is easy to compute the **unitig identifier** $\text{unitig}(x)$ given the k-mer x .
- Now \mathcal{L} stores $\text{Color}(x)$ for each unitig in the order given by $\text{unitig}(x)$.



Properties of colored compacted dBGs

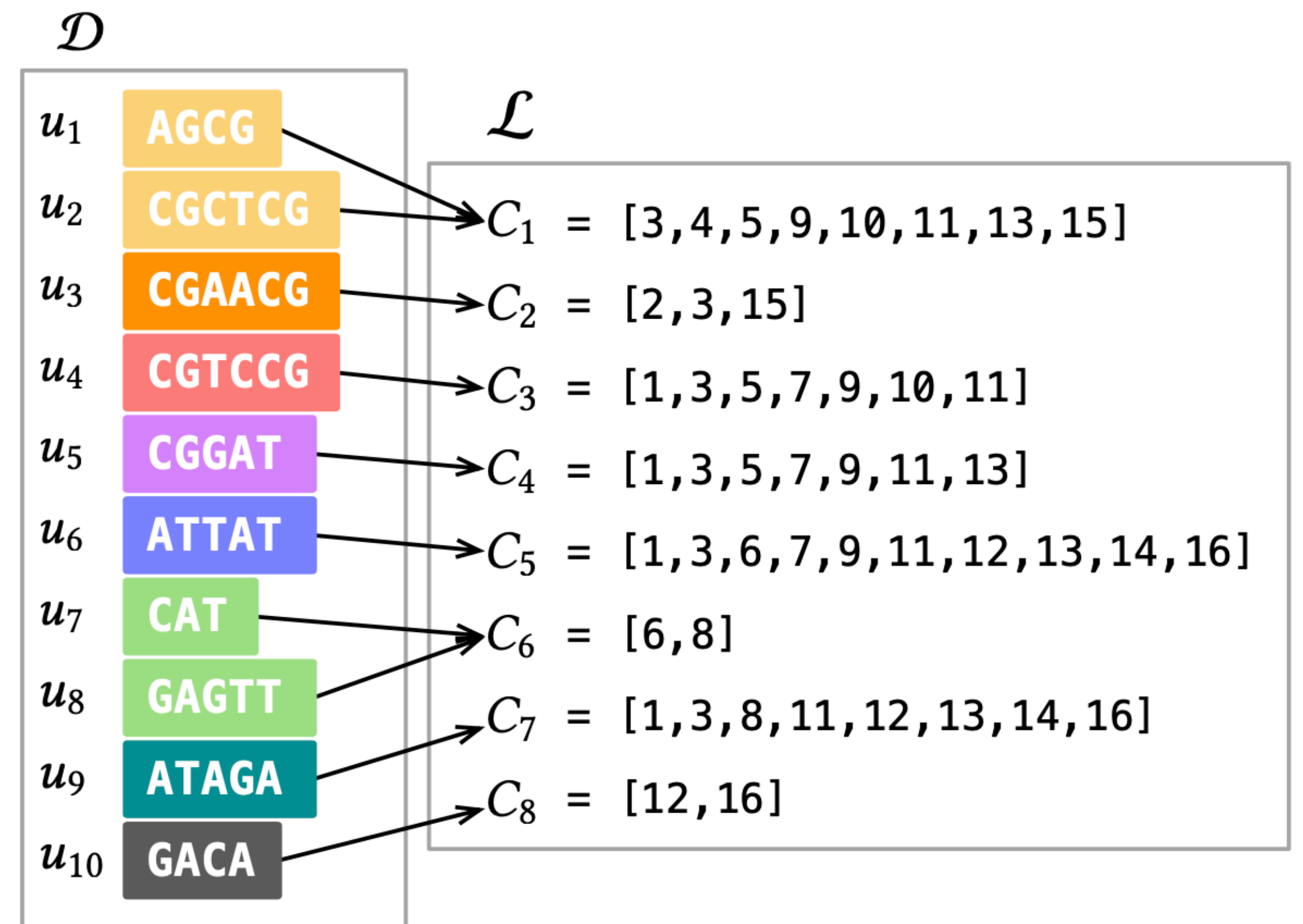
3. **Unitigs co-occur.** → Distinct unitigs often have the same color, i.e., they co-occur in the same subset of references. We have way less distinct colors than unitigs.
We need an efficient **map from unitigs to colors** $unitig(x) \rightarrow Color(x)$.



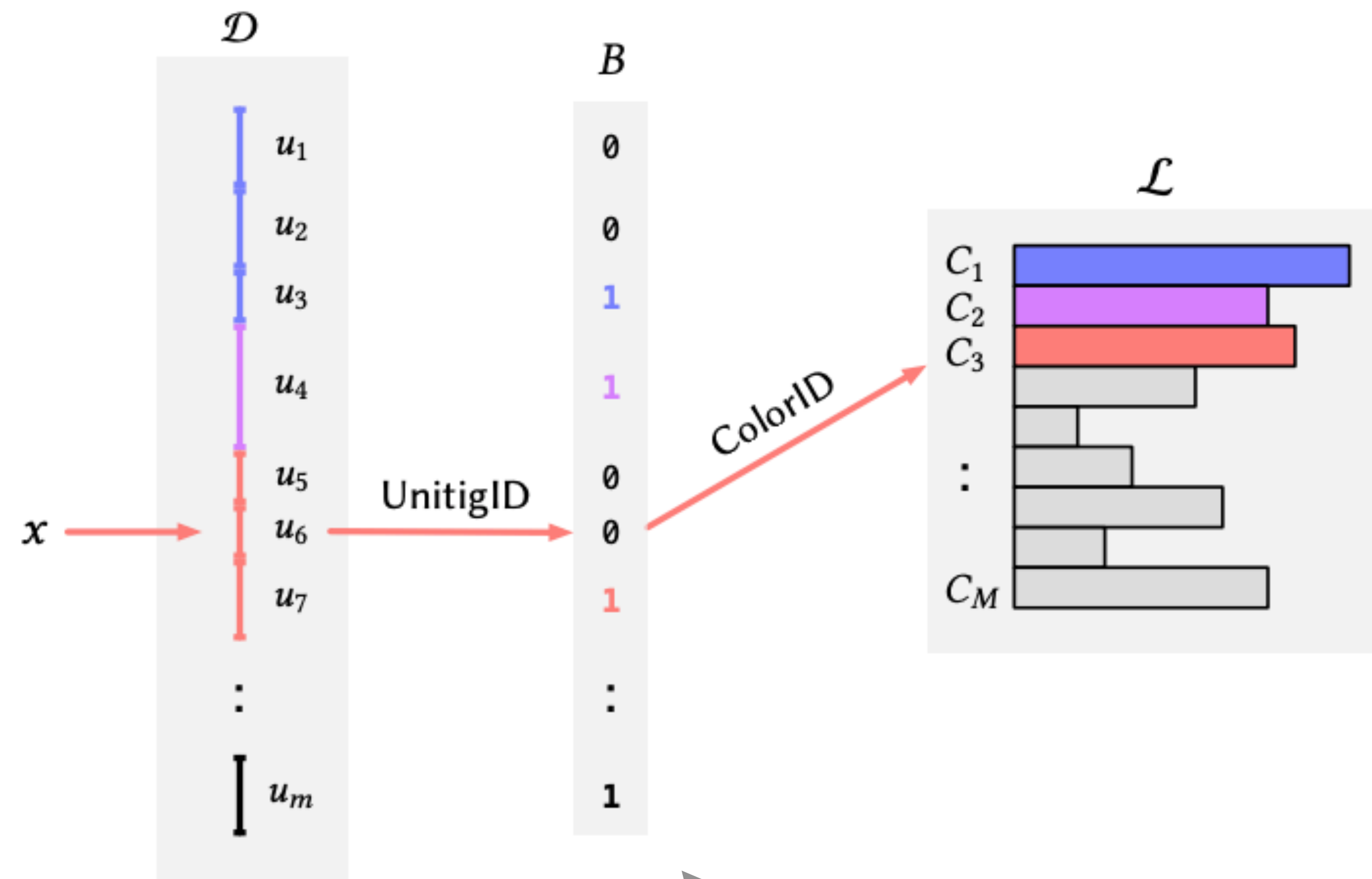
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- Represent \mathcal{D} with **SSHash** [P., 2022].
- SSSHash stores a set of unitigs in any wanted order, so we can **permute** the unitigs in \mathcal{D} so that **consecutive unitigs have the same color**.
- Then, mapping a unitig to its color is as simple as a Rank query over a bitmap.



Mapping unitigs to colors in succinct space



Just $1 + o(1)$ bits per unitig.

Results

- Results on some large pangenomes of different complexities.
- We implemented the method in a tool called **Fulgor** [Fan et al., 2023]: <https://github.com/jermp/fulgor/releases/tag/v1.0.0>

	<i>E. Coli</i> (EC)	<i>S. Enterica</i> (SE)					Gut bacteria (GB)
Genomes	3,682	5,000	10,000	50,000	100,000	150,000	30,691
Distinct colors ($\times 10^6$)	5.59	2.69	4.24	13.92	19.36	23.61	227.80
Integers in colors ($\times 10^9$)	5.74	5.77	15.68	133.49	303.53	490.04	10.04
k -mers in dBG ($\times 10^6$)	170.65	104.69	239.88	806.23	1,018.69	1,194.44	13,936.86
Unitigs in dBG ($\times 10^6$)	9.31	4.95	8.24	30.64	41.16	49.60	566.39

