

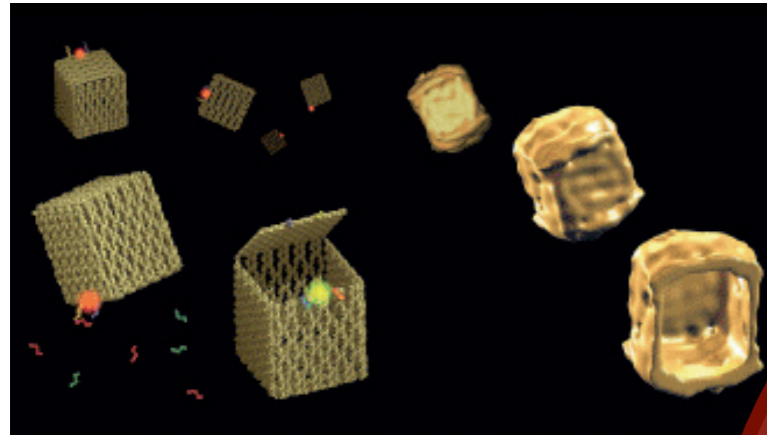
# **Oritatami:** **A computational model for** **cotranscriptional folding**

**Nicolas Schabanel**

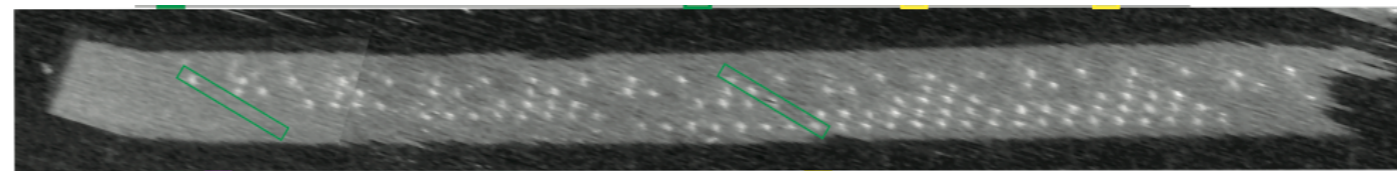
**CNRS - LIP, ENS Lyon & IXXI - France**

# Context: Biomolecular Computing & Engineering

■ ~100 nm



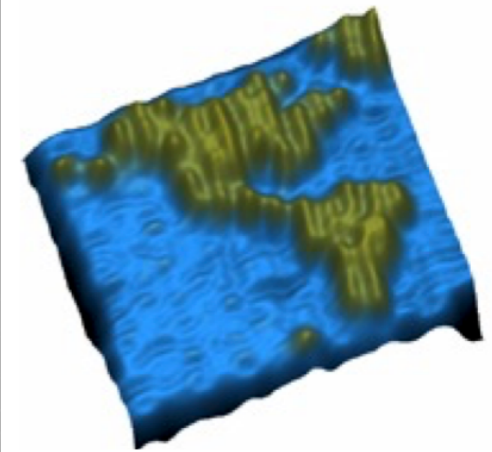
*Andersen et al, 2000*



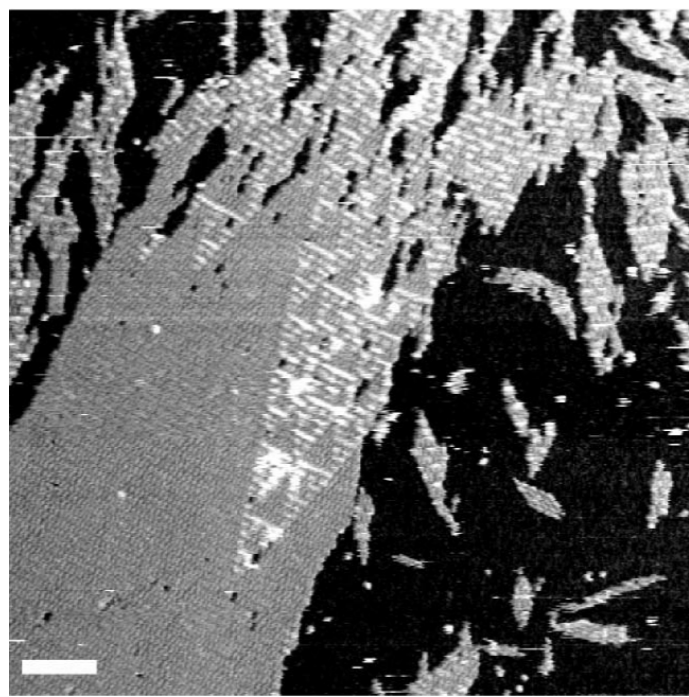
0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0
0	1	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0
0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	
0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1

Constantine Evans PhD Thesis, Caltech 2014

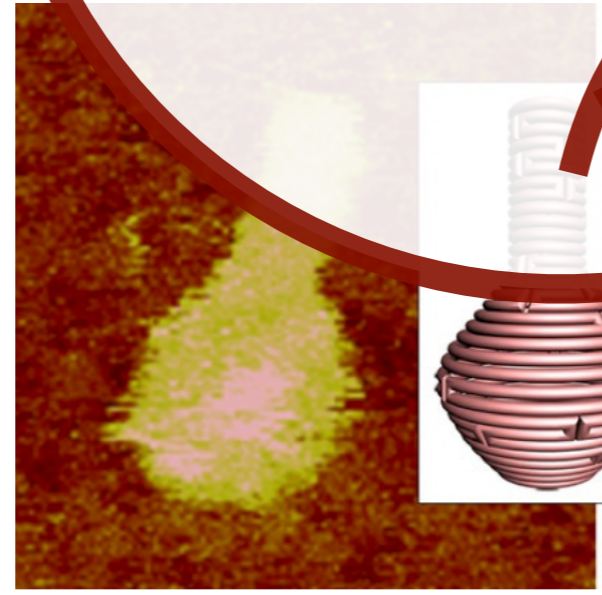
**X X**  
 $T^{\circ} \geq 50^{\circ} C$   
 (with a red curved line pointing to the right)



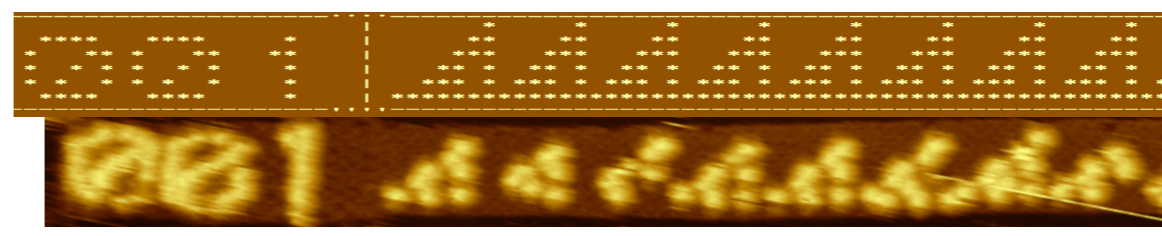
*Rothemund, Nature 2006*



*Fujibayashi et al, 2007*



**Han et al, Science 2011**



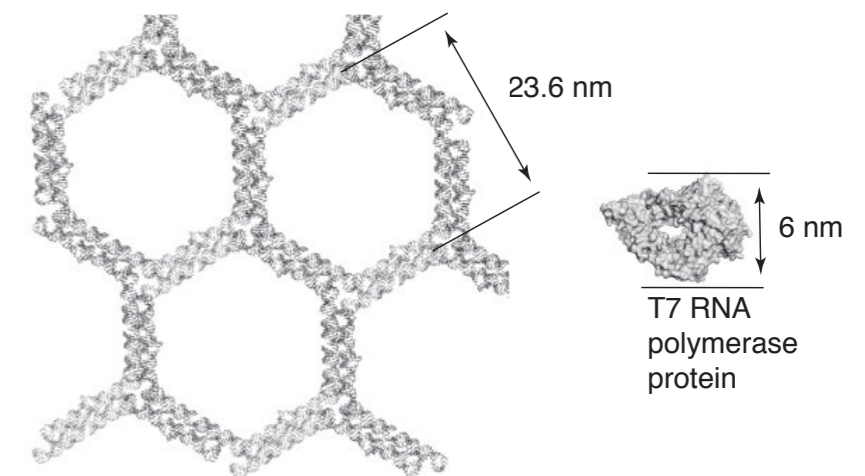
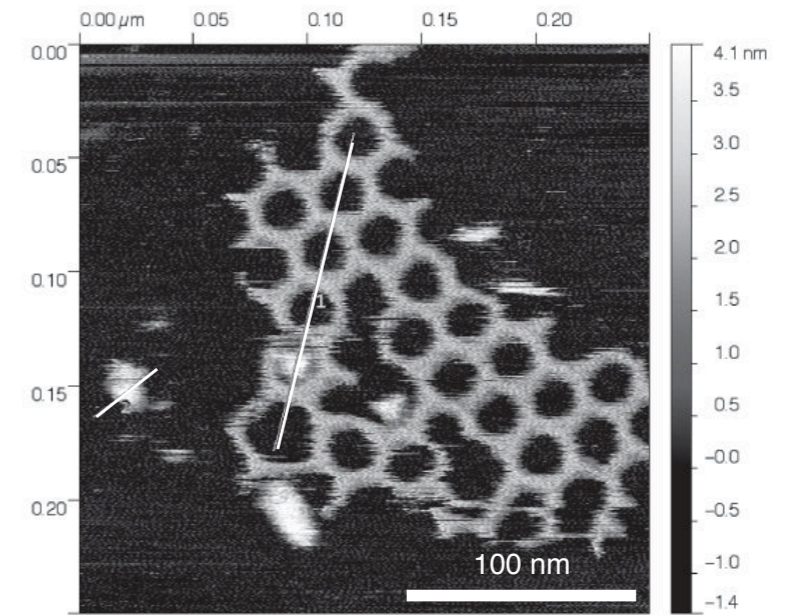
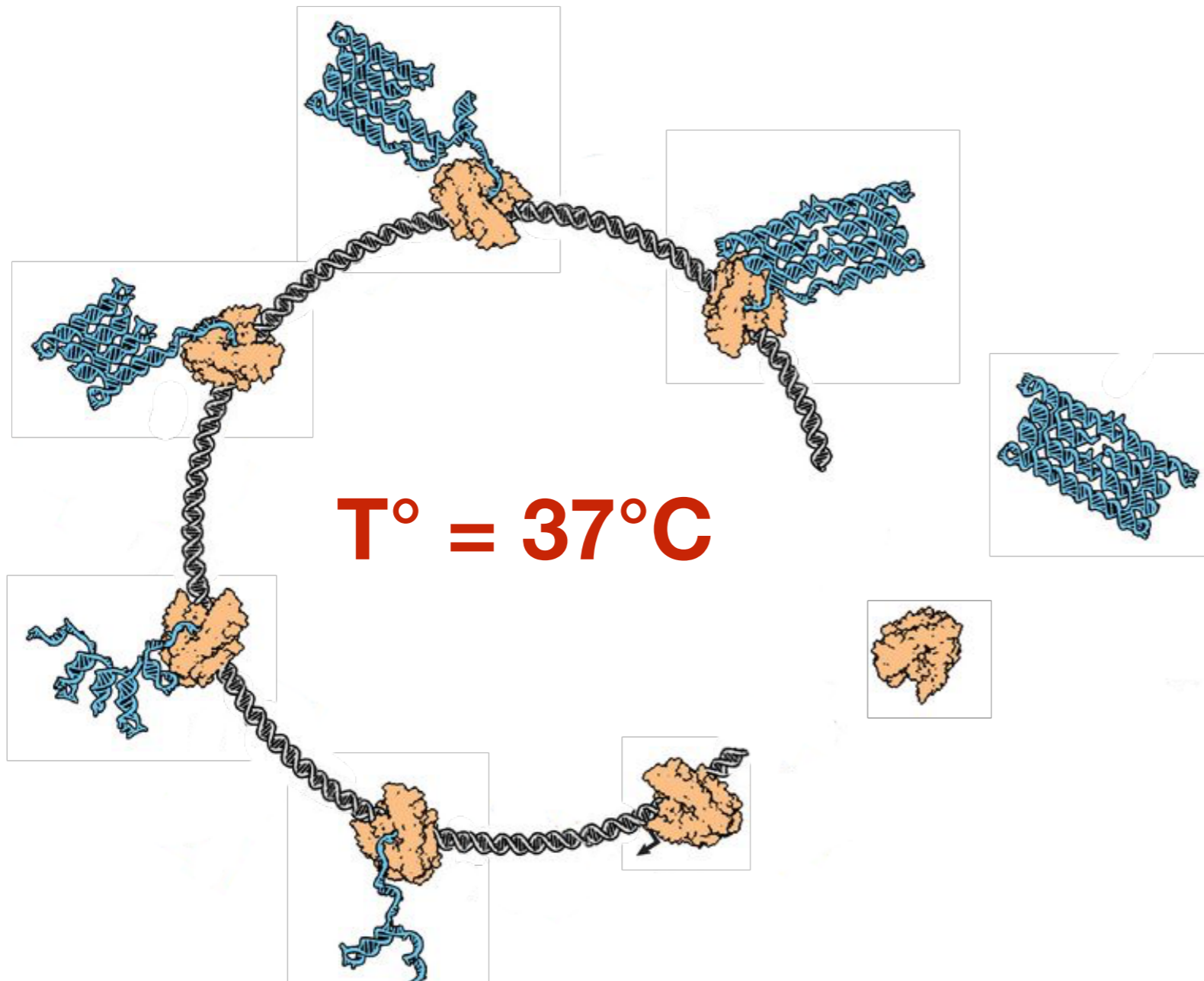
*Rule 110 on input 001 - Woods et al, Nature 2019*