Index space in GB

Genomes		Fulgor			Themisto			MetaGraph			COBS
		dBG	Colors	Total	dBG	Colors	Total	dBG	Colors	Total	Total
EC	3,682	0.29	1.36	1.65	0.22	1.85	2.08	0.10	0.23	0.33	7.53
SE	5,000	0.16	0.59	0.75	0.14	1.29	1.43	0.07	0.19	0.26	9.11
	10,000	0.35	1.66	2.01	0.32	3.50	3.81	0.13	0.38	0.51	18.68
	50,000	1.26	17.03	18.30	1.07	32.42	33.48	0.36	1.95	2.31	88.61
	100,000	1.72	40.70	42.44	1.35	75.94	77.28	0.45	3.50	3.95	173.58
	150,000	2.03	68.60	70.66	1.58	125.16	126.74	—	—	—	265.49
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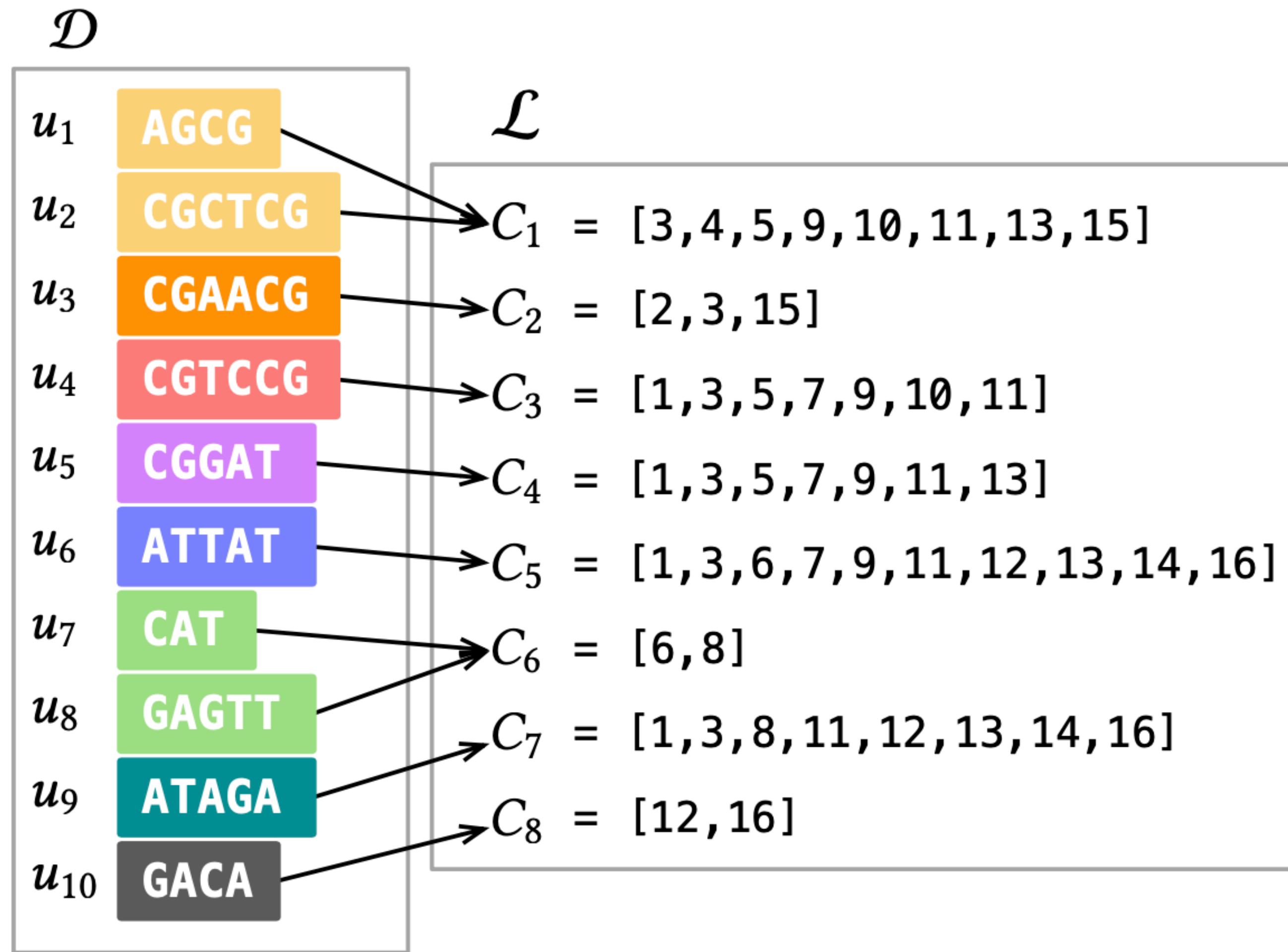
Pseudoalignment efficiency

Genomes Rate			Fulgor		Themisto		MetaG.-B		MetaG.-NB		COBS	
			mm:ss	GB	h:mm:ss	GB	mm:ss	GB	h:mm:ss	GB	h:mm:ss	GB
EC	3,682	98.99	2:10	1.68	0:03:40	2.46	22:00	30.44	1:05:41	0.40	0:45:11	34.93
SE	5,000	89.49	1:16	0.82	0:03:50	1.82	14:14	36.54	0:20:32	0.33	0:38:34	41.93
	10,000	89.71	2:26	2.11	0:07:35	4.16	28:15	92.18	0:43:40	0.61	1:01:14	84.20
	50,000	91.25	19:15	18.53	0:42:02	33.14	—	—	4:30:03	2.72	3:54:18	408.82
	100,000	91.41	27:30	42.78	1:22:00	75.93	—	—	9:40:06	4.82	8:07:29	522.56
	150,000	91.52	42:30	70.55	2:00:13	124.27	—	—	—	—	7:47:14	522.63
GB	30,691	92.91	01:10	30.02	0:01:20	48.47	28:55	15.86	0:22:05	9.91	0:34:45	225.57

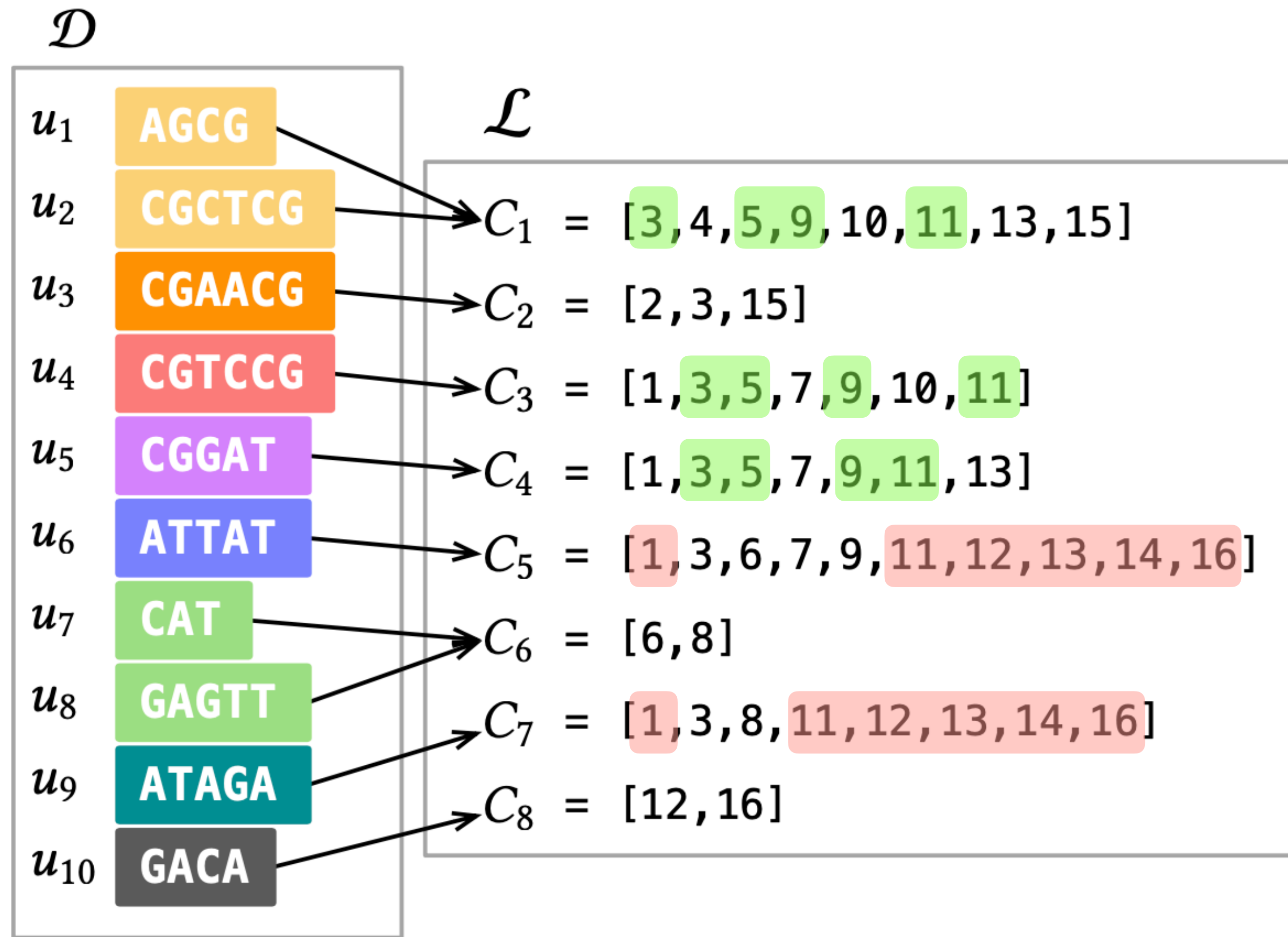
Yet another property!

1. Unitigs spell references in \mathcal{R} .
2. Unitigs are monochromatic.
3. Unitigs co-occur.
4. **Colors are similar when indexing pangenomes.** → Opportunity to achieve **much better compression** if colors are not compressed *individually* (each set independently of the others) but *common patterns are factored out and compressed once*.

Colors are similar when indexing pangénomies

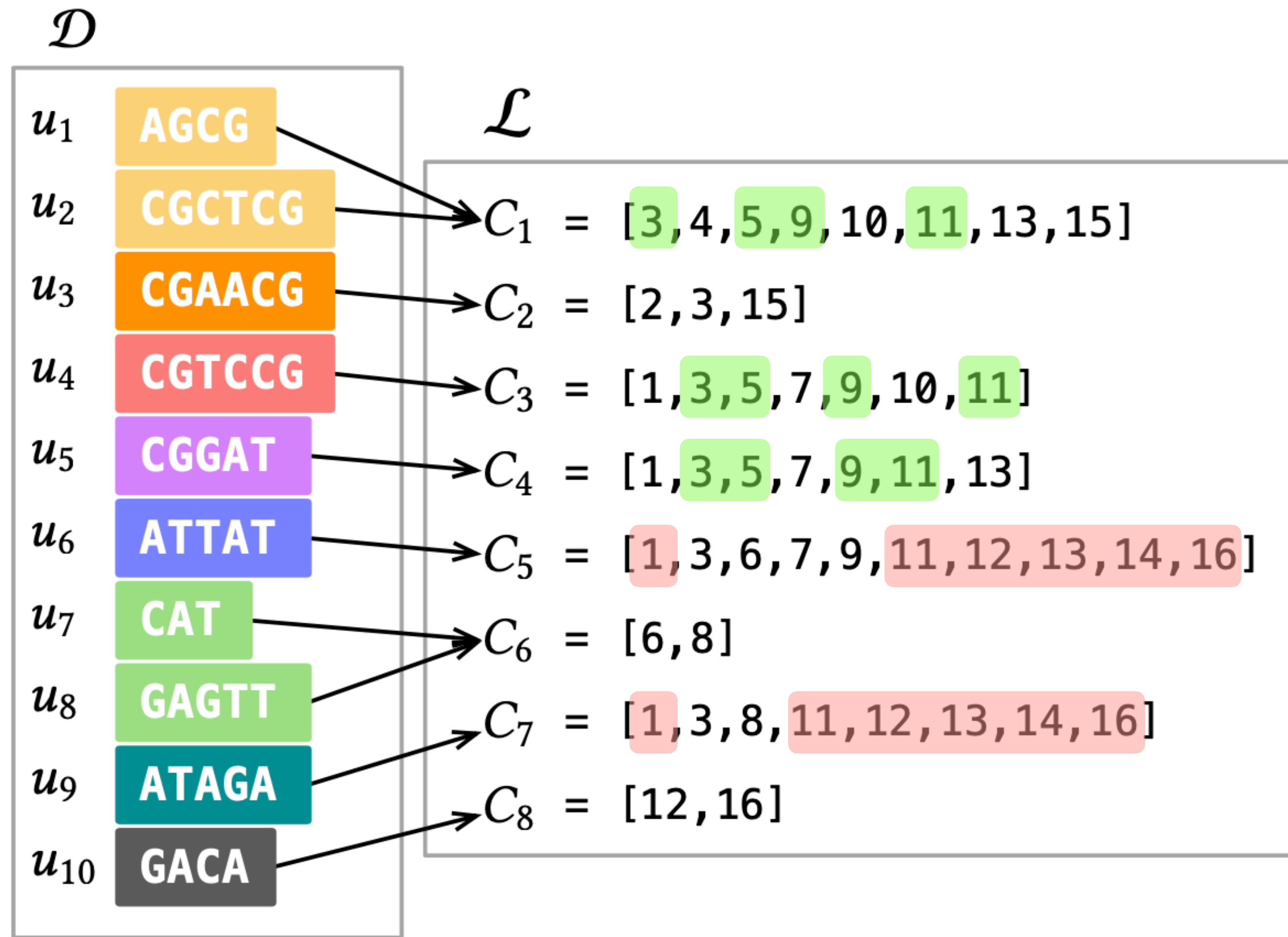


Colors are similar when indexing pangénomies



- The pattern $\{3, 5, 9, 11\}$ is currently represented **three times**.
- The pattern $\{1, 11, 12, 13, 14, 16\}$ is represented **twice**.

Colors are similar when indexing pangénomies




- The pattern $\{3, 5, 9, 11\}$ is currently represented **three times**.
- The pattern $\{1, 11, 12, 13, 14, 16\}$ is represented **twice**.
- **Q.** How to factor out this redundancy?

Introducing meta and partial colors

- Determine a **partition** of $[N] = \{1, \dots, N\}$ so that references in the same partition are *similar*. Take the set of distinct **partial** colors for each partition \rightarrow factor out the redundancy.
- **Intuition:** Similar references induce similar colors and thus *share patterns* \rightarrow the number of distinct partial colors in a partition is small.
- Now we can render each original color as a sequence of references — or **meta** colors — to those **partial** colors.

Meta and partial colors — Example

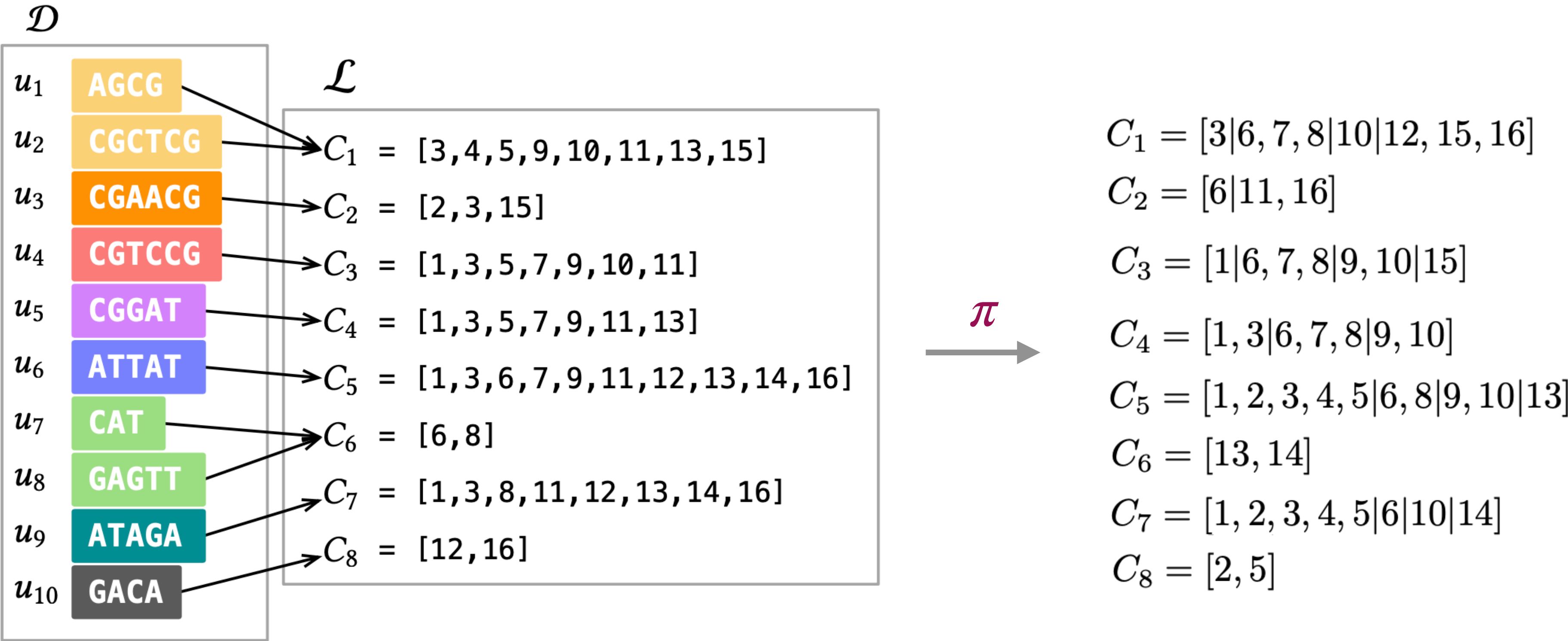
- Example for **N = 16** references and **4** partitions.

new identifiers \rightarrow $\begin{array}{cccccc} \{ & 1 & 12 & 13 & 14 & 16 & \} & \{ & 3 & 5 & 9 & \} & \{ & 7 & 11 & \} & \{ & 2 & 4 & 6 & 8 & 10 & 15 & \} \\ 1 & 2 & 3 & 4 & 5 & & 6 & 7 & 8 & & 9 & 10 & & 11 & 12 & 13 & 14 & 15 & 16 \end{array}$  this defines a permutation π

Meta and partial colors — Example

- Example for **N = 16** references and **4** partitions.

$\{ 1\ 12\ 13\ 14\ 16 \} \{ 3\ 5\ 9 \} \{ 7\ 11 \} \{ 2\ 4\ 6\ 8\ 10\ 15 \}$
new identifiers \rightarrow 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 ← this defines a permutation π