# Co-transcriptional folding



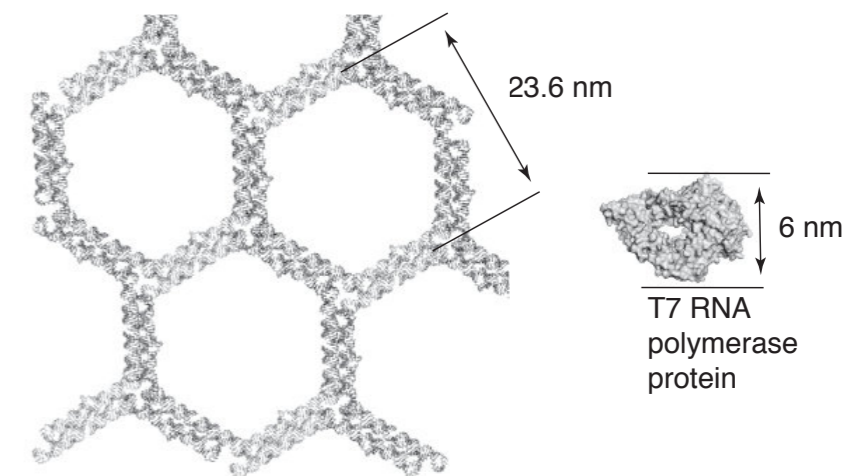
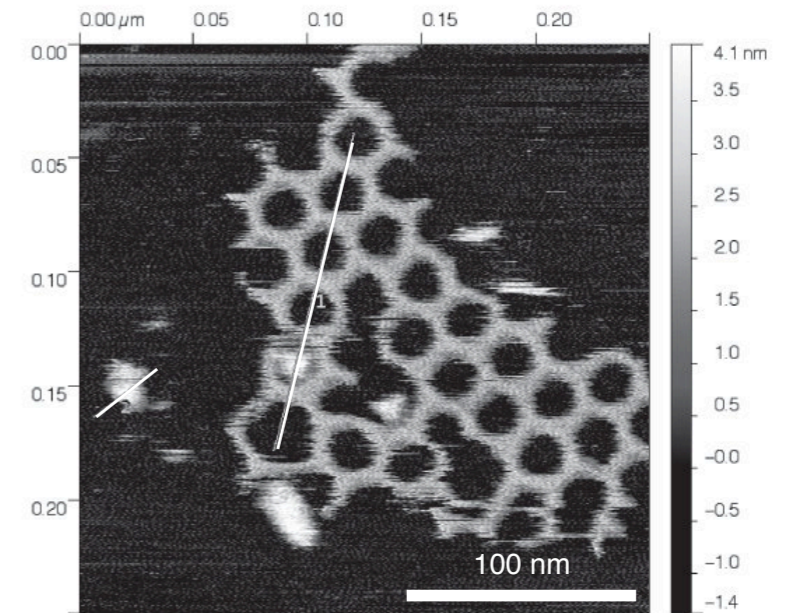
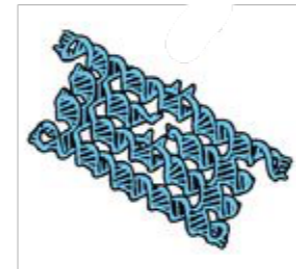
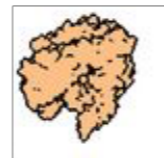
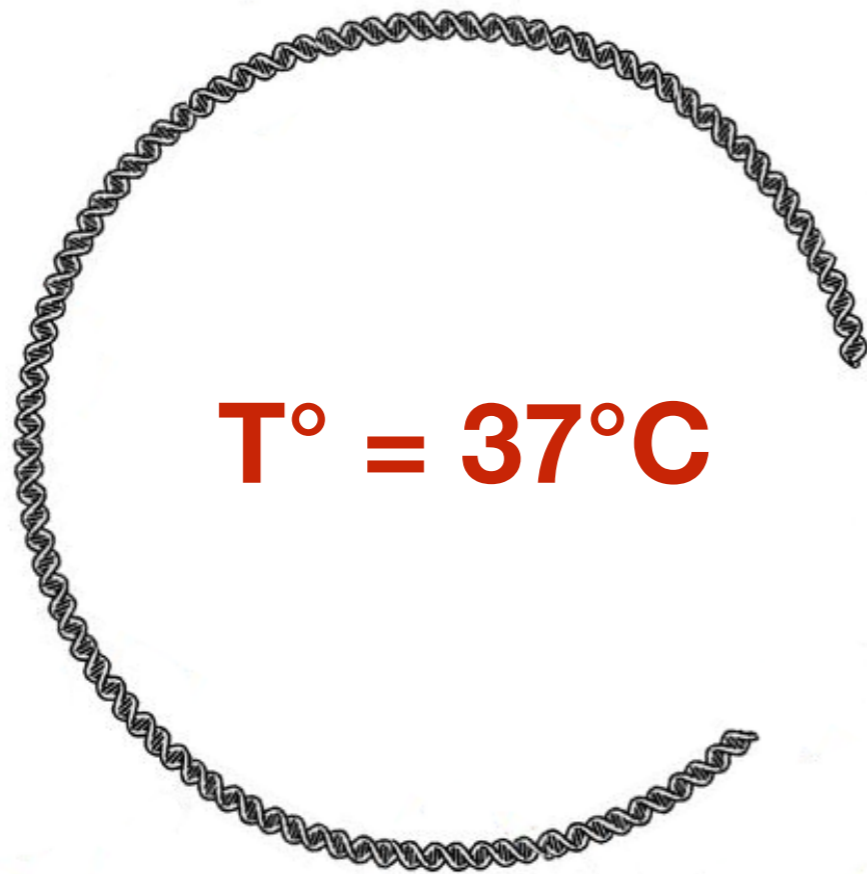
*Geary, Rothmund, Andersen, Science 2014*

# RNA co-transcriptional folding

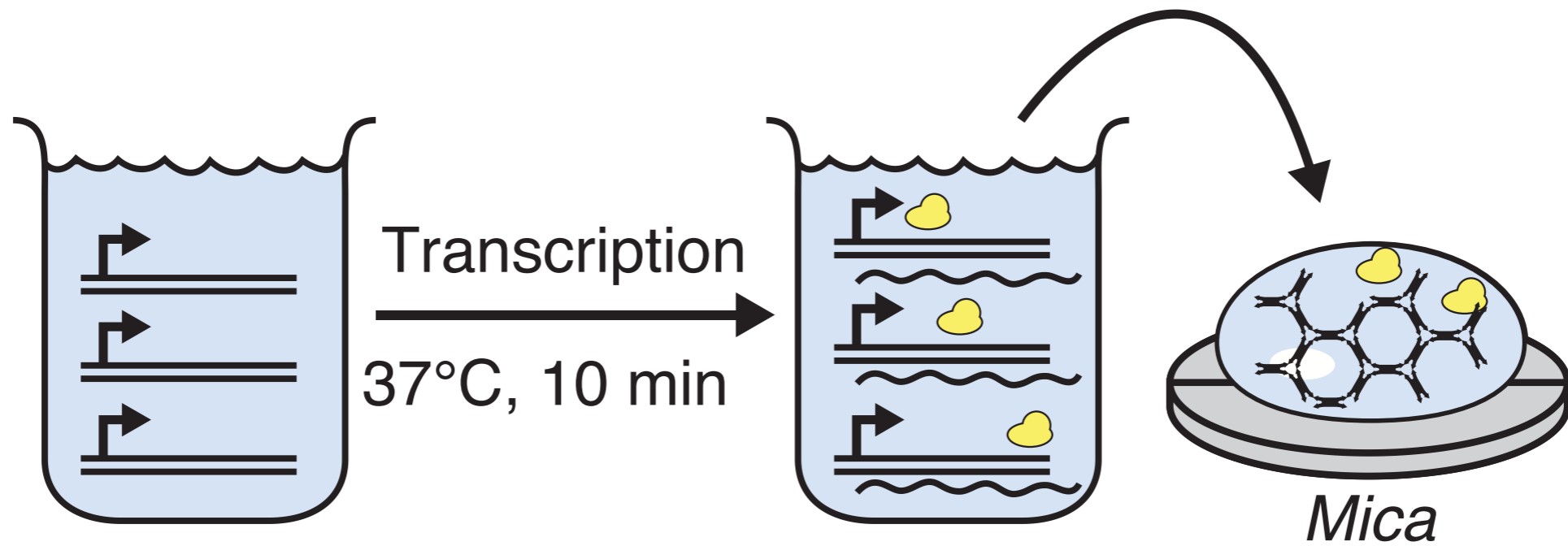


Geary, Rothmund, Andersen, Science 2014

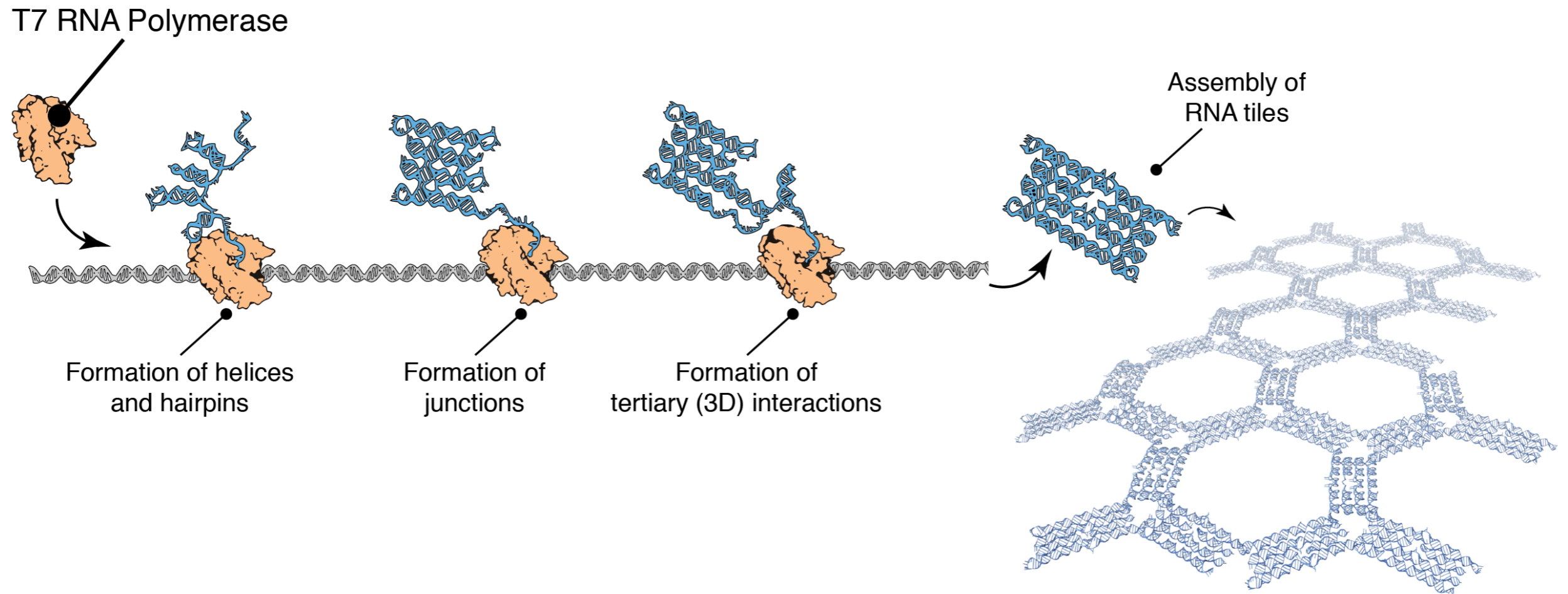
# RNA co-transcriptional folding



# Protocol



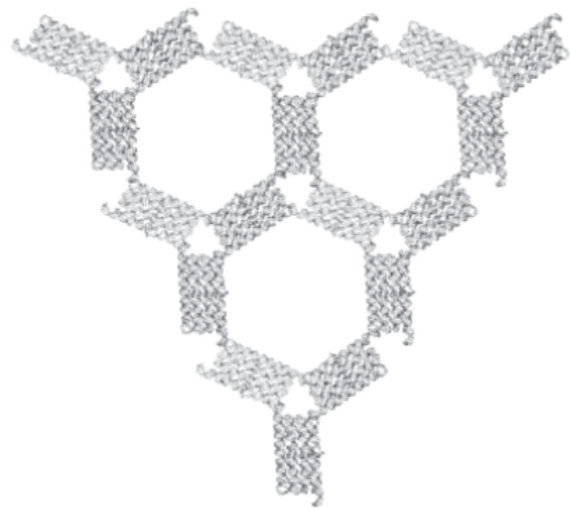
# RNA Origami in Real Time



T7 RNA polymerase produces RNA directionally from 5' to 3', **at a rate much slower than the RNA folds up (few microseconds).**

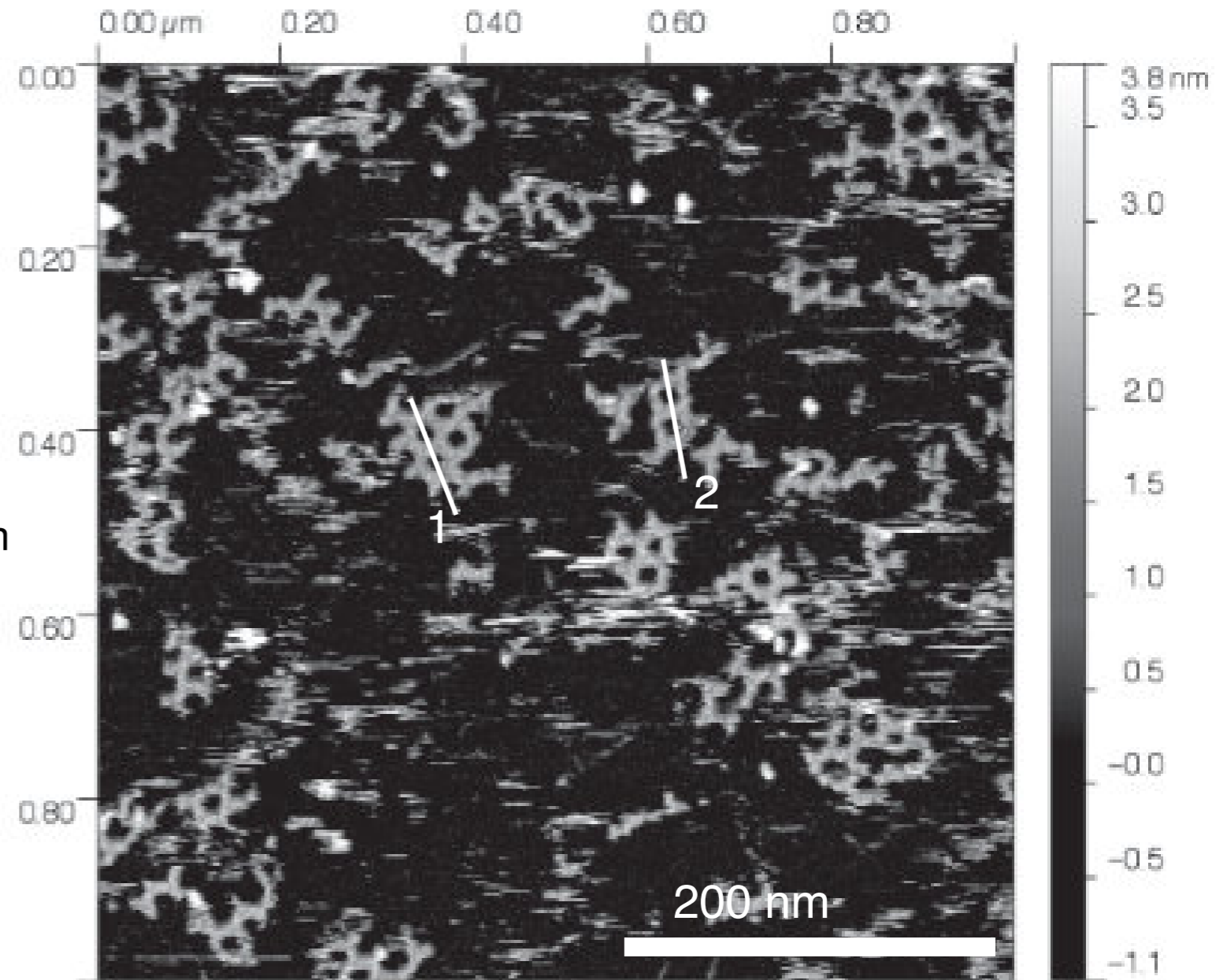
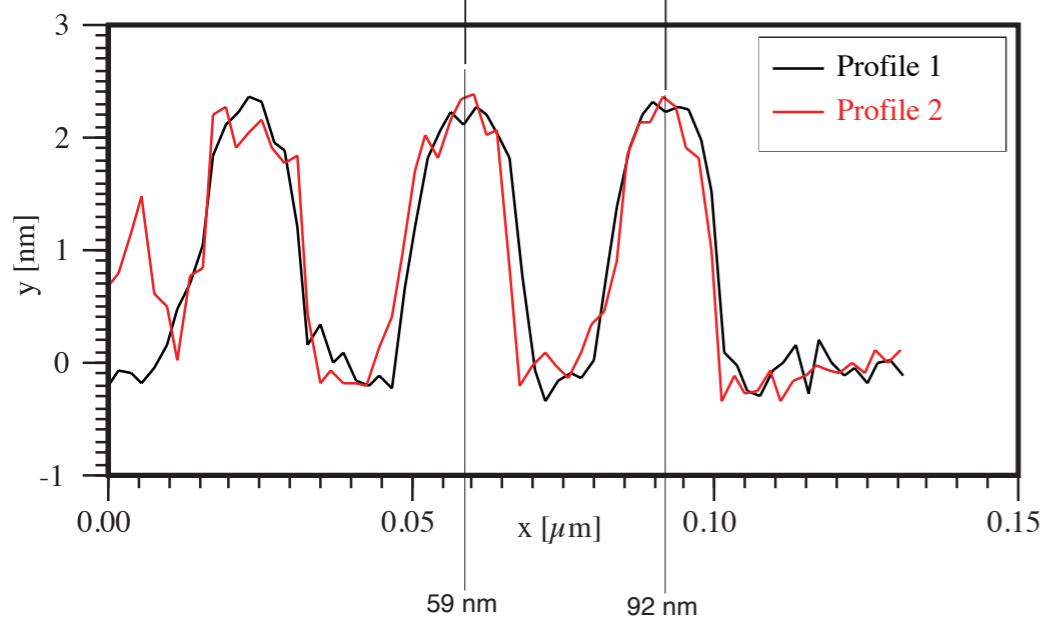
The polymerase reads the DNA gene, and becomes an RNA origami production factory, **synthesizing a new RNA origami roughly every 1 second.**

# AFM imaging of 4H-AE co-transcriptional assembly



period = 33.0 nm

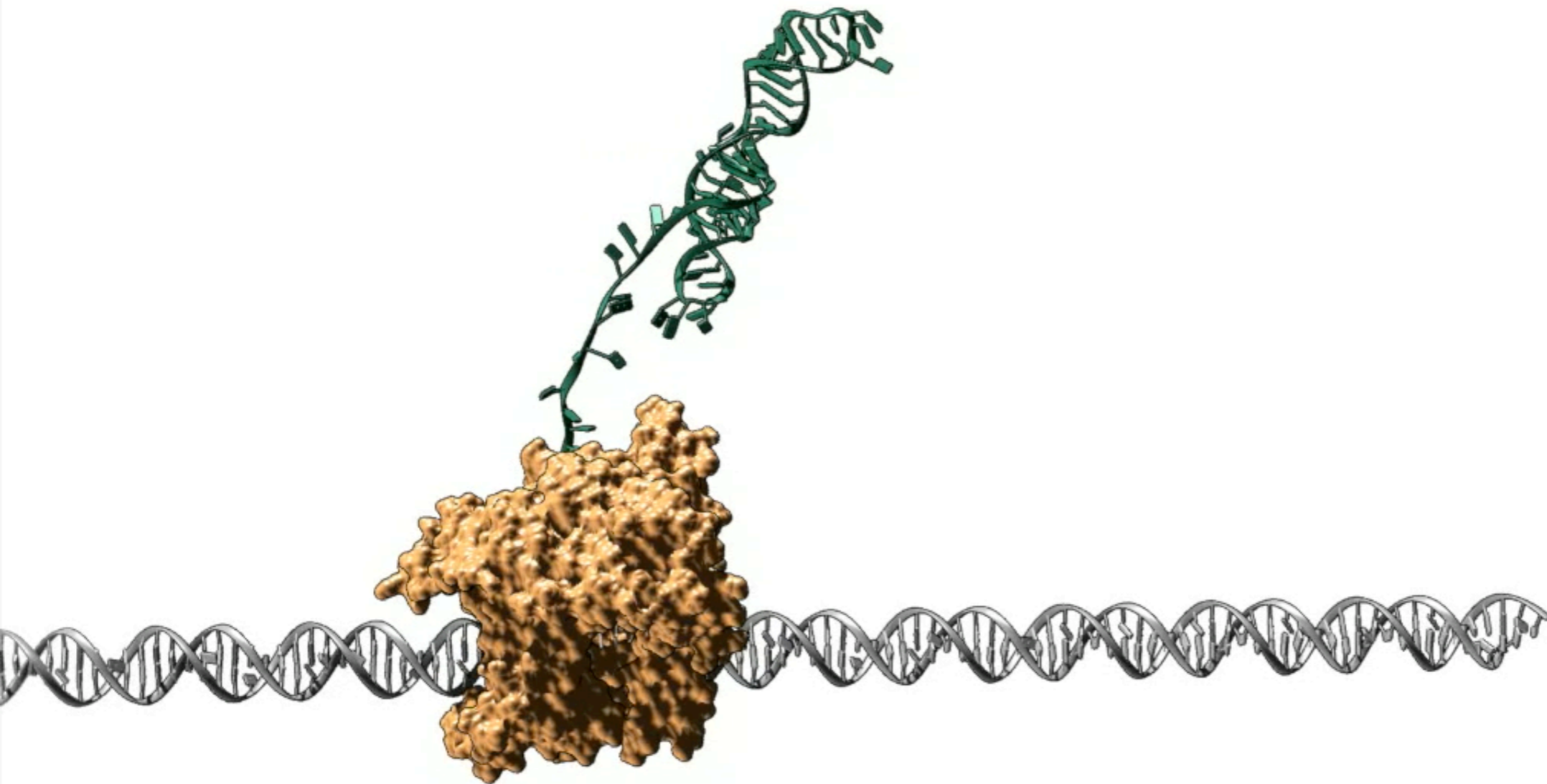
Note that the modeled spacing was 33.5nm



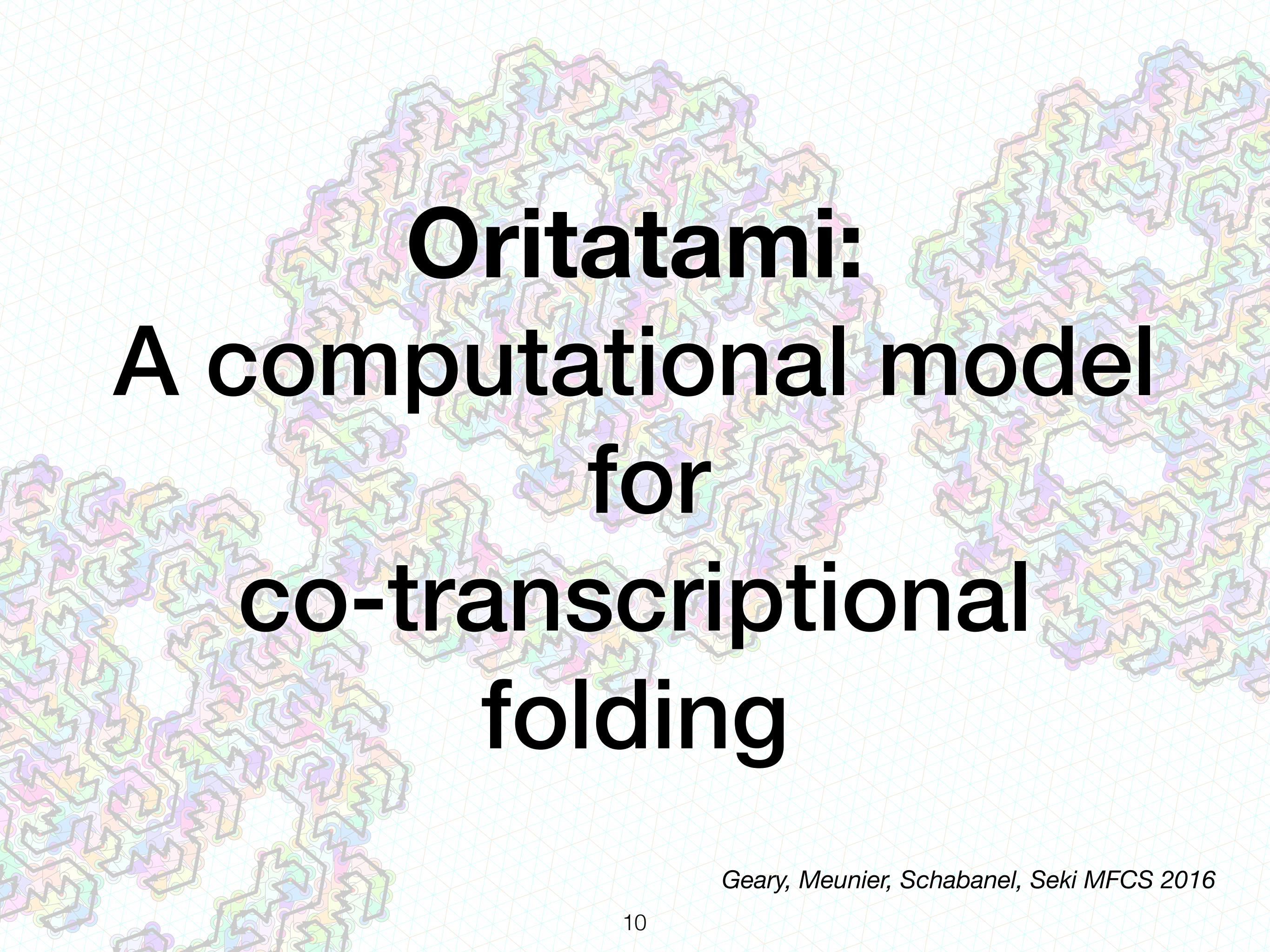


# RNA Folding

(Real time: ~1 second)



*Video: Geary*

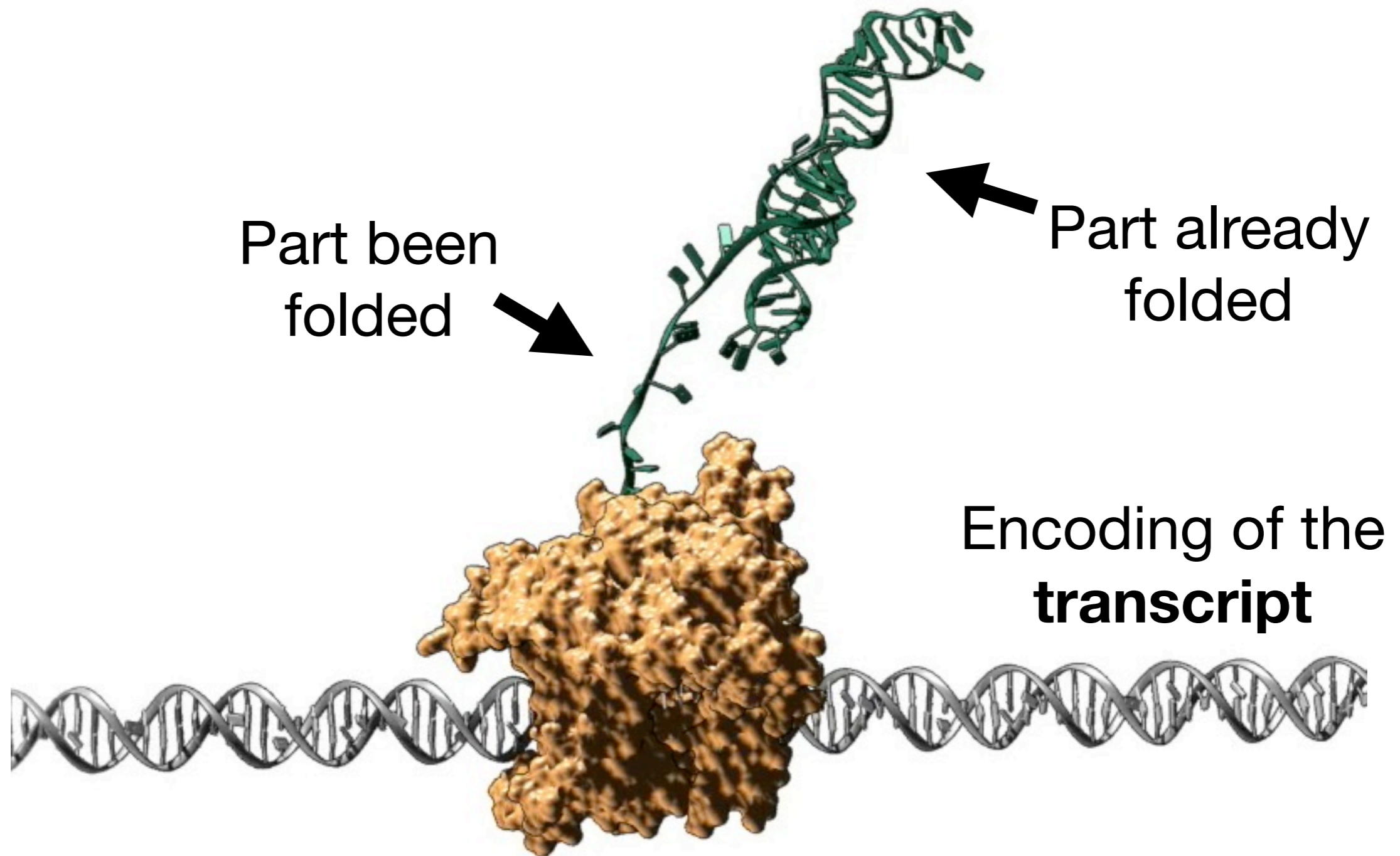
The background features a light blue and green grid with a pattern of overlapping, colorful, irregular geometric shapes in shades of purple, green, yellow, and blue. The text is centered over this pattern.

**Oritatami:  
A computational model  
for  
co-transcriptional  
folding**

*Geary, Meunier, Schabanel, Seki MFCS 2016*

# RNA Folding

(Real time: ~1 second)



# Oritatami:

## A model for co-transcriptional folding

### The program:

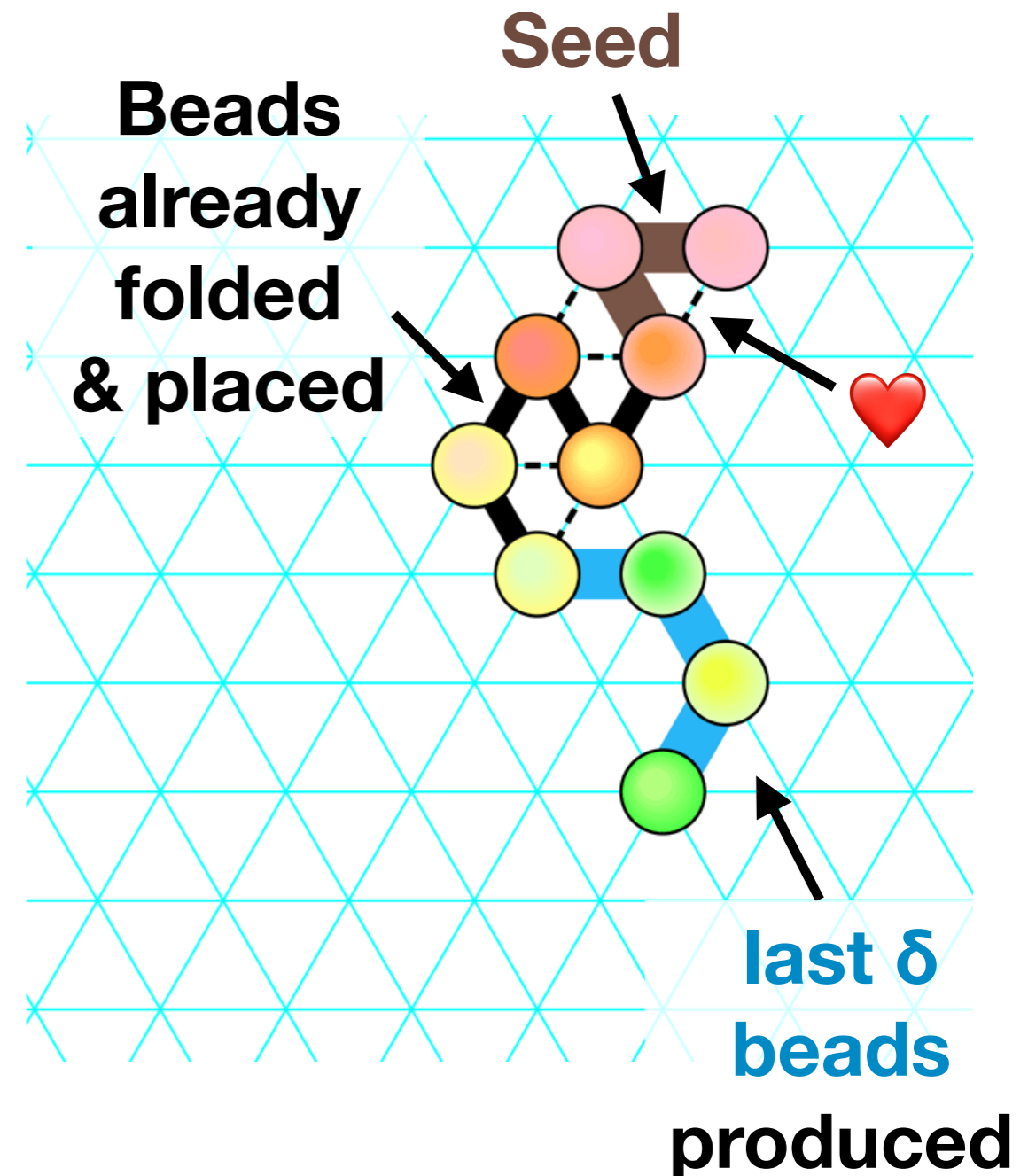
- a sequence of **bead types** (the **transcript**)

### The instructions:

- the rule **a**♥**b** if bead types **a** and **b** attract each other

### The input configuration:

- Some beads placed beforehand (the **seed**)