 u_5

CGGAT

 u_6

ATTAT

 u_7

CAT

 u_8

GAGTT

 u_9

ATAGA

 u_{10}

GACA

\mathcal{L}

$\rightarrow C_1 = [3, 4, 5, 9, 10, 11, 13, 15]$

$\rightarrow C_2 = [2, 3, 15]$

$\rightarrow C_3 = [1, 3, 5, 7, 9, 10, 11]$

$\rightarrow C_4 = [1, 3, 5, 7, 9, 11, 13]$

$\rightarrow C_5 = [1, 3, 6, 7, 9, 11, 12, 13, 14, 16]$

$\rightarrow C_6 = [6, 8]$

$\rightarrow C_7 = [1, 3, 8, 11, 12, 13, 14, 16]$

$\rightarrow C_8 = [12, 16]$

$\xrightarrow{\pi}$

$C_1 = [3|6, 7, 8|10|12, 15, 16]$

$C_2 = [6|11, 16]$

$C_3 = [1|6, 7, 8|9, 10|15]$

$C_4 = [1, 3|6, 7, 8|9, 10]$

$C_5 = [1, 2, 3, 4, 5|6, 8|9, 10|13]$

$C_6 = [13, 14]$

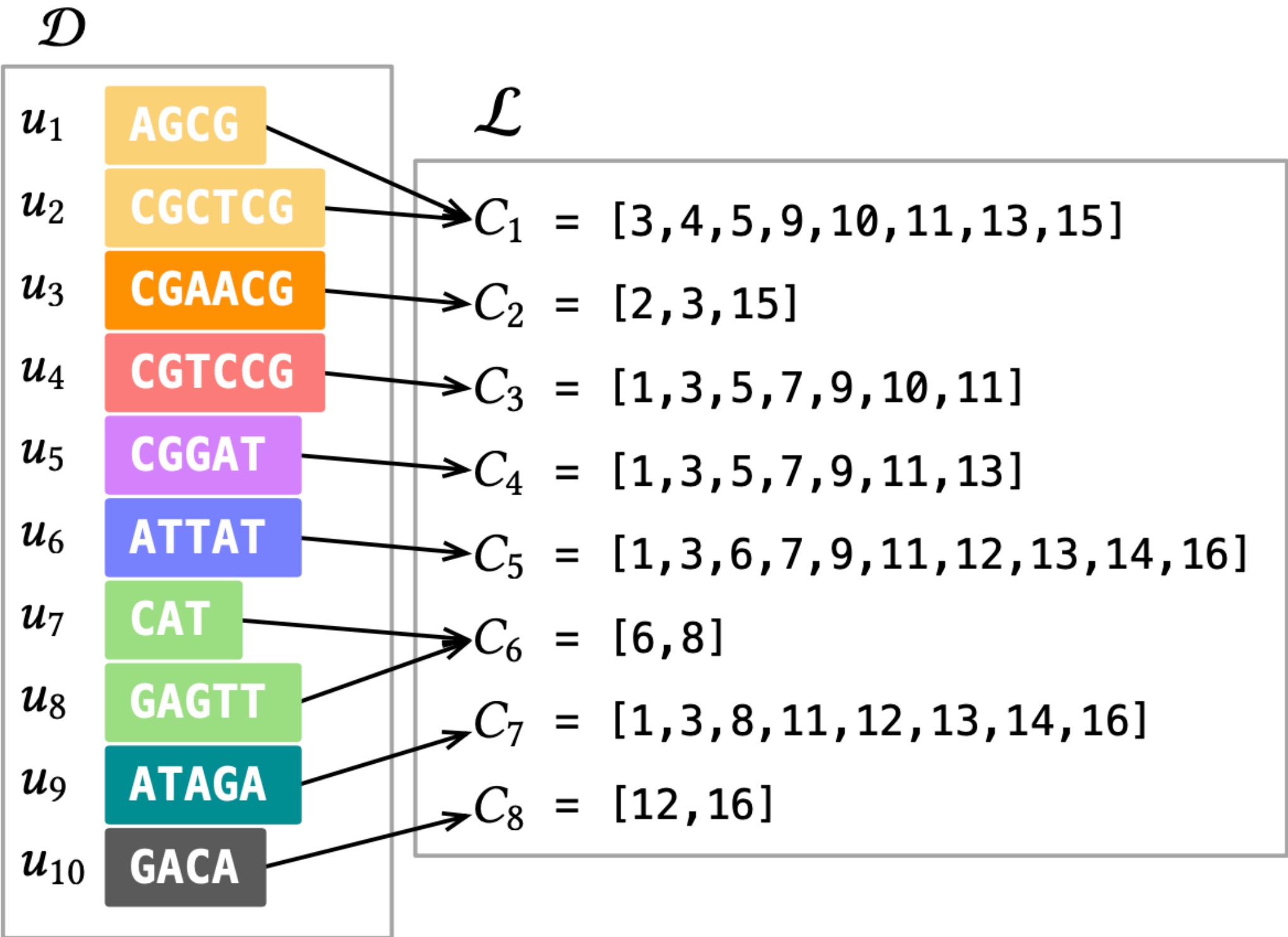
$C_7 = [1, 2, 3, 4, 5|6|10|14]$

$C_8 = [2, 5]$

Meta and partial colors — Example

- Example for **N = 16** references and **4** partitions.

$\{ 1\ 12\ 13\ 14\ 16 \} \{ 3\ 5\ 9 \} \{ 7\ 11 \} \{ 2\ 4\ 6\ 8\ 10\ 15 \}$
new identifiers $\rightarrow 1\ 2\ 3\ 4\ 5\ \boxed{6\ 7\ 8}\ 9\ 10\ 11\ 12\ 13\ 14\ 15\ 16$ ← this defines a permutation π
partition 2



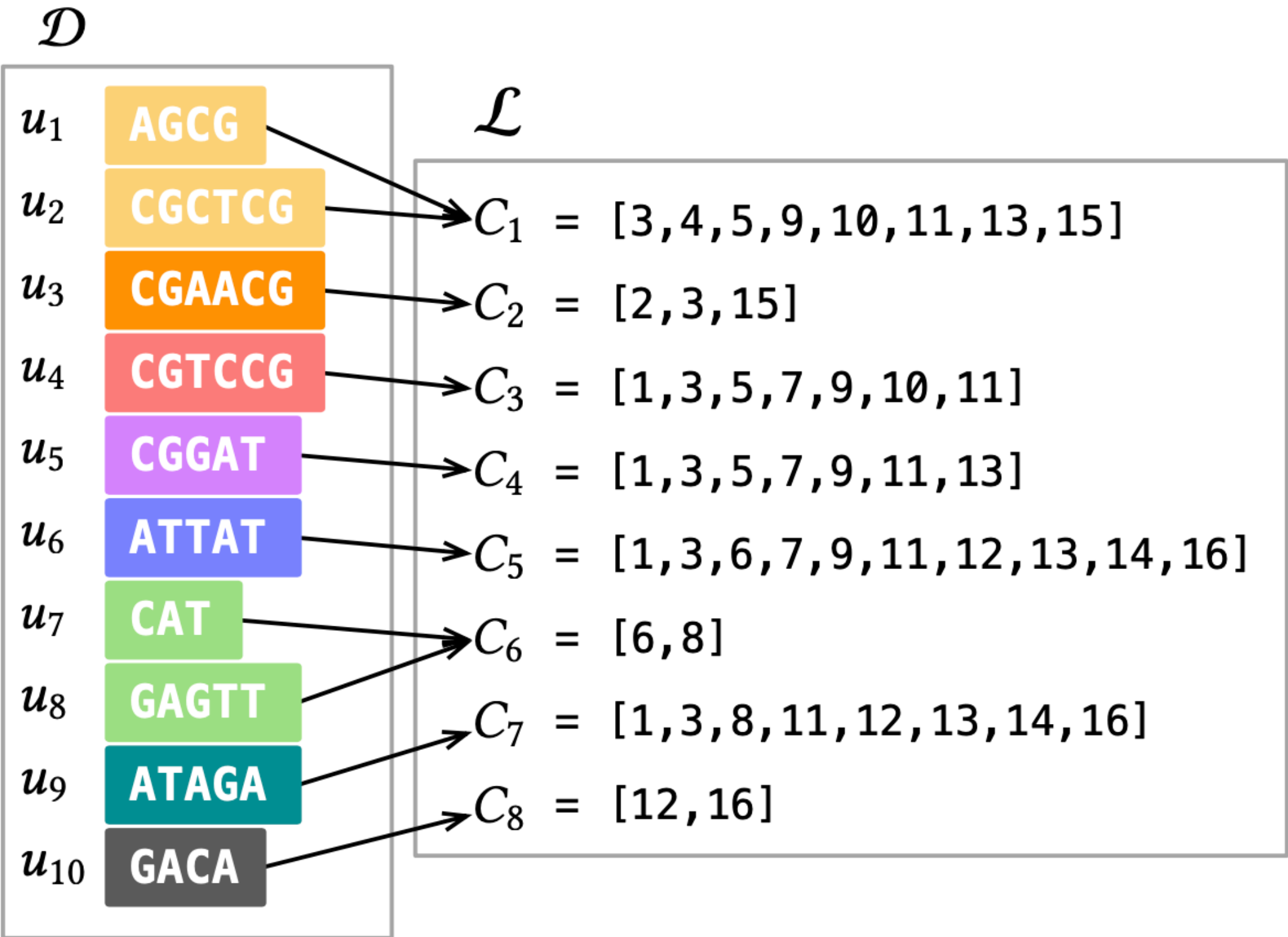
π

$C_1 = [3|6, 7, 8|10|12, 15, 16]$
 $C_2 = [6|11, 16]$
 $C_3 = [1|6, 7, 8|9, 10|15]$
 $C_4 = [1, 3|6, 7, 8|9, 10]$
 $C_5 = [1, 2, 3, 4, 5|6, 8|9, 10|13]$
 $C_6 = [13, 14]$
 $C_7 = [1, 2, 3, 4, 5|6|10|14]$
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Meta and partial colors — Example

- Example for **N = 16** references and **4** partitions.

$\{ 1\ 12\ 13\ 14\ 16 \} \{ 3\ 5\ 9 \} \{ 7\ 11 \} \{ 2\ 4\ 6\ 8\ 10\ 15 \}$
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partition 2

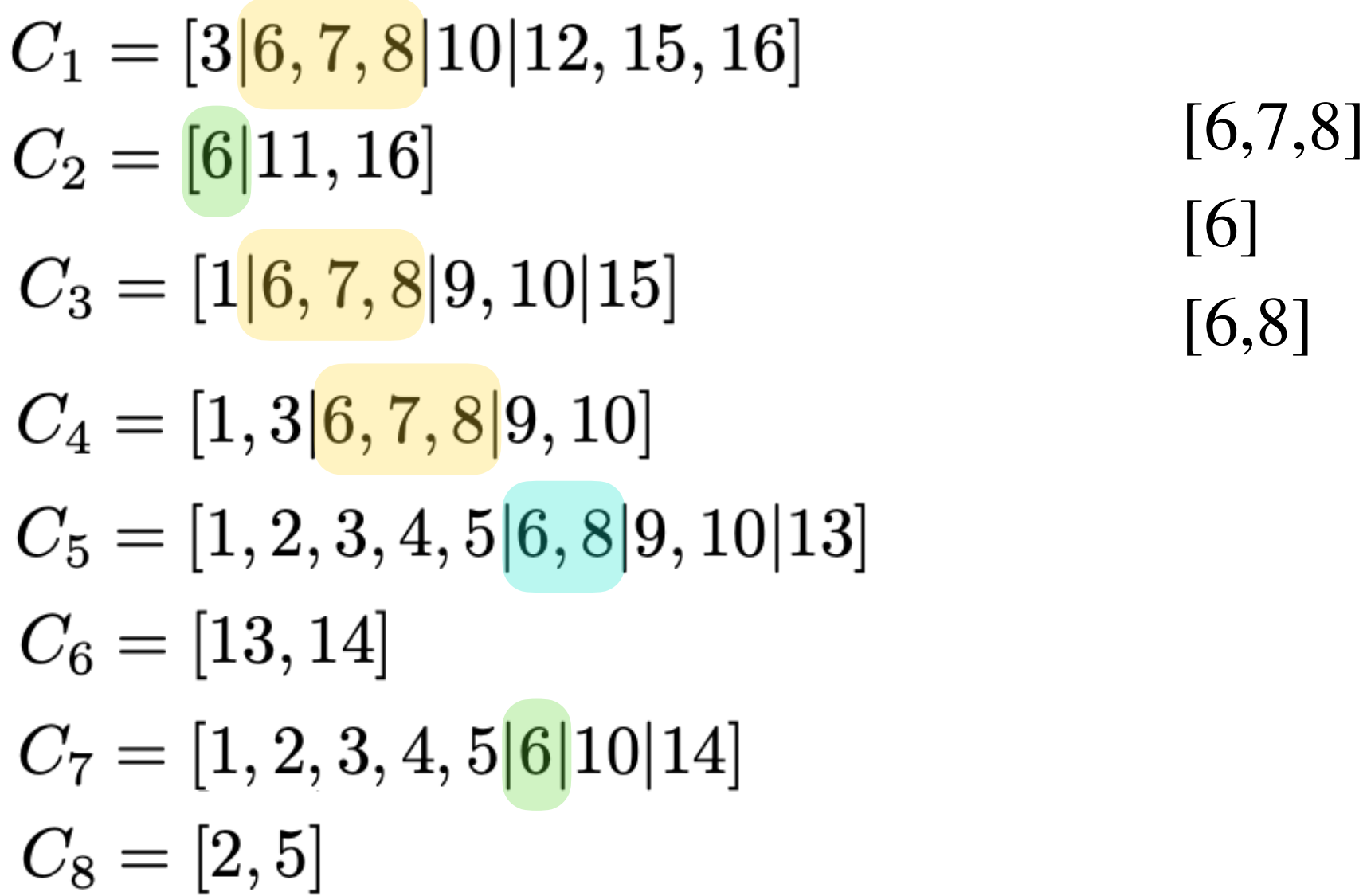
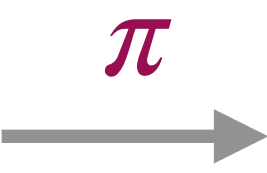
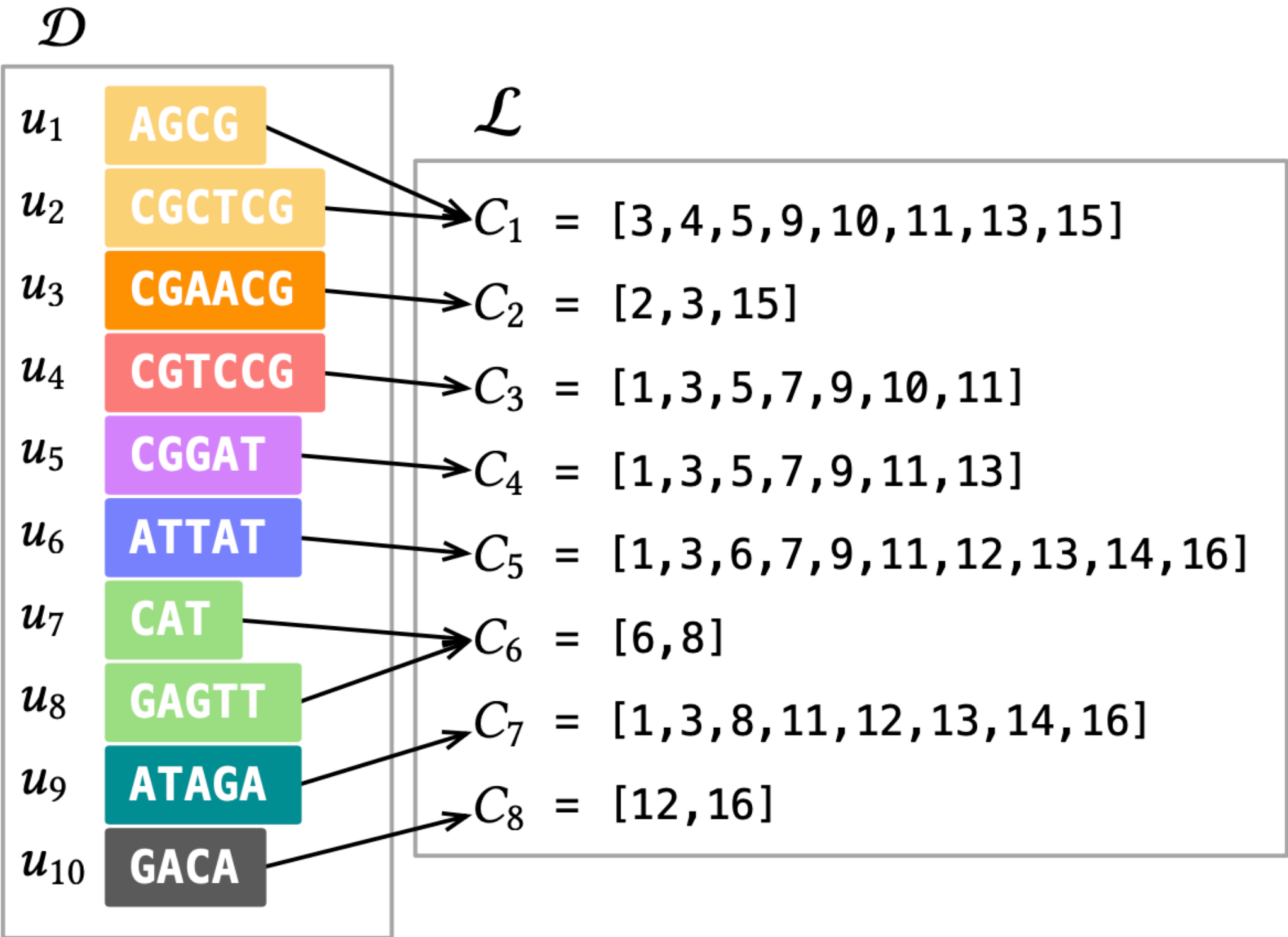
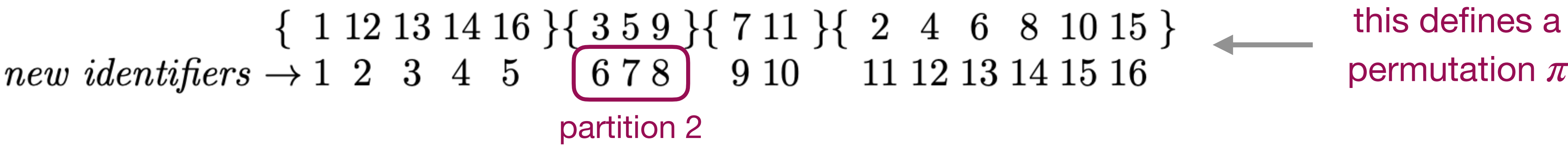


π

$C_1 = [3|6, 7, 8|10|12, 15, 16]$
 $C_2 = [6|11, 16]$
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 $C_6 = [13, 14]$
 $C_7 = [1, 2, 3, 4, 5|6|10|14]$
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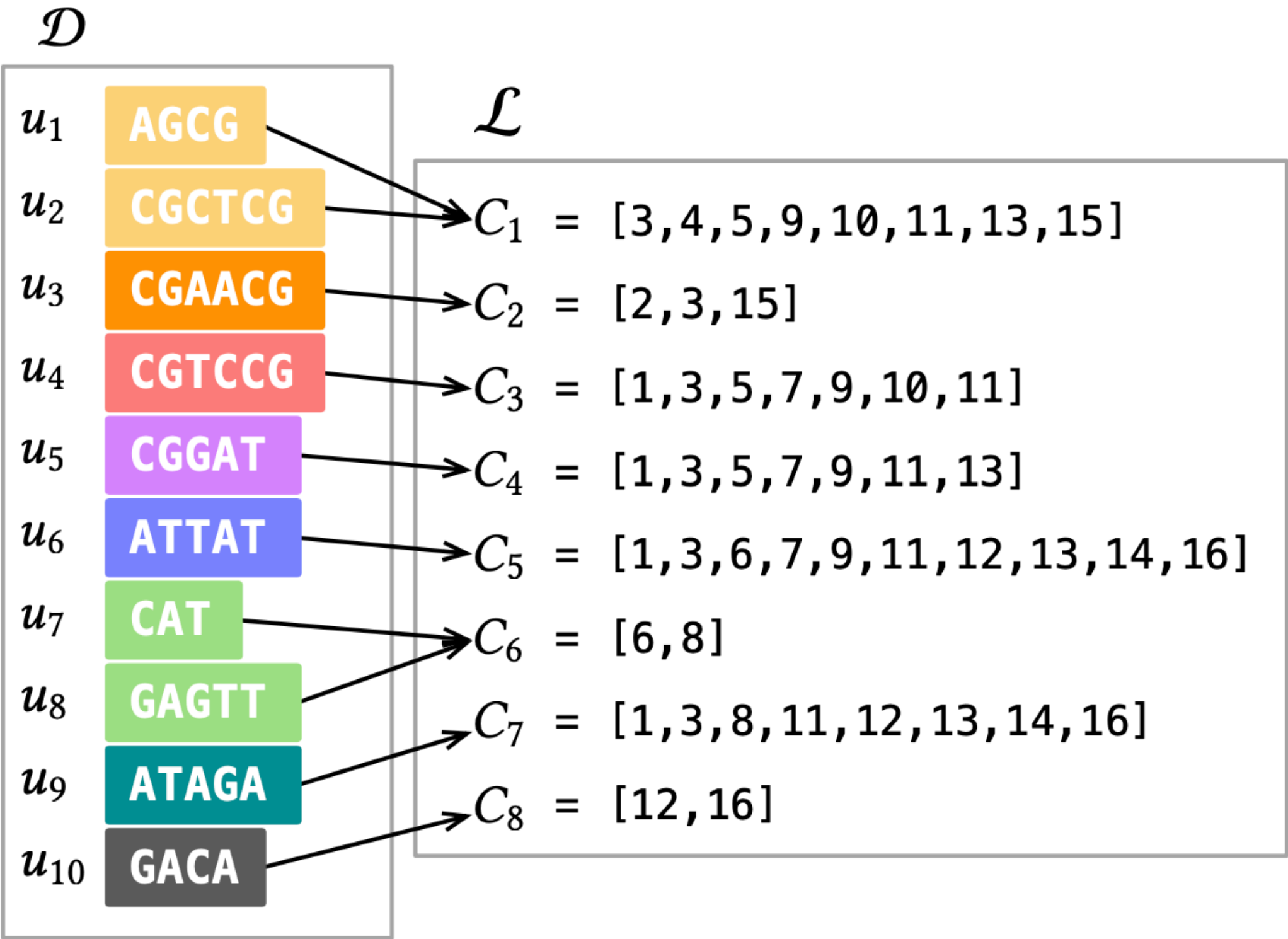
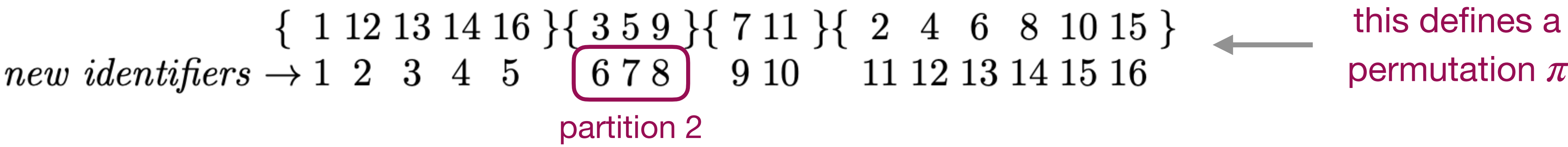
Meta and partial colors — Example