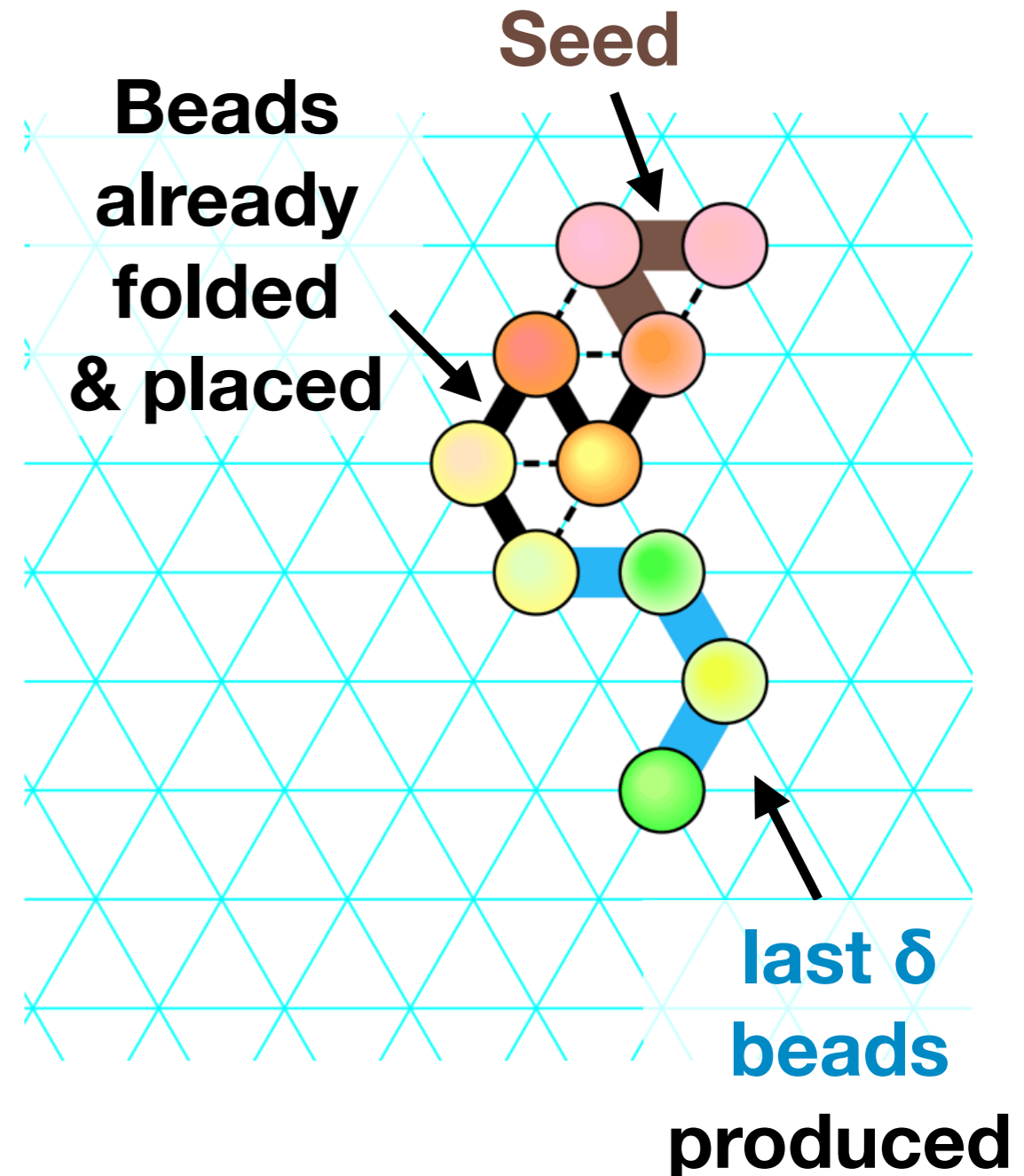


# Oritatami: A model for co-transcriptional folding

## The dynamics

- Starting from the seed, the sequence is *produced one bead at a time*
- **Only the  $\delta$  last produced beads** are free to move and explore the accessible positions to settle in the ones **maximizing the number of bonds**
- All other beads remain in their last locations

here, delay  $\delta = 3$ <sub>13</sub>

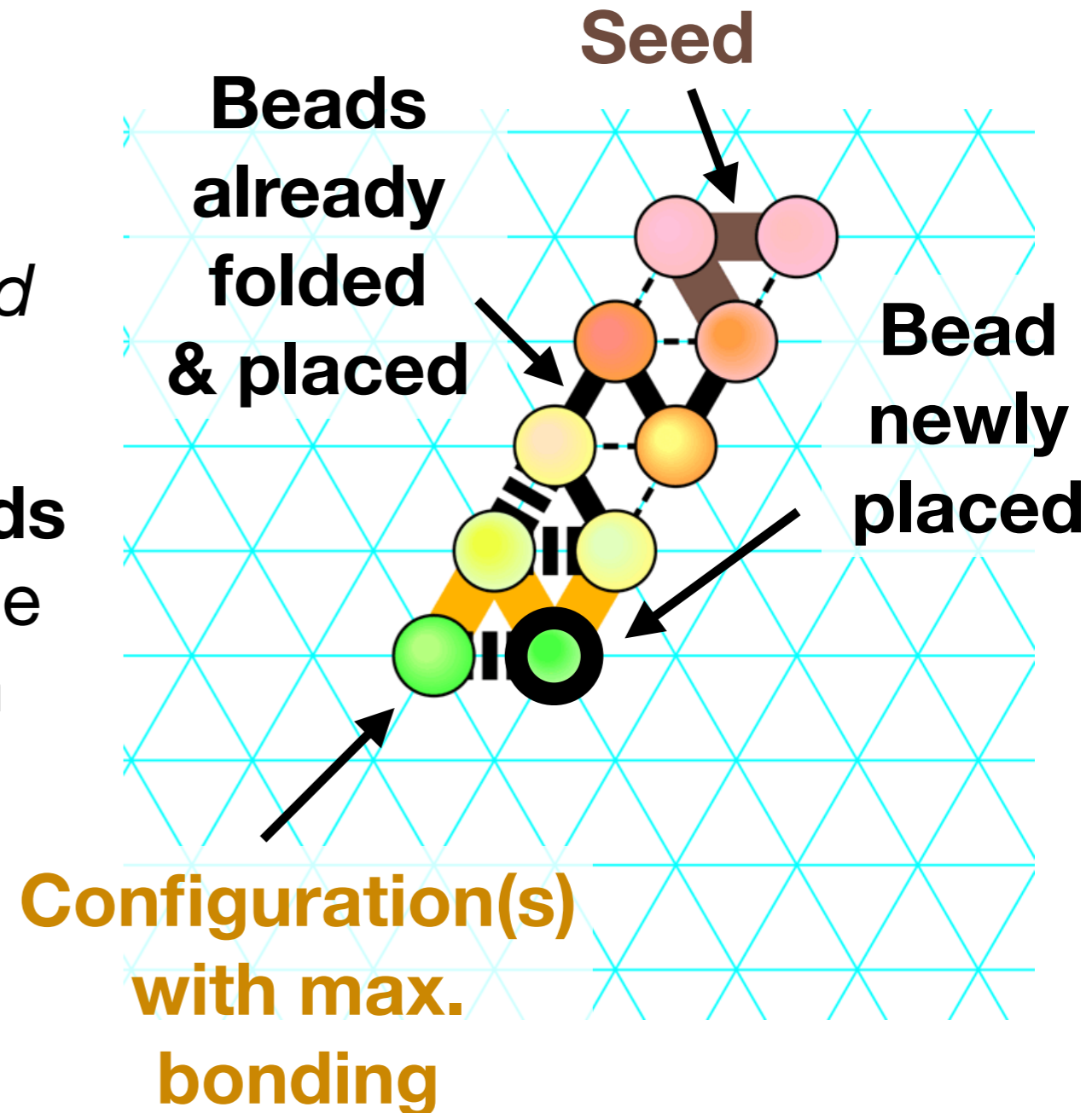


# Oritatami:

## A model for co-transcriptional folding

### The dynamics.

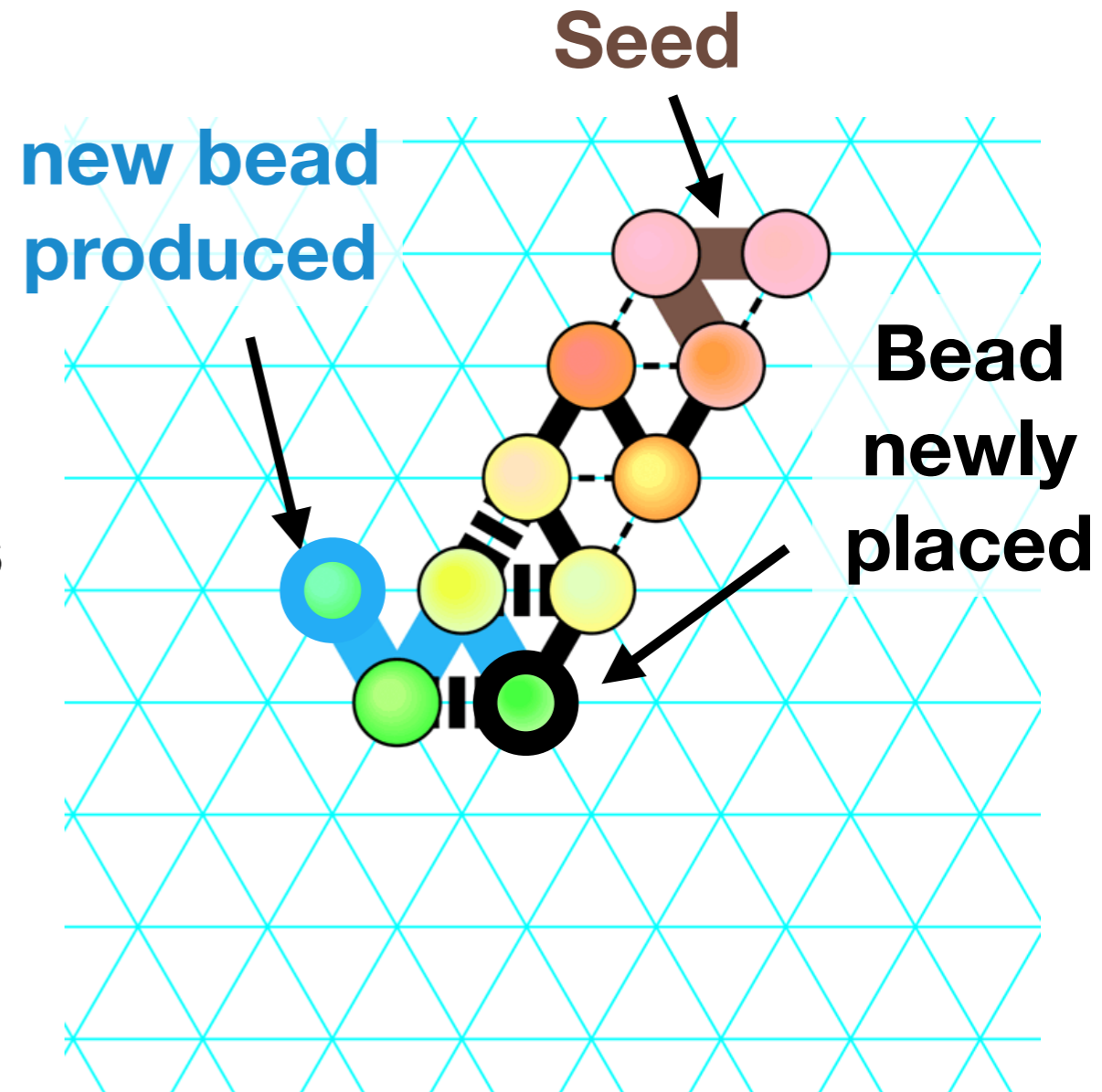
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# Oritatami: A model for co-transcriptional folding

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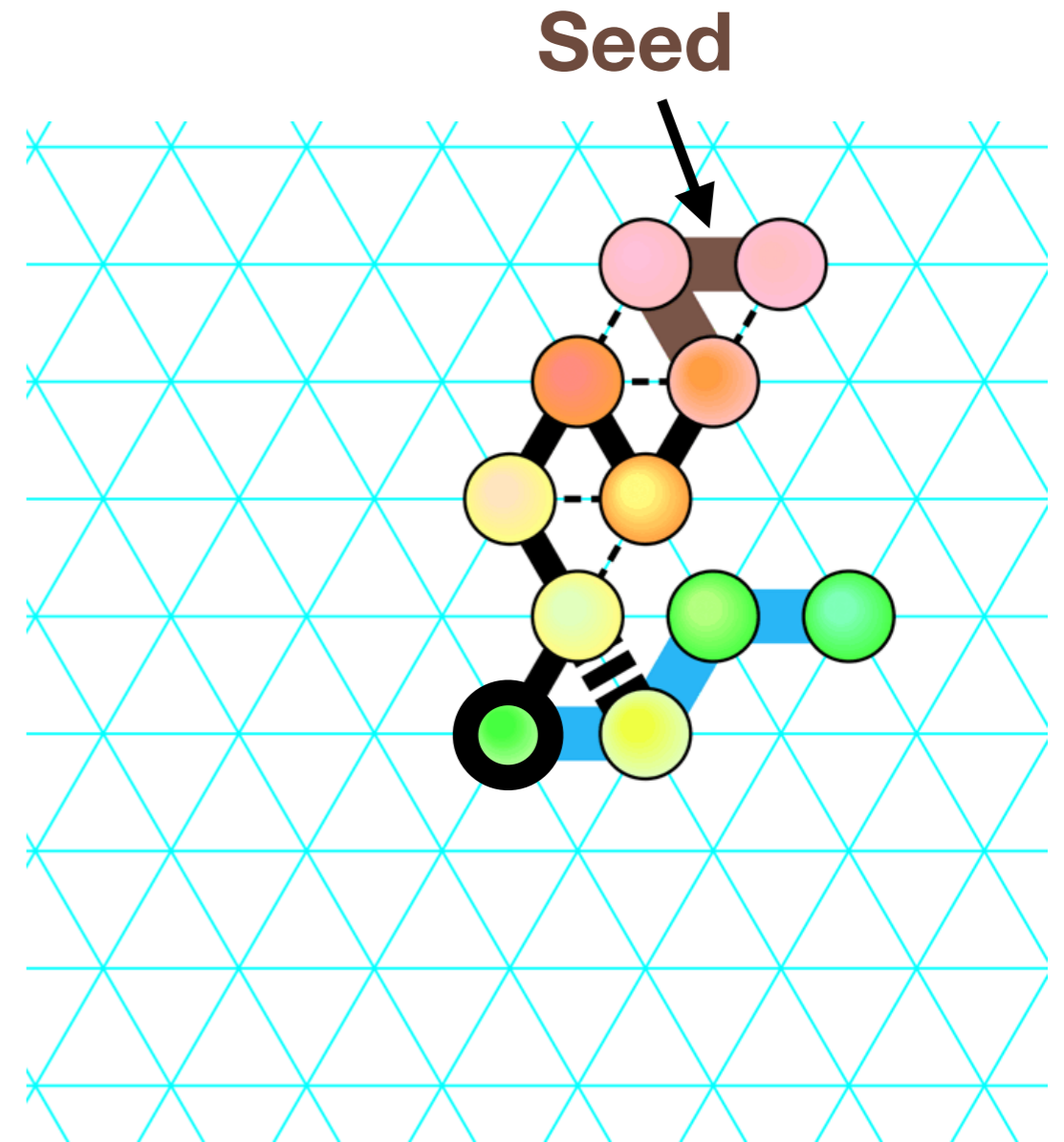
- Starting from the seed, the sequence is *produced one bead at a time*
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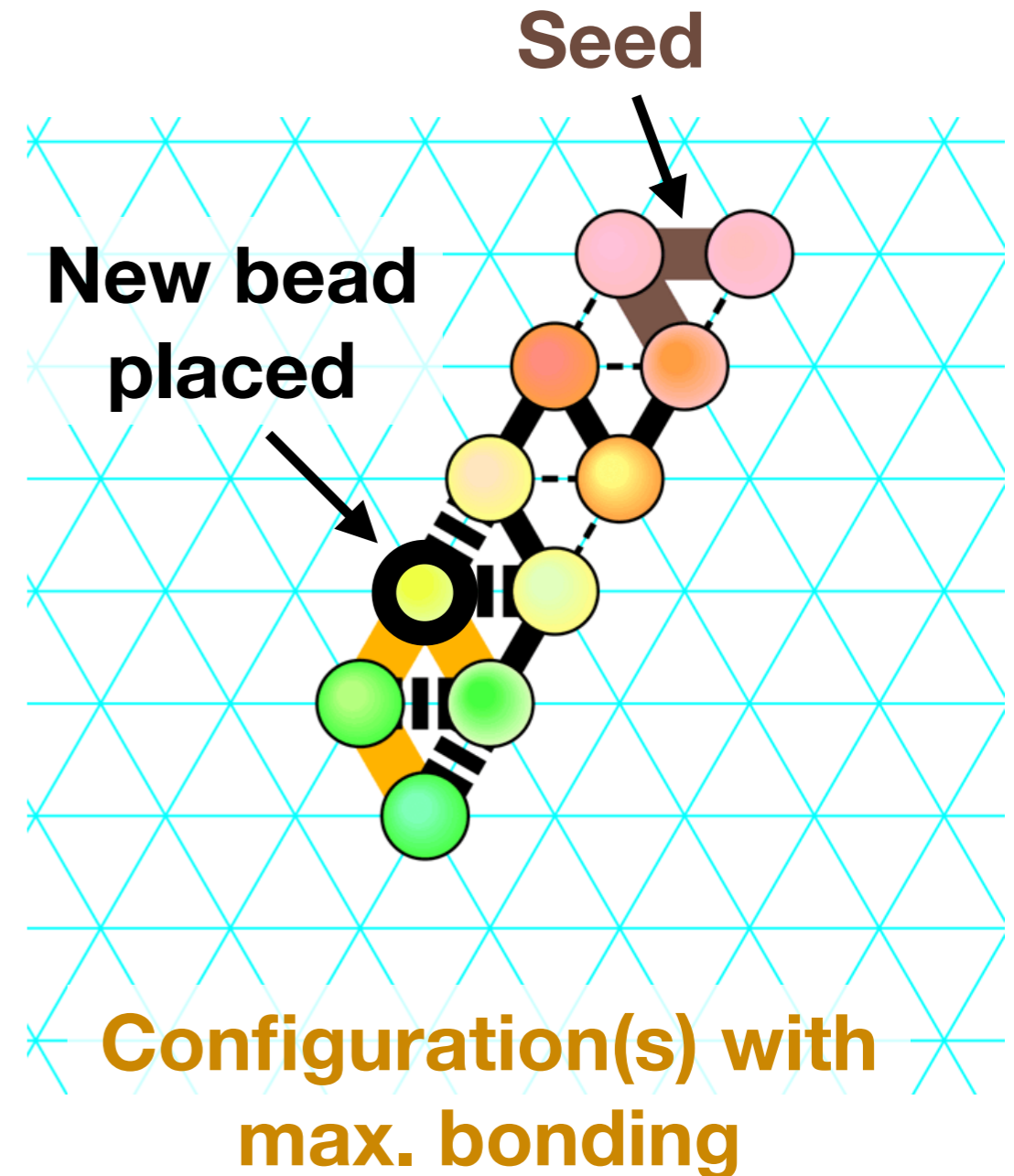