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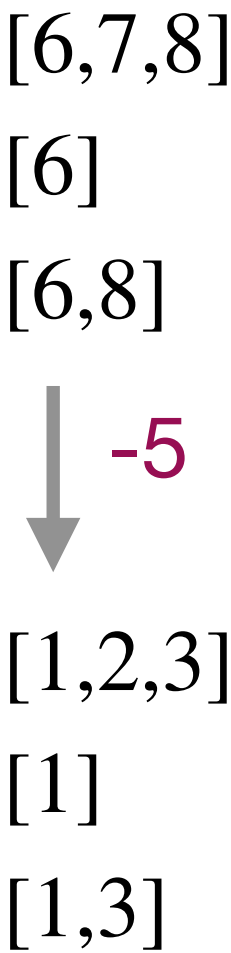
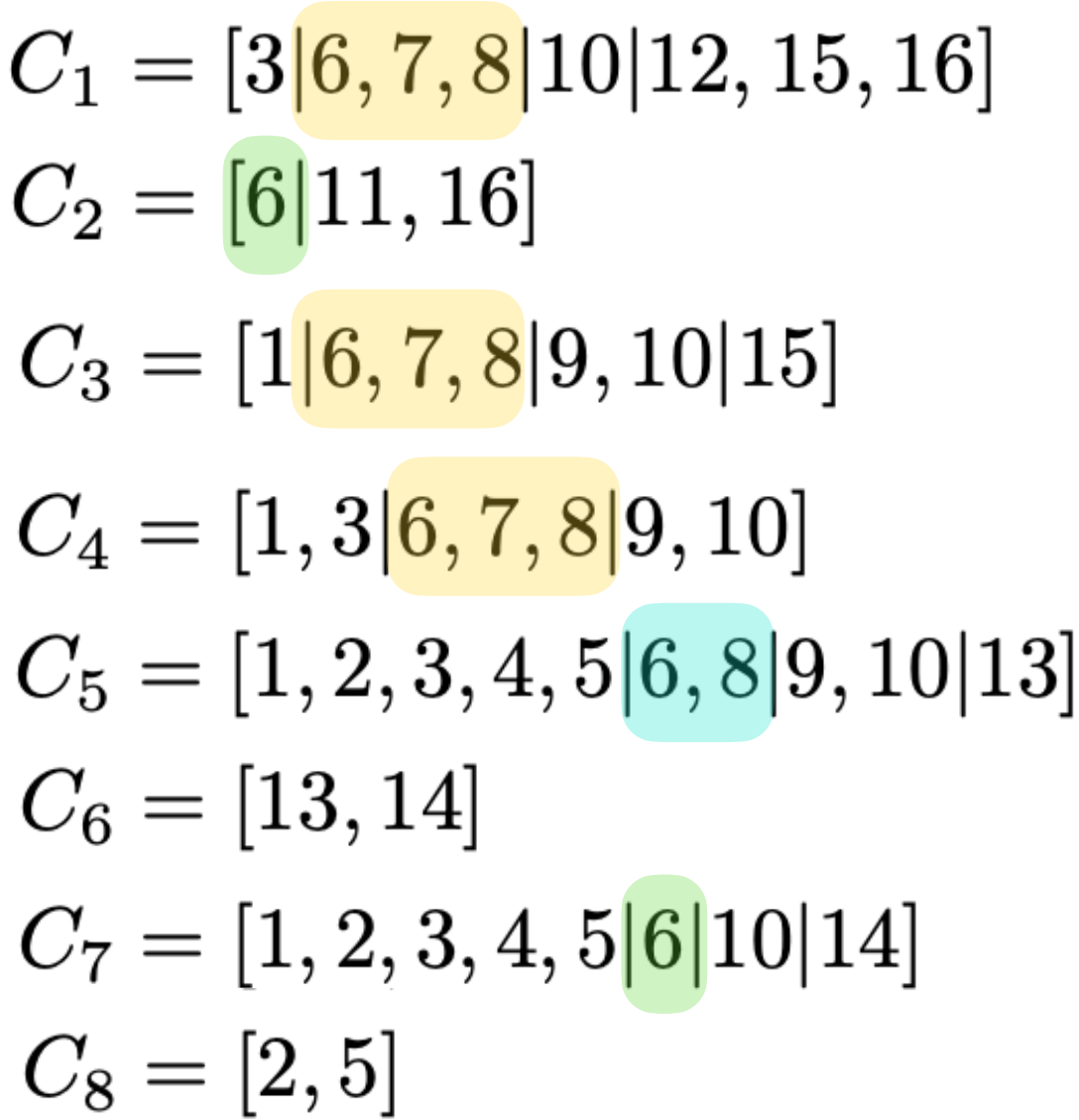


Meta and partial colors — Example

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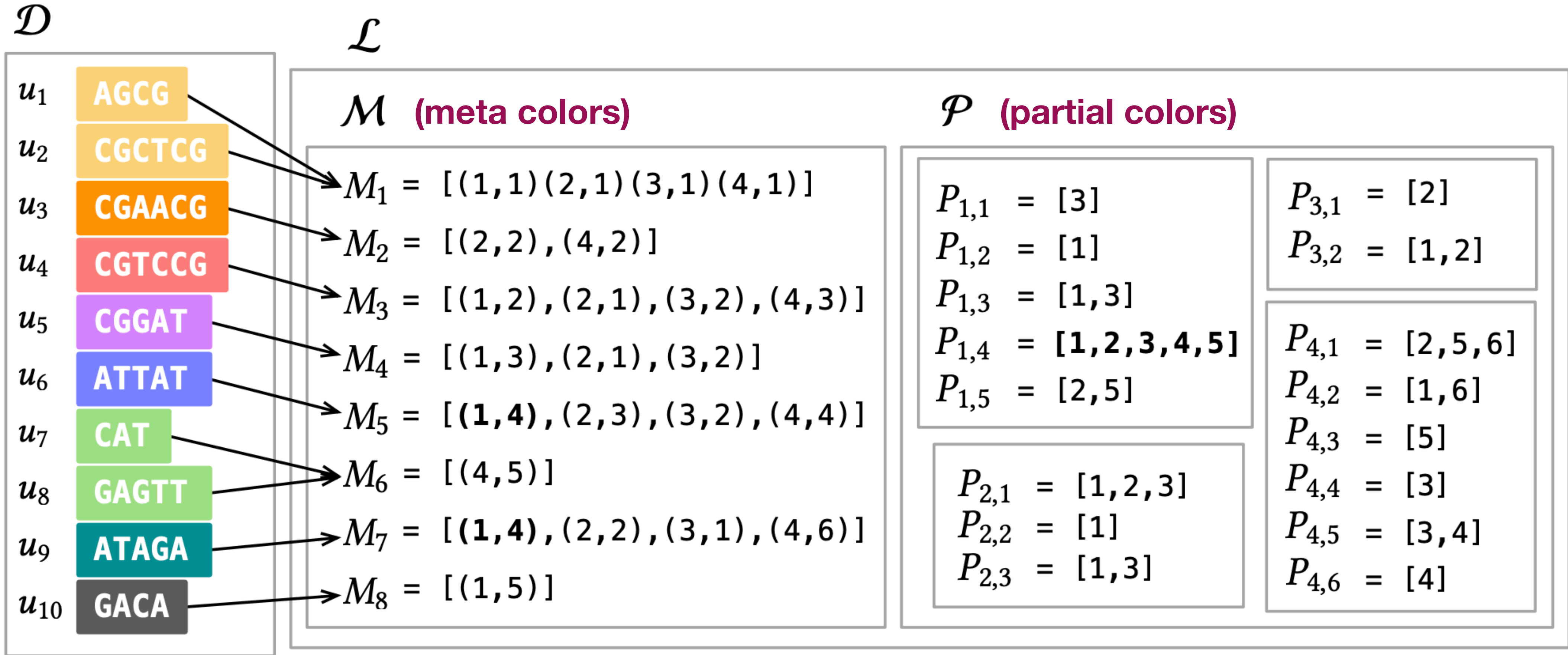