# Oritatami: A model for co-transcriptional folding

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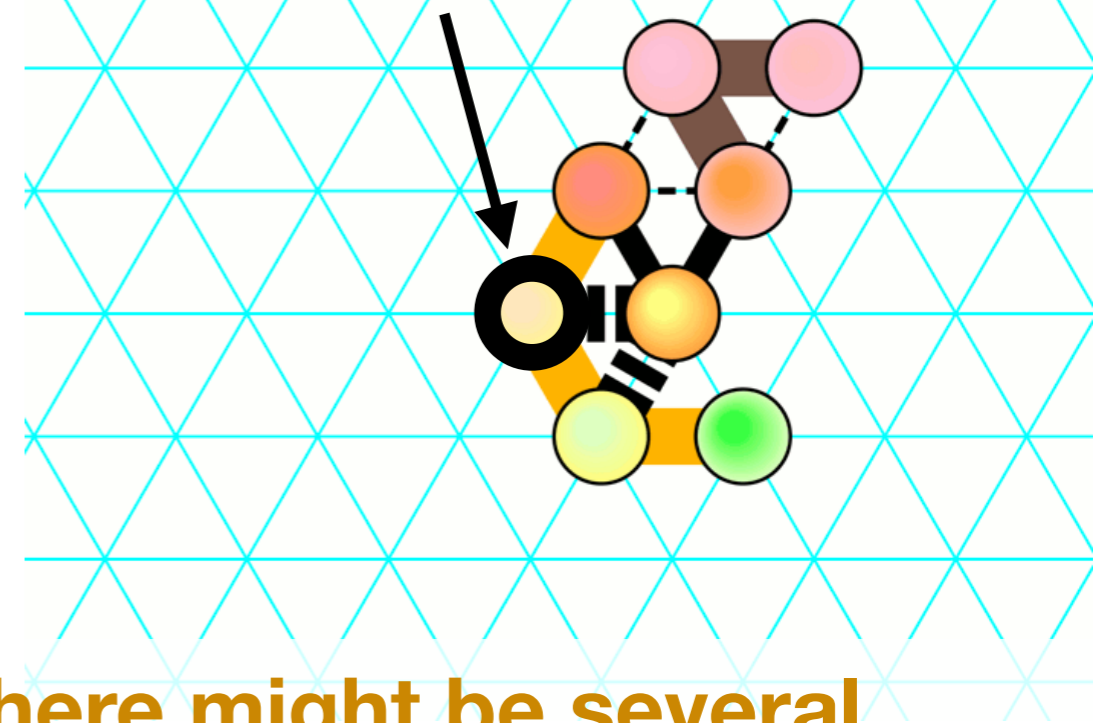
**There might be several configurations with max. bonding**

# Oritatami: A model for co-transcriptional folding

## The dynamics.

- Starting from the seed, the sequence is *produced one bead at a time*
- **Only the  $\delta$  last produced beads** are free to move and explore the accessible positions to settle in the ones **maximizing the number of bonds**
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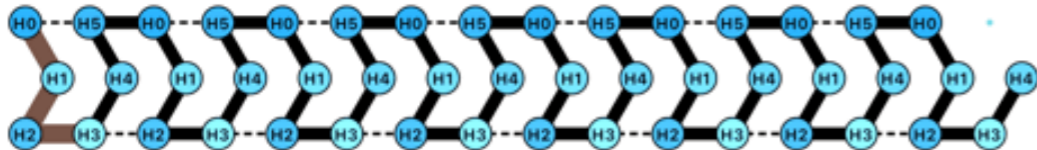
The bead has same position in all maximal extension  
 $\Rightarrow$  *deterministic*



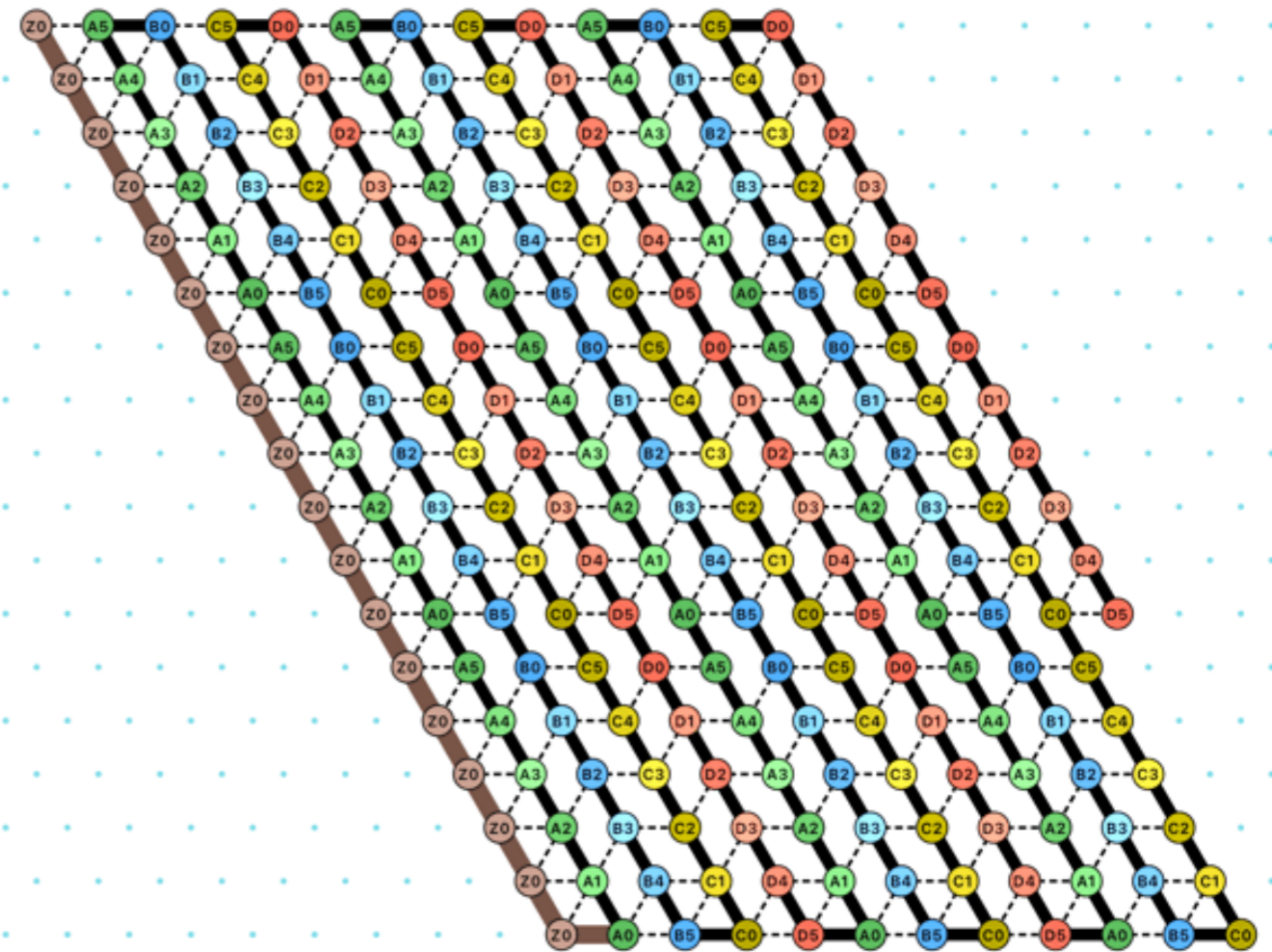
**There might be several configurations with max. bonding**

# Oritatami: a first construction

here, delay  $\delta = 3$



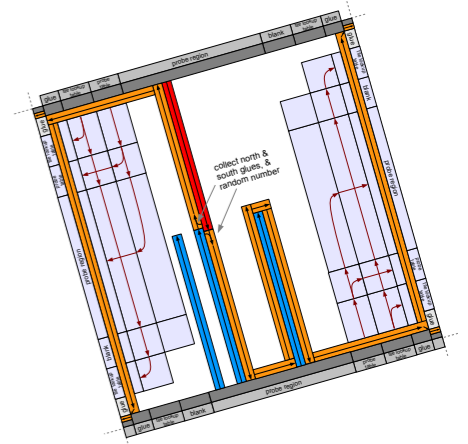
A glider



A switchback

Both can be combined together

# Oritatami vs aTAM

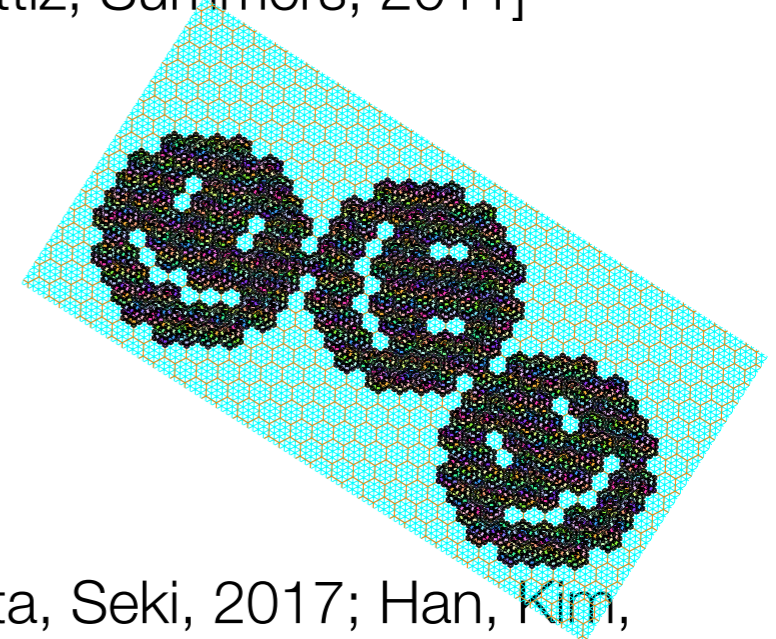


## Some self-assembly seminal work (mostly aTAM)

- Tile assembly systems are **Turing universal** [Winfree, 1998]
- **Arbitrary shape assembly** with optimal tile set size [Soloveichik, Winfree, 2007]
- **Uncomputable limit configurations** [Lathrop, Lutz, Pattiz, Summers, 2011]
- **Intrinsic universality** [Doty et al, 2012]

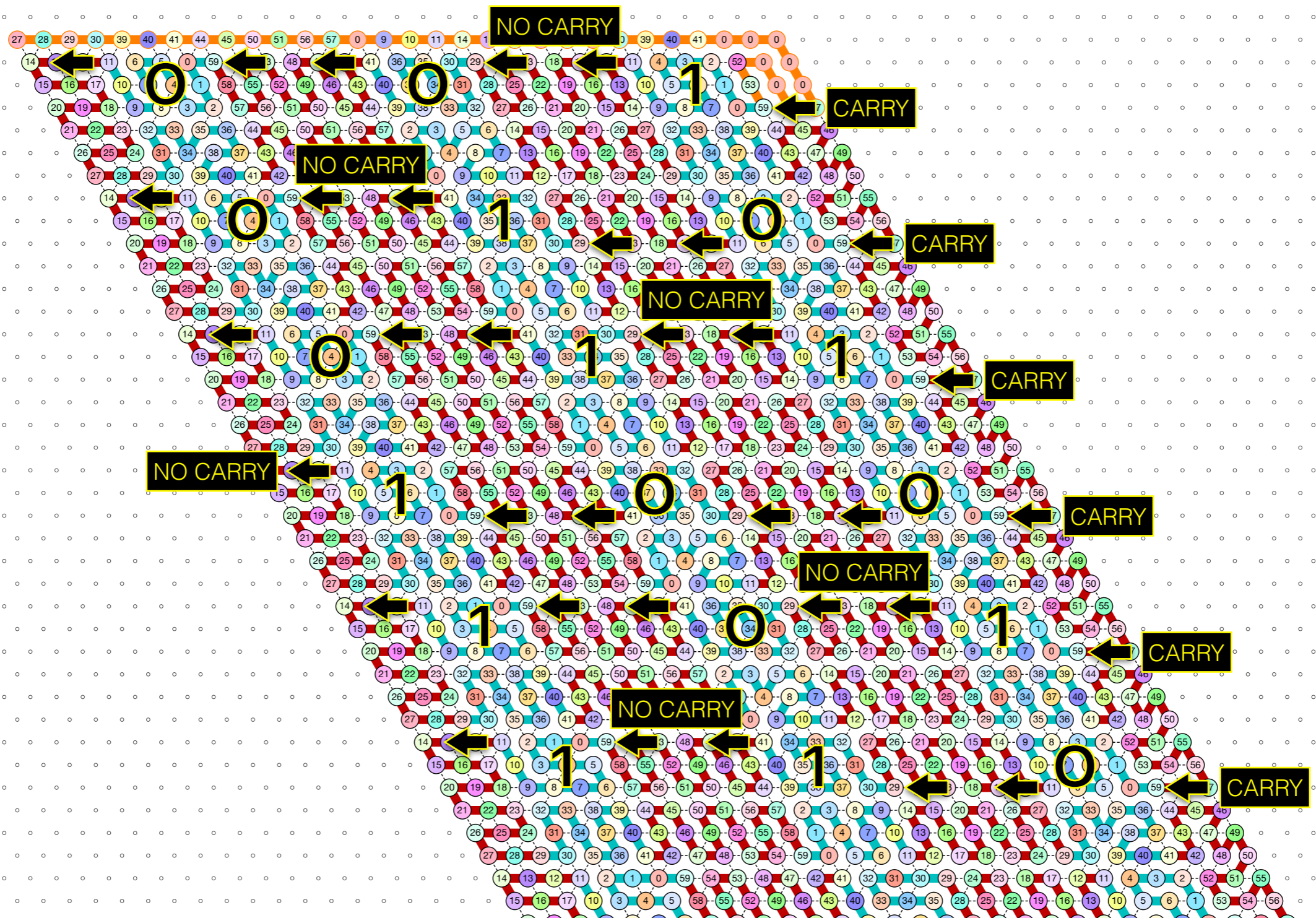
## Oritatami

- A **binary counter** [Geary, Meunier, S., Seki, 2016]
- Heighdragon **fractal** [Masuda, Seki, Ubukata, 2018]
- Folding **arbitrary shapes** [Demaine et al, 2018]
- **NP-hardness** for oritatami design [Geary et al, 2016; Ota, Seki, 2017; Han, Kim, 2017] and for non-deterministic oritatami equivalence [Han et al, 2016]
- **Efficient Turing Machine simulation** through tag-systems [Geary et al, 2018]
- Intrinsic simulation of **1D cellular automata** [Pchelina et al, 2020]
- Intrinsic simulation of **Turedo: uncomputable and arbitrary dense** limit configurations, building **arbitrary object** from asymptotically minimal seed [Pchelina et al, 2022]