π



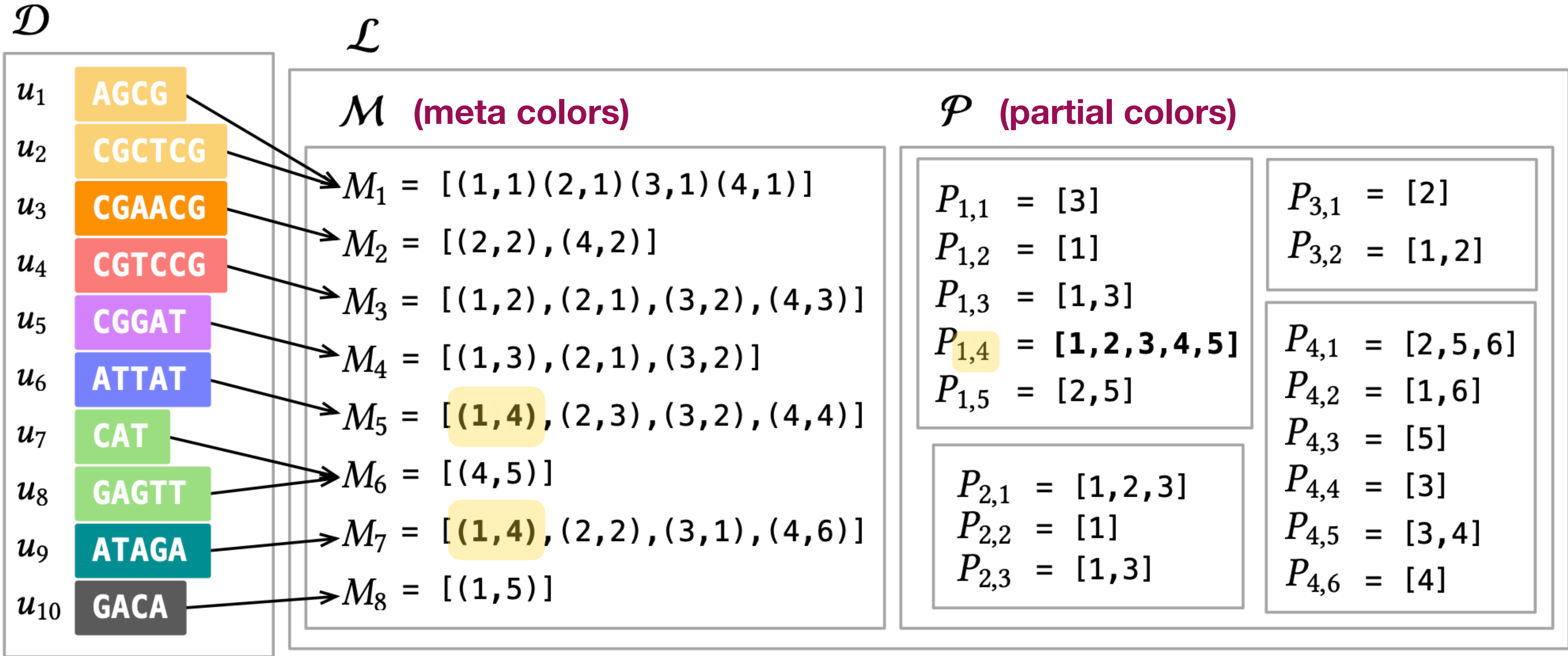
Meta and partial colors — Example

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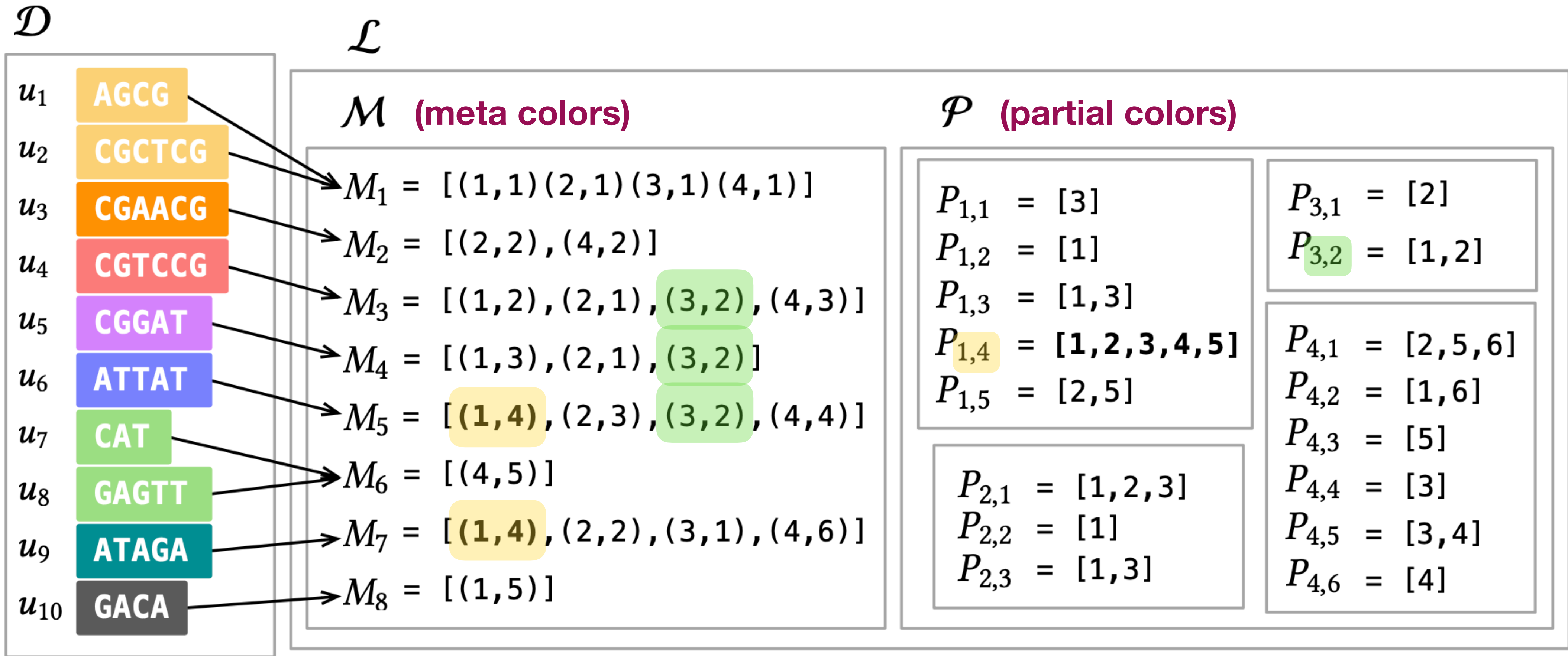
Meta and partial colors — Example

- Example for **N = 16** references and **4** partitions.



Meta and partial colors — Example

- Example for **N = 16** references and **4** partitions.



Results

- We applied the meta/partial color optimisation to Fulgor.
- We call it the *meta-colored* compacted dBG (**Mac-dBG**, or **Fulgor-v2**).
- <https://github.com/jermp/fulgor/releases/tag/v2.0.0>

Space in GB

Genomes		Mac-dBG			Fulgor		
		dBG	Colors	Total	dBG	Colors	Total
EC	3,682	0.29	0.52	0.81	0.29	1.36	1.65
SE	5,000	0.16	0.16	0.32	0.16	0.59	0.75
	10,000	0.35	0.33	0.68	0.35	1.66	2.01
	50,000	1.26	2.14	3.40	1.26	17.03	18.30
	100,000	1.72	3.83	5.55	1.72	40.70	42.44
	150,000	2.03	5.37	7.40	2.03	68.60	70.66
GB	30,691	21.31	7.85	29.16	21.31	15.45	36.85

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Genomes		Mac-dBG			Fulgor		
		dBG	Colors	Total	dBG	Colors	Total
EC	3,682	0.29	0.52	0.81	0.29	1.36	1.65
SE	5,000	0.16	0.16	0.32	0.16	0.59	0.75
	10,000	0.35	0.33	0.68	0.35	1.66	2.01
	50,000	1.26	2.14	3.40	1.26	17.03	18.30
	100,000	1.72	3.83	5.55	1.72	40.70	42.44
	150,000	2.03	5.37	7.40	2.03	68.60	70.66
GB	30,691	21.31	7.85	29.16	21.31	15.45	36.85

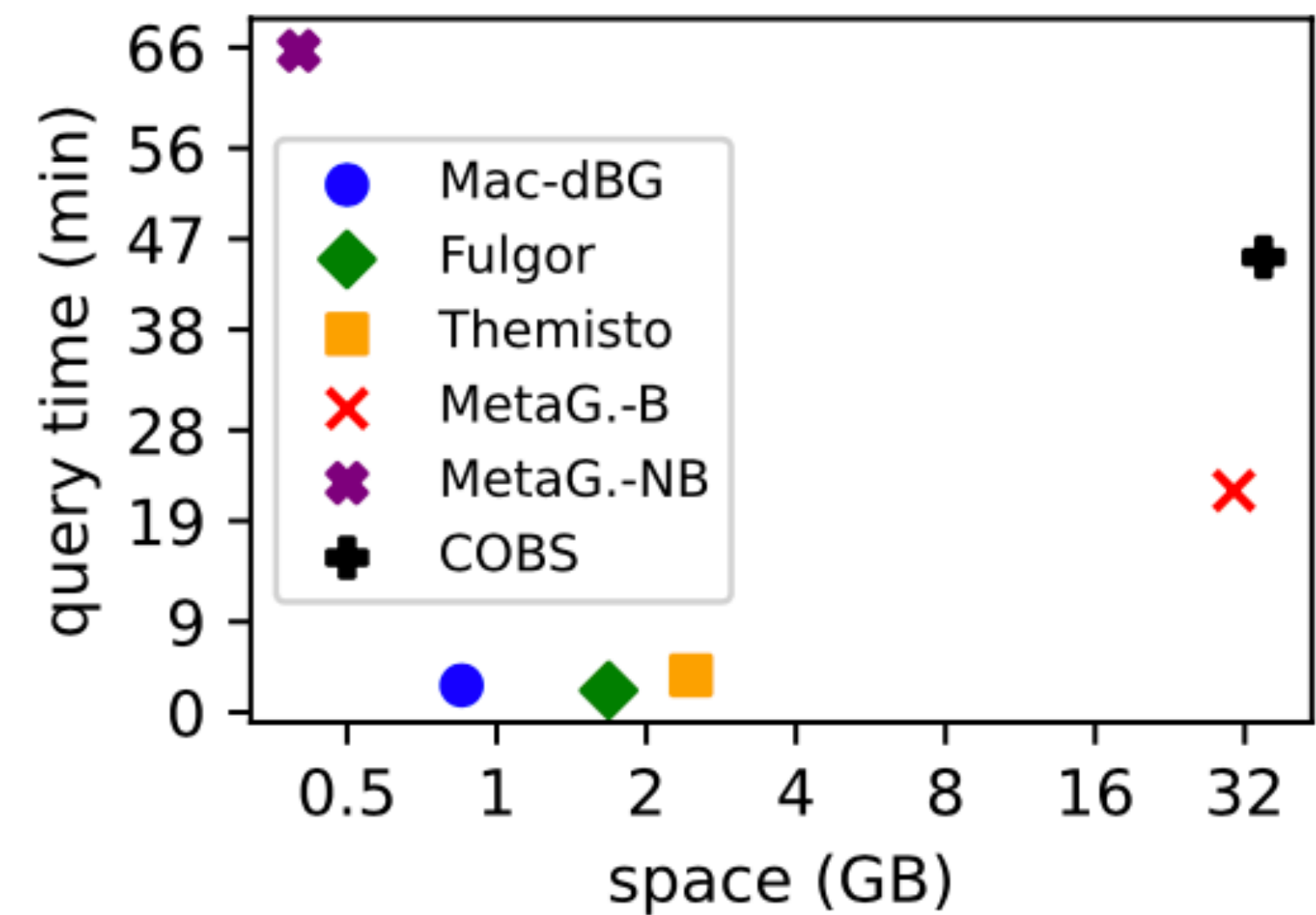
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Genomes		Mac-dBG			Fulgor		
		dBG	Colors	Total	dBG	Colors	Total
EC	3,682	0.29	0.52	0.81	0.29	1.36	1.65
SE	5,000	0.16	0.16	0.32	0.16	0.59	0.75
	10,000	0.35	0.33	0.68	0.35	1.66	2.01
	50,000	1.26	2.14	3.40	1.26	17.03	18.30
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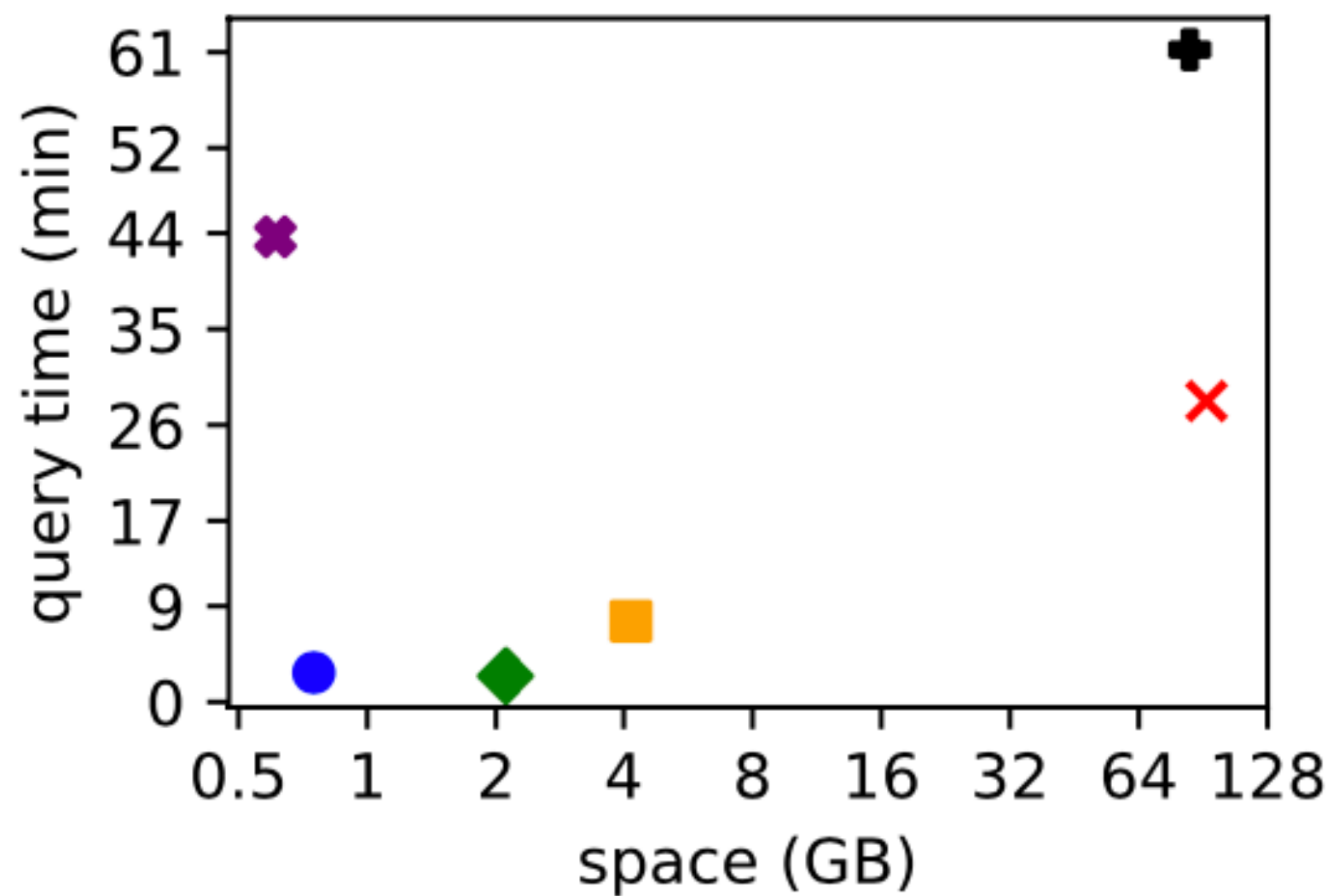
Pseudoalignment efficiency

	Genomes	Rate	Mac-dBG		Fulgor	
			mm:ss	GB	mm:ss	GB
EC	3,682	98.99	2:40	0.85	2:10	1.68
SE	5,000	89.49	1:16	0.37	1:16	0.82
	10,000	89.71	2:45	0.75	2:26	2.11
	50,000	91.25	14:00	3.65	19:15	18.53
	100,000	91.41	26:48	6.29	27:30	42.78
	150,000	91.52	41:30	8.51	42:30	70.55
GB	30,691	92.91	01:03	28.51	01:10	30.02

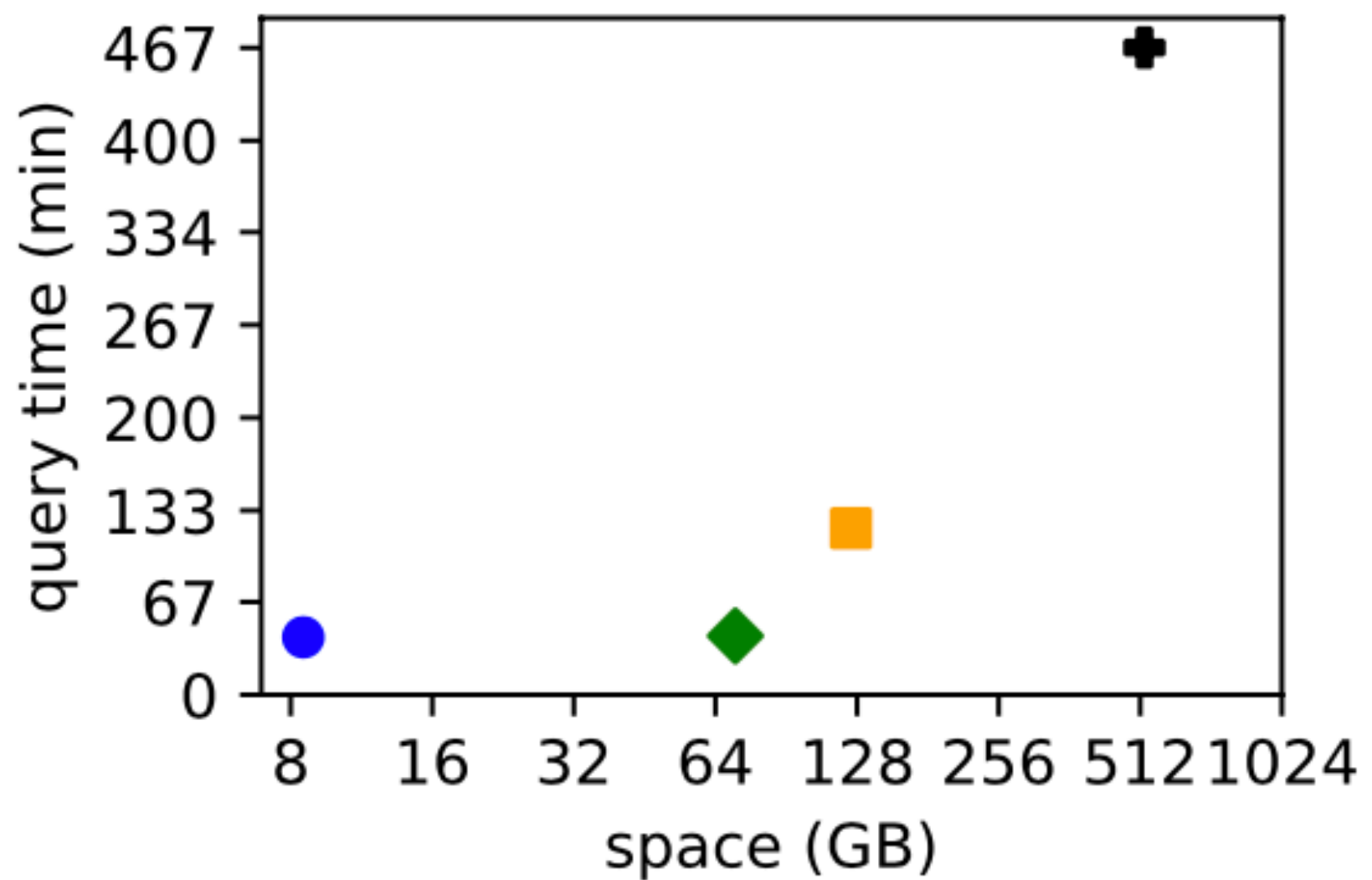
Overall space/time trade-off



(a) EC



(b) SE 10,000



(c) SE 150,000

Conclusions

- SSHash to obtain an **efficient map from k-mers to unitigs**.
- Permute unitigs in color order to enable a **space-efficient mapping from unitigs to colors**.
- Factorize the redundancy in large color matrixes via **meta/partial colors**.
- Result: the meta-colored DBG embodies a superior space/time trade-off compared to the state of the art. Space improvement can be dramatic but query efficiency not harmed.
- Many **open problems and future directions**, check our pre-print out:
<https://doi.org/10.1101/2023.07.21.550101>.

Conclusions

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Thank you for the attention!