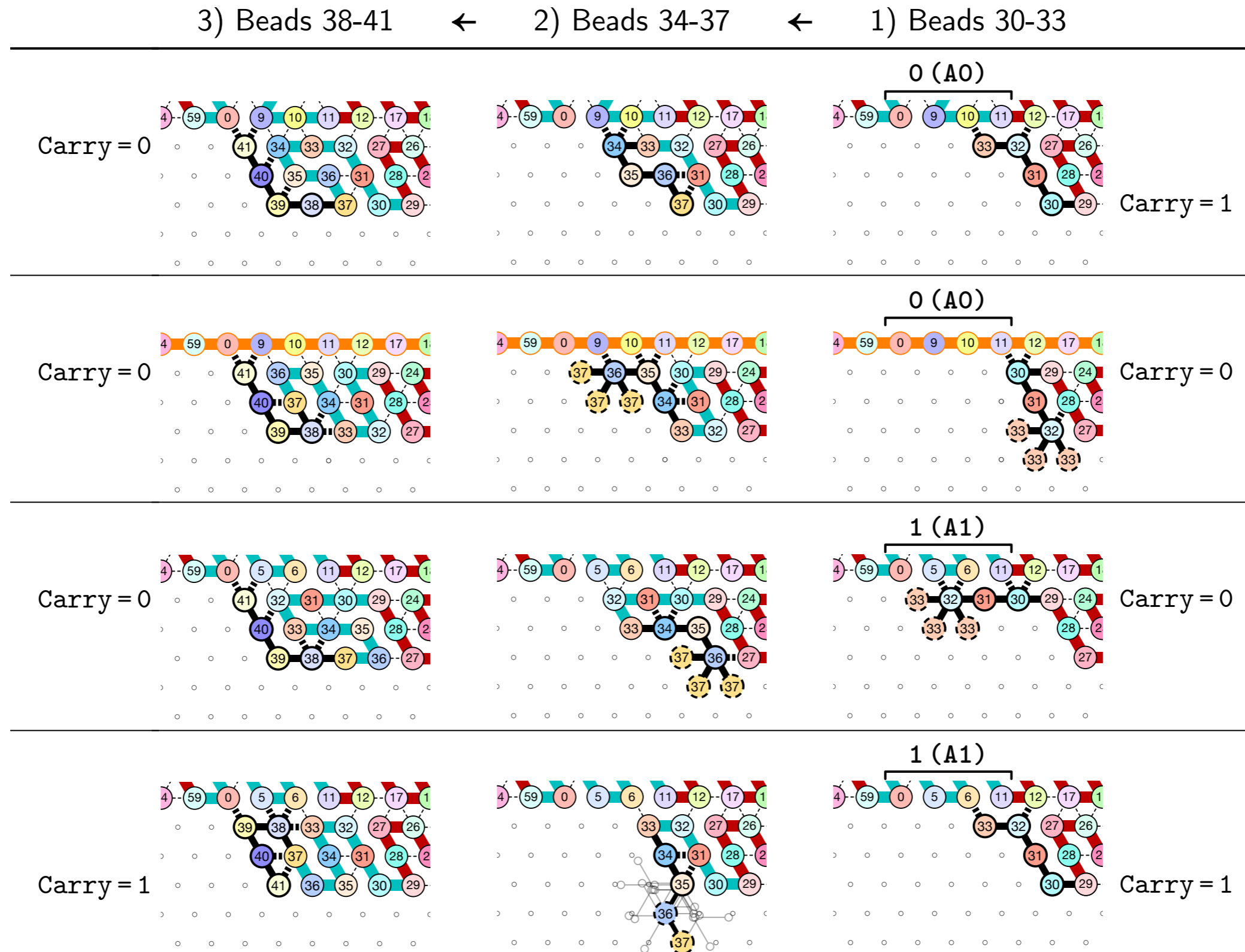


# Oritatami. A binary counter

Information is encoded in the geometry



# How does computation work?



**Oritatami is  
Turing complete**

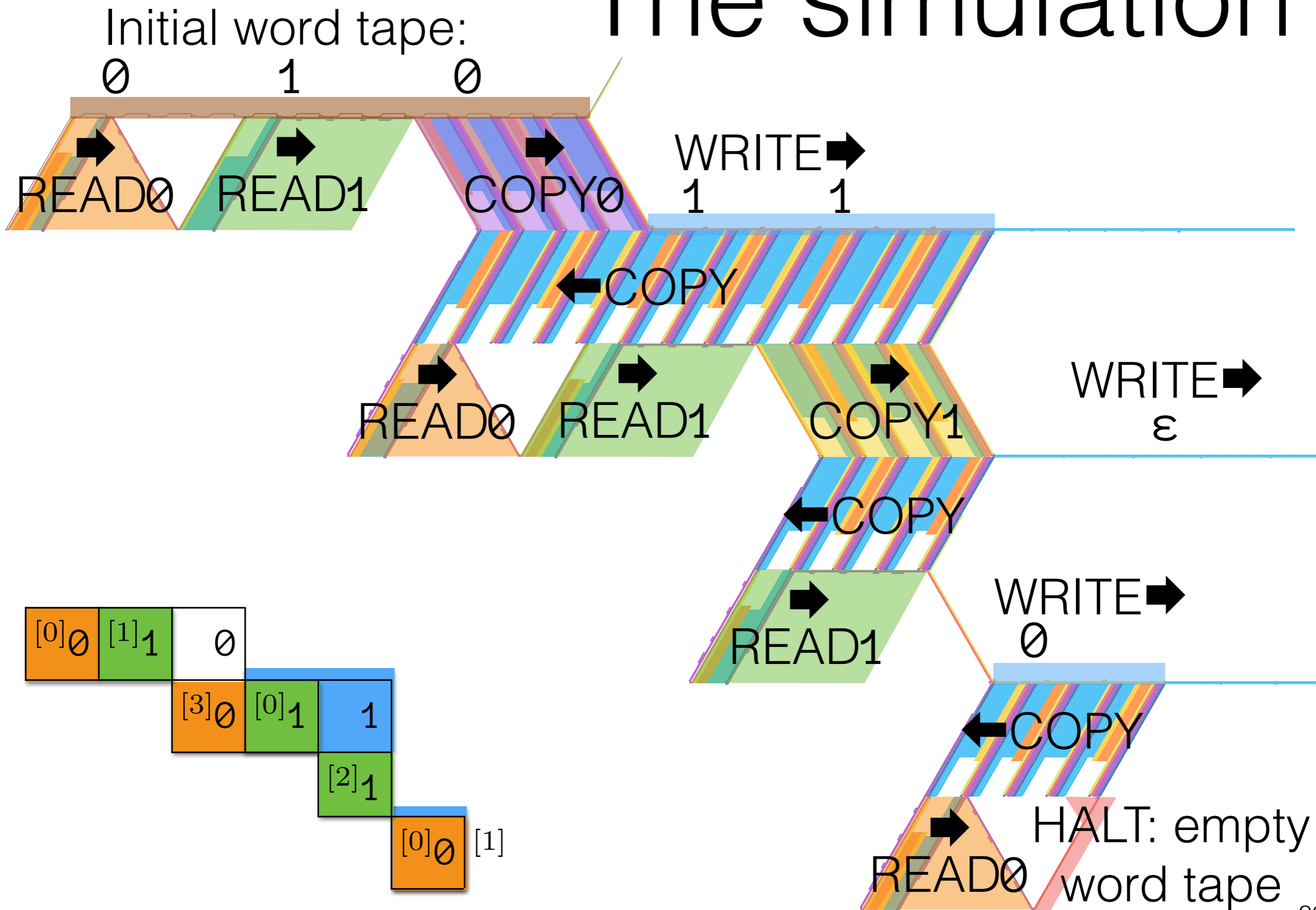


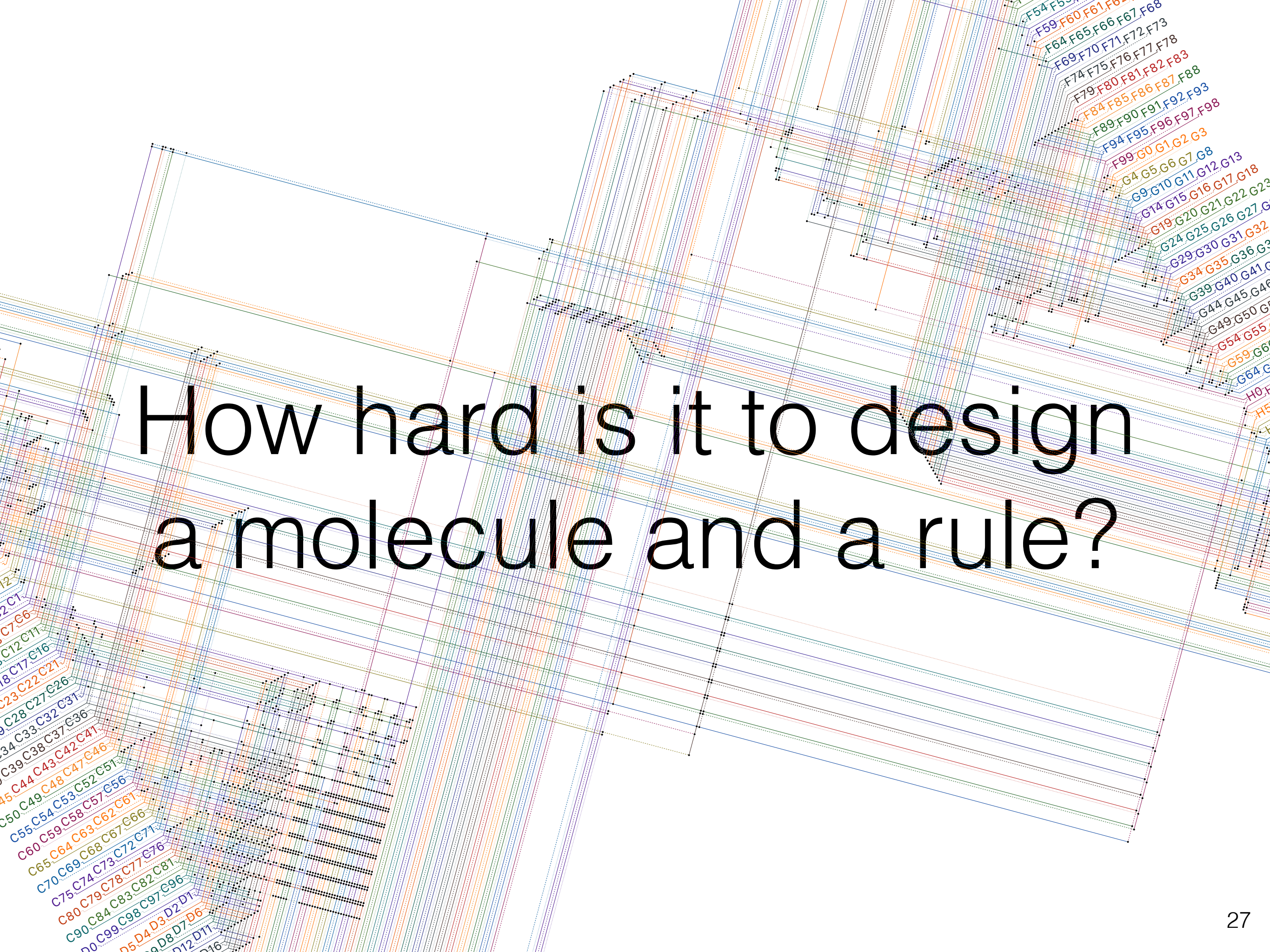
# Trimmed space-time diagram

Consider the following productions:  $p = \langle \overset{[0]}{1}\overset{[1]}{1}\overset{[2]}{0}, \epsilon, \overset{[2]}{1}\overset{[3]}{1}, \overset{[3]}{0} \rangle$

$[0]010 \rightarrow [1]10 \xrightarrow[\substack{\text{Append} \\ [2]:11}]{} [3]011 \rightarrow [0]11 \xrightarrow[\substack{\text{Append} \\ [1]:\epsilon}]{} [2]1 \xrightarrow[\substack{\text{Append} \\ [3]:0}]{} [0]0 \rightarrow [1] \text{Halt}$

# The simulation

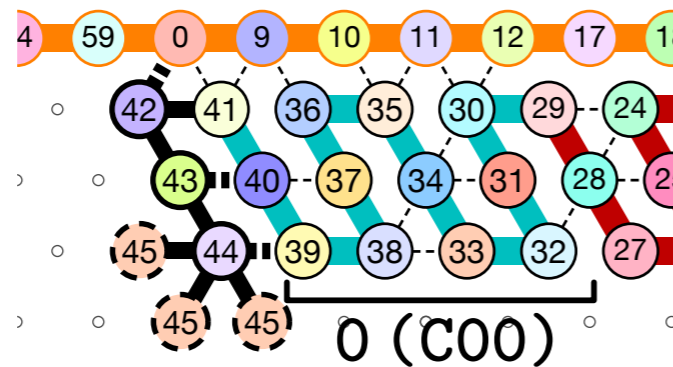


A complex network diagram with many nodes and edges, overlaid with a large text question. The nodes are arranged in a grid-like pattern and are labeled with alphanumeric strings such as 'F54 F55', 'G4 G5 G6 G7 G8', 'C28 C27 C26', and 'D5 D4 D3 D2 D1'. The edges are represented by thin, colored lines connecting the nodes. The overall structure is dense and multi-layered, suggesting a complex system or a large-scale network.

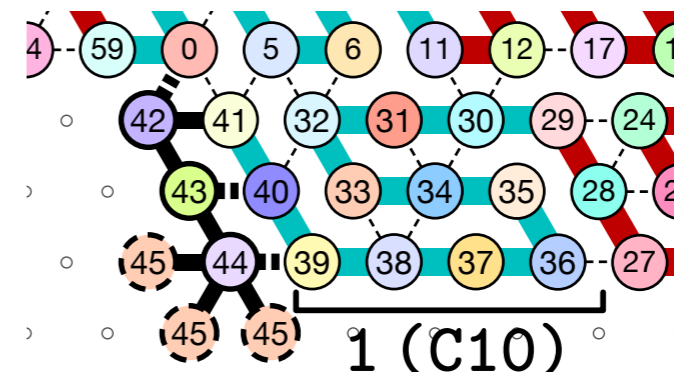
How hard is it to design  
a molecule and a rule?

# The first challenge: Designing the desired shapes

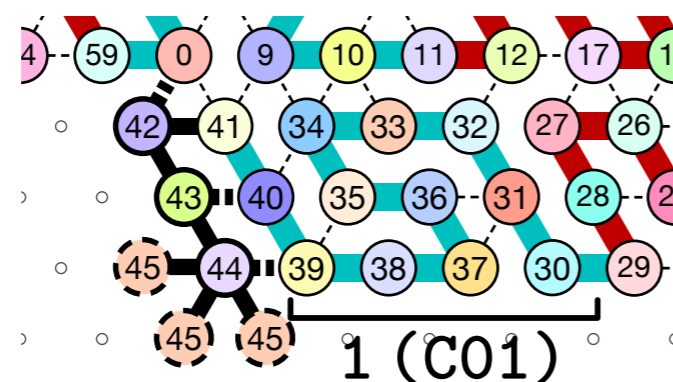
- Design shapes for which a **common** rule  exists



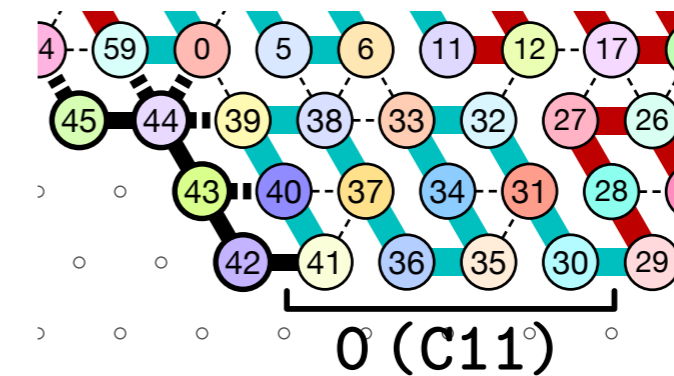
$$0+0 = 0 + \text{no } C$$



$$1+0 = 1 + \text{no } C$$




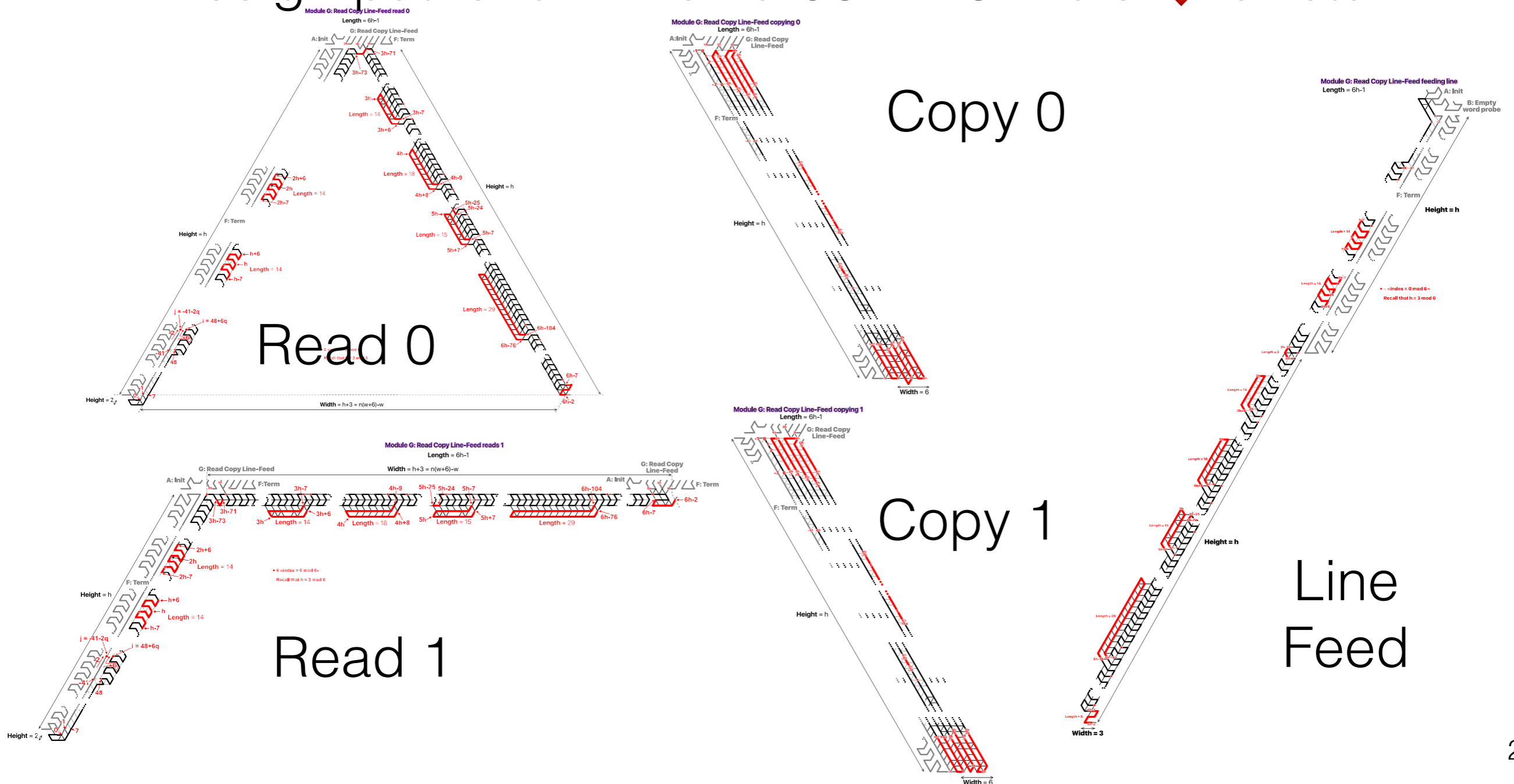
$$0+1 = 1 + \text{no } C$$



$$1+1 = 0 + C$$

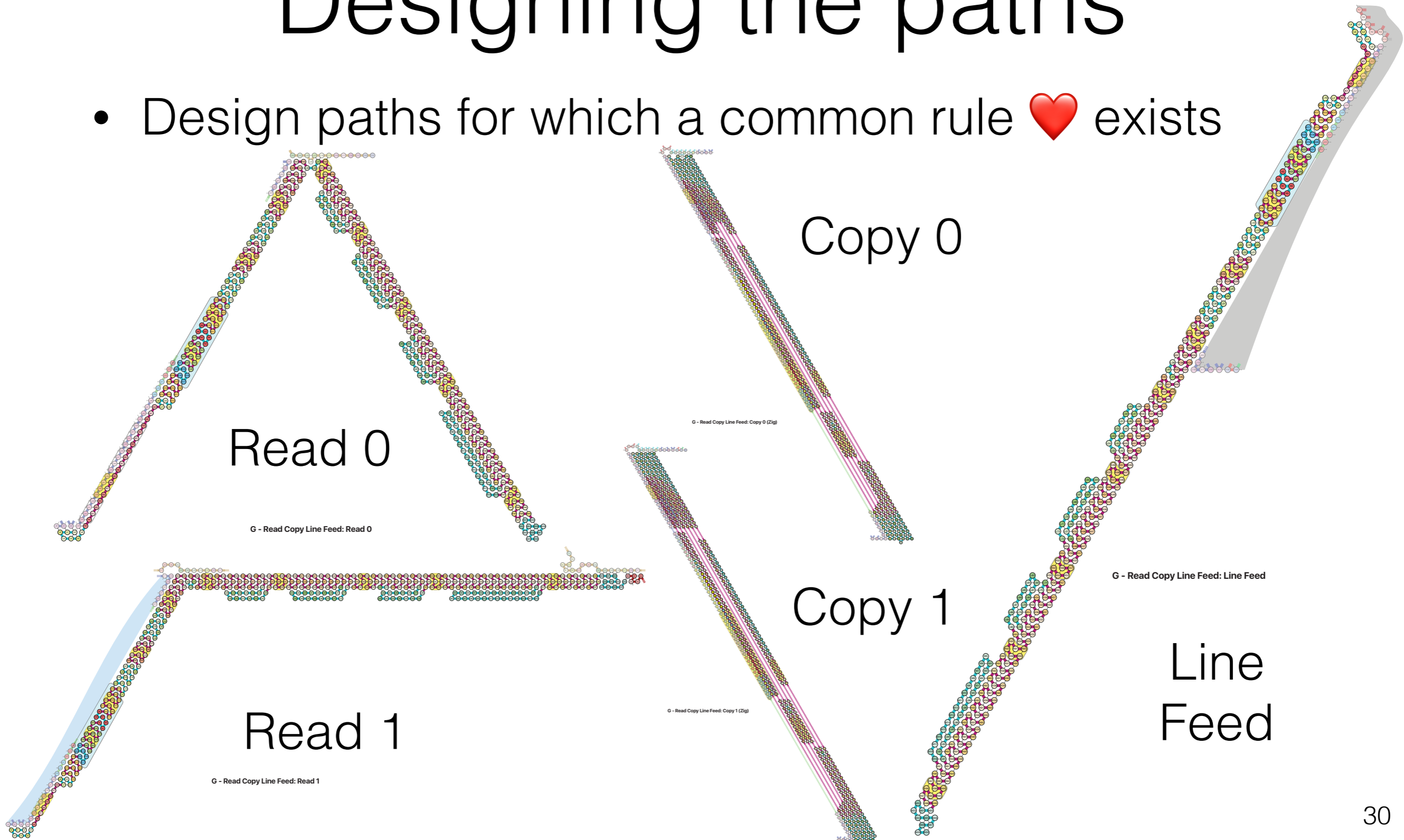
# The first challenge: Designing the desired paths

- Design paths for which a **common** rule  exists



# The first challenge: Designing the paths

- Design paths for which a common rule ❤️ exists

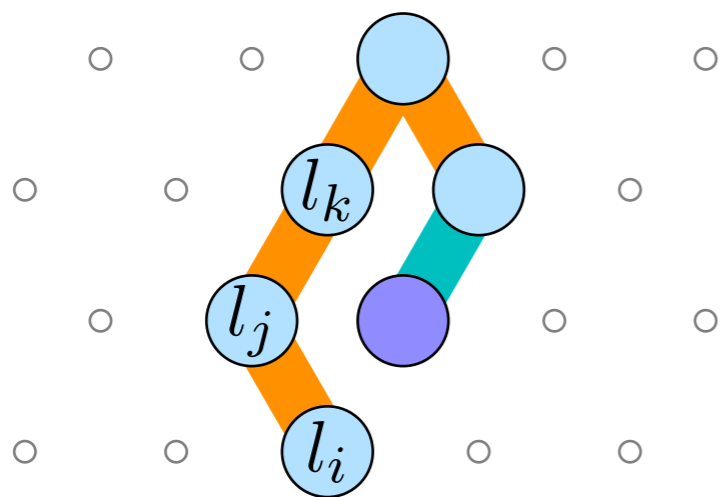


# Oritatami design is NP-hard

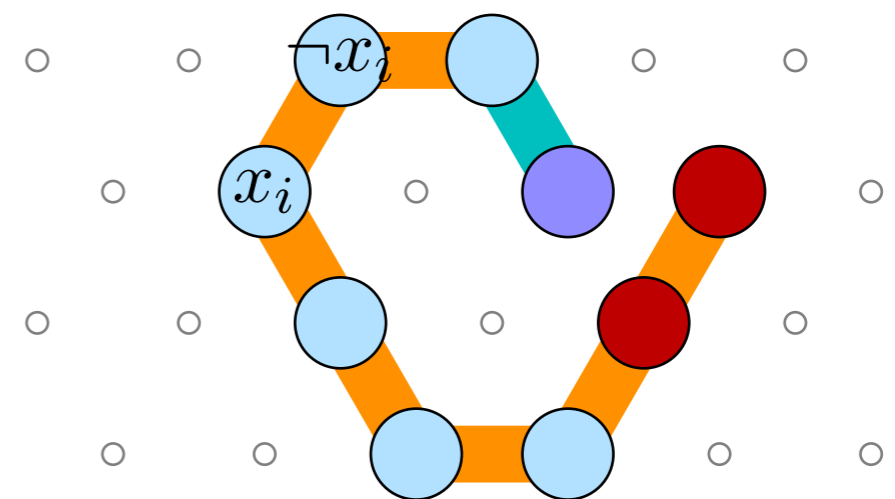
INPUT:	a delay time $\delta$ , a list of $n > 0$ seeds $\sigma_1, \sigma_2, \dots, \sigma_n$ , and a list of $n$ conformations $c_1, c_2, \dots, c_n$ of the same length $l$
OUTPUT:	an attraction rule $\heartsuit$ such that for all $i \in \{1, 2, \dots, n\}$ , Oritatami system $\mathcal{O}_i = (s, \sigma_i, \heartsuit, \delta)$ deterministically folds into conformation $c_i$ , where $s$ is the sequence of length $l$ such that for all $i \in \{1, 2, \dots, l\}$ , $s_i = i$ .

## The reduction (*length=1, $\delta$ arbitrary*)


Ensures it binds to at least one literal in  $l_i \vee l_j \vee l_k$



Ensures it binds to at most one of  $x_i$  and  $\neg x_i$



# The second challenge: Designing the rule

**Theorem.** There is a **FPT algorithm** with respect to  $L$  that designs **in linear time in  $L$**  (but exponential in  $k$  and  $\delta$ ) a **rule ** that folds the sequence  $1, \dots, L$  of length  $L$  into  $k$  prescribed conformations when folded in  $k$  prescribed environments.

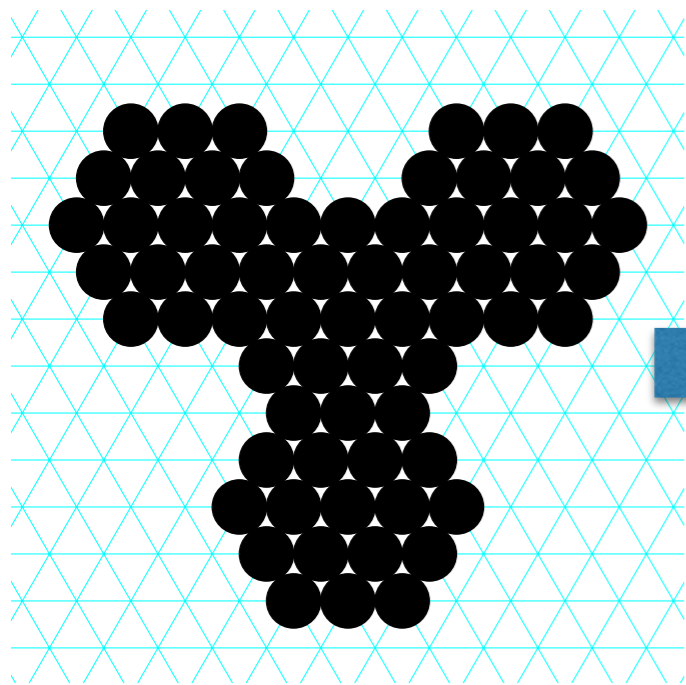
*Proof.* • **Locality:** each bead only sees a bounded number (exponential in  $\delta$ ) of other beads when folded.

- Then, compute all valid local rules for each of these neighborhoods
- And use dynamic programming to decide whether there is a global rule compatible with at least one of the local rule for each environment.

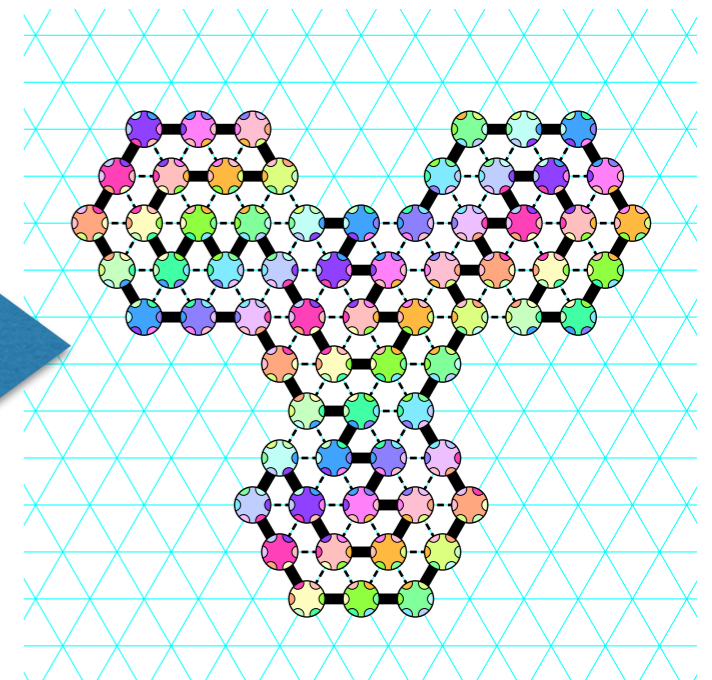
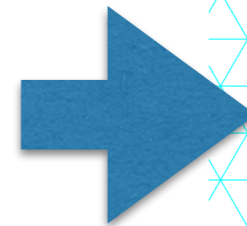
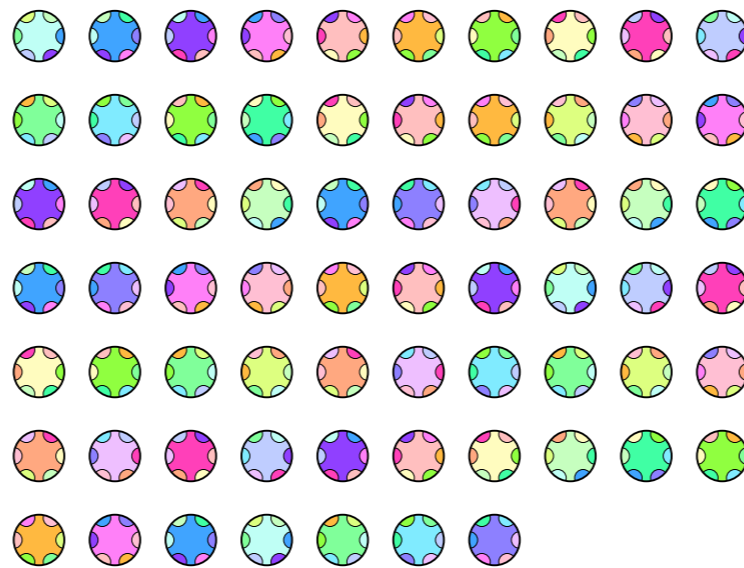


# Building shapes

**Goal: Given a shape  $S$ ,  
Find an oritatami system, i.e. a  
*sequence of bead types*,  
that folds into  $S$**

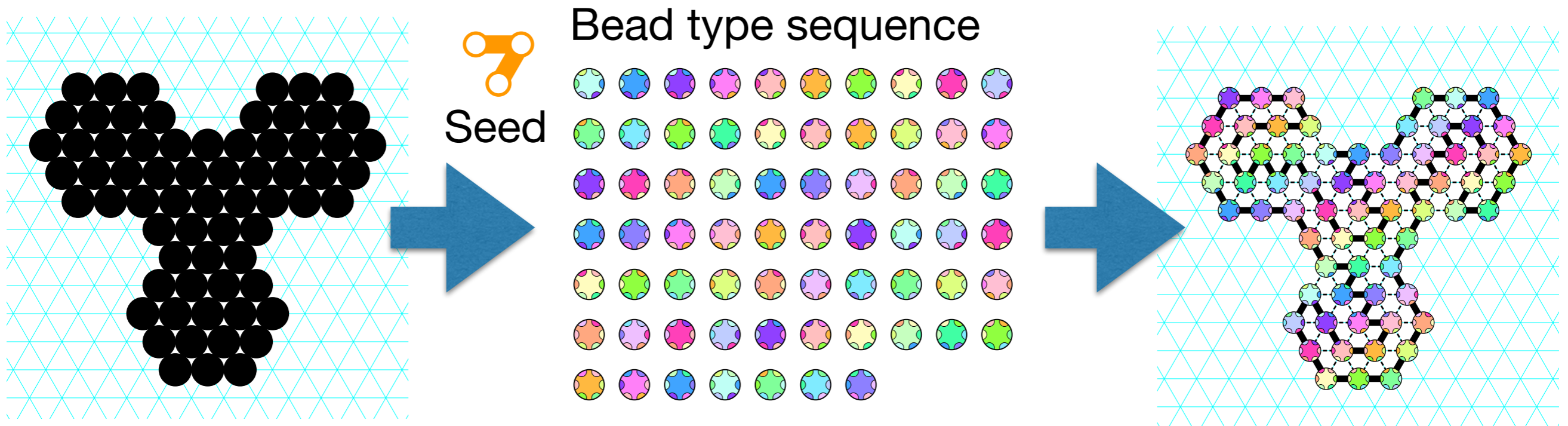


Bead type sequence



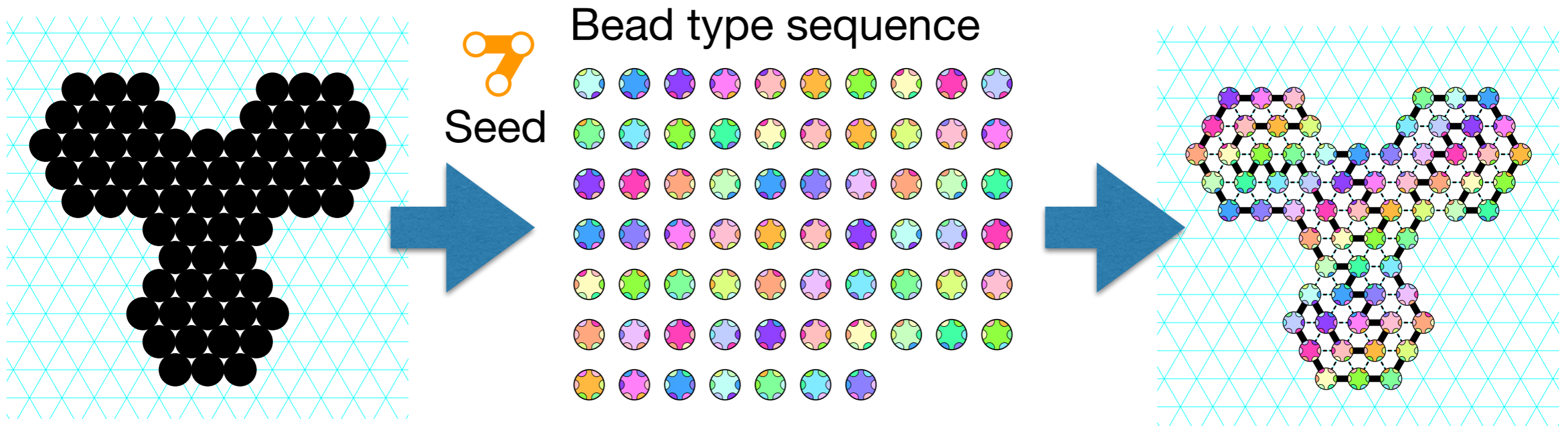
# An Oritatami system folds a shape if:

**Starting from the seed configuration,**  
it folds deterministically to occupy all the positions of  
the shape and only them

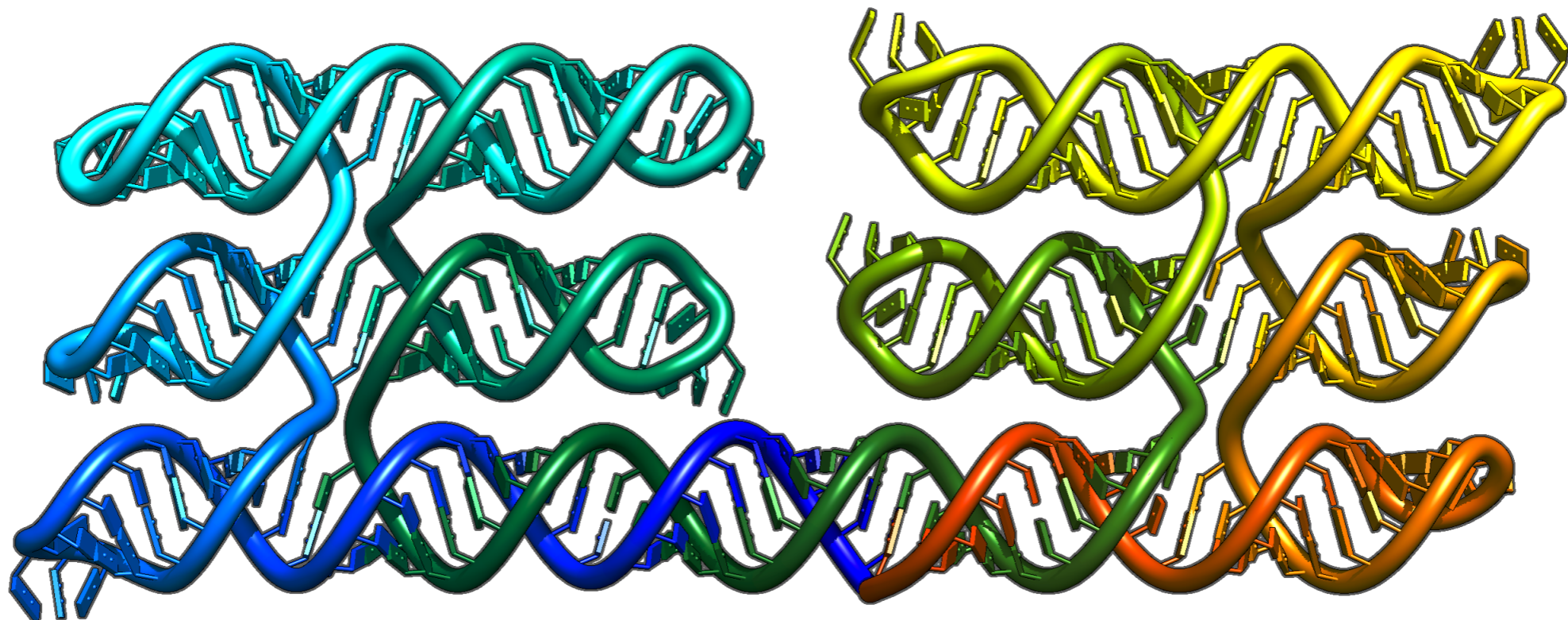
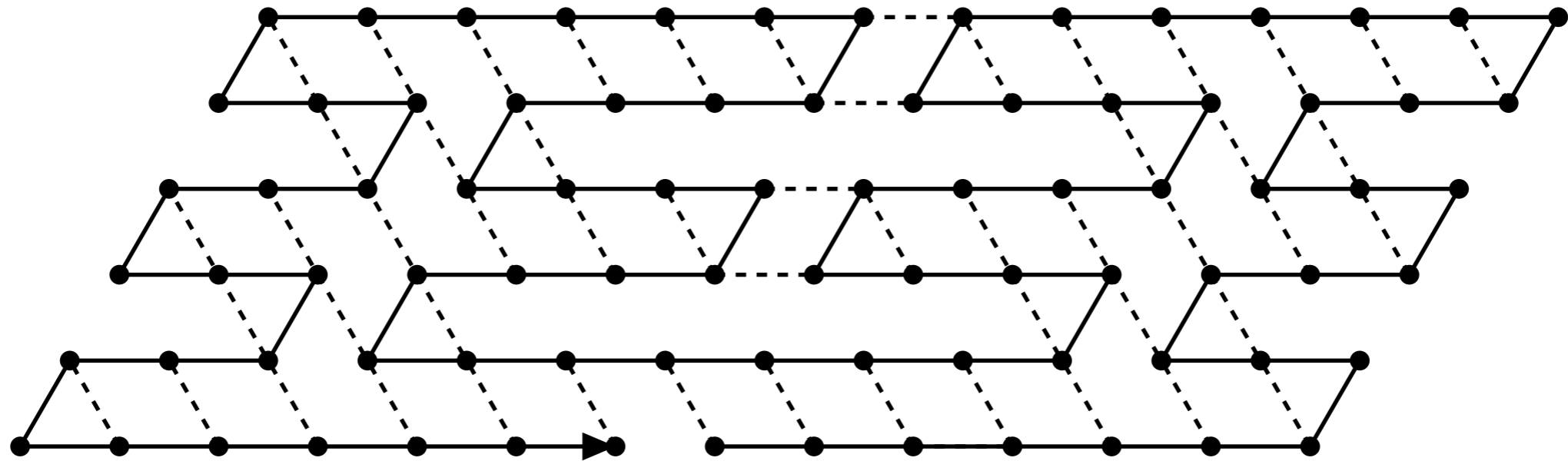


# Seek an Universal construction

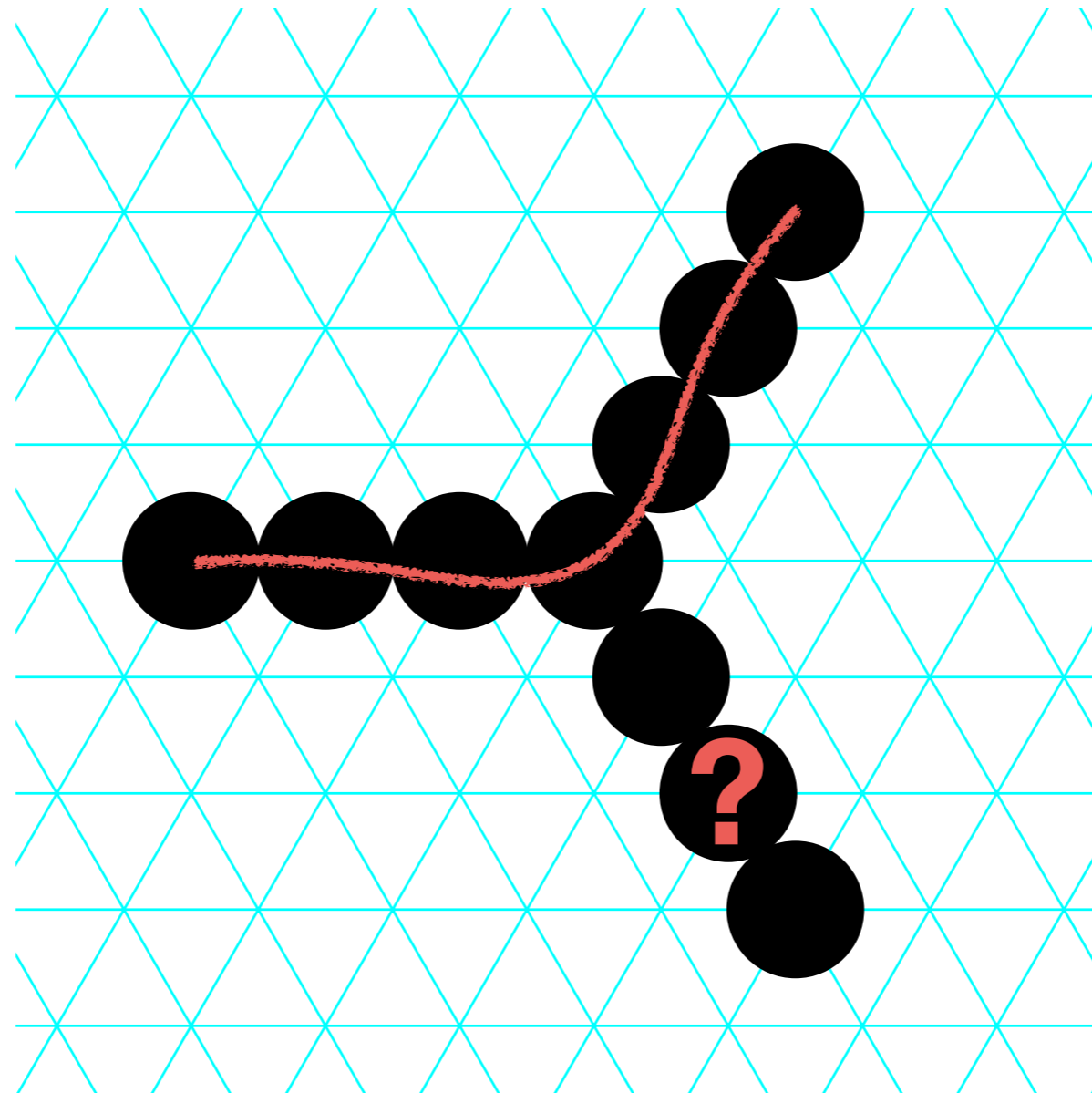
- **Fixed** finite size seed
- **Fixed** finite set of bead types  
*(independent of the shape)*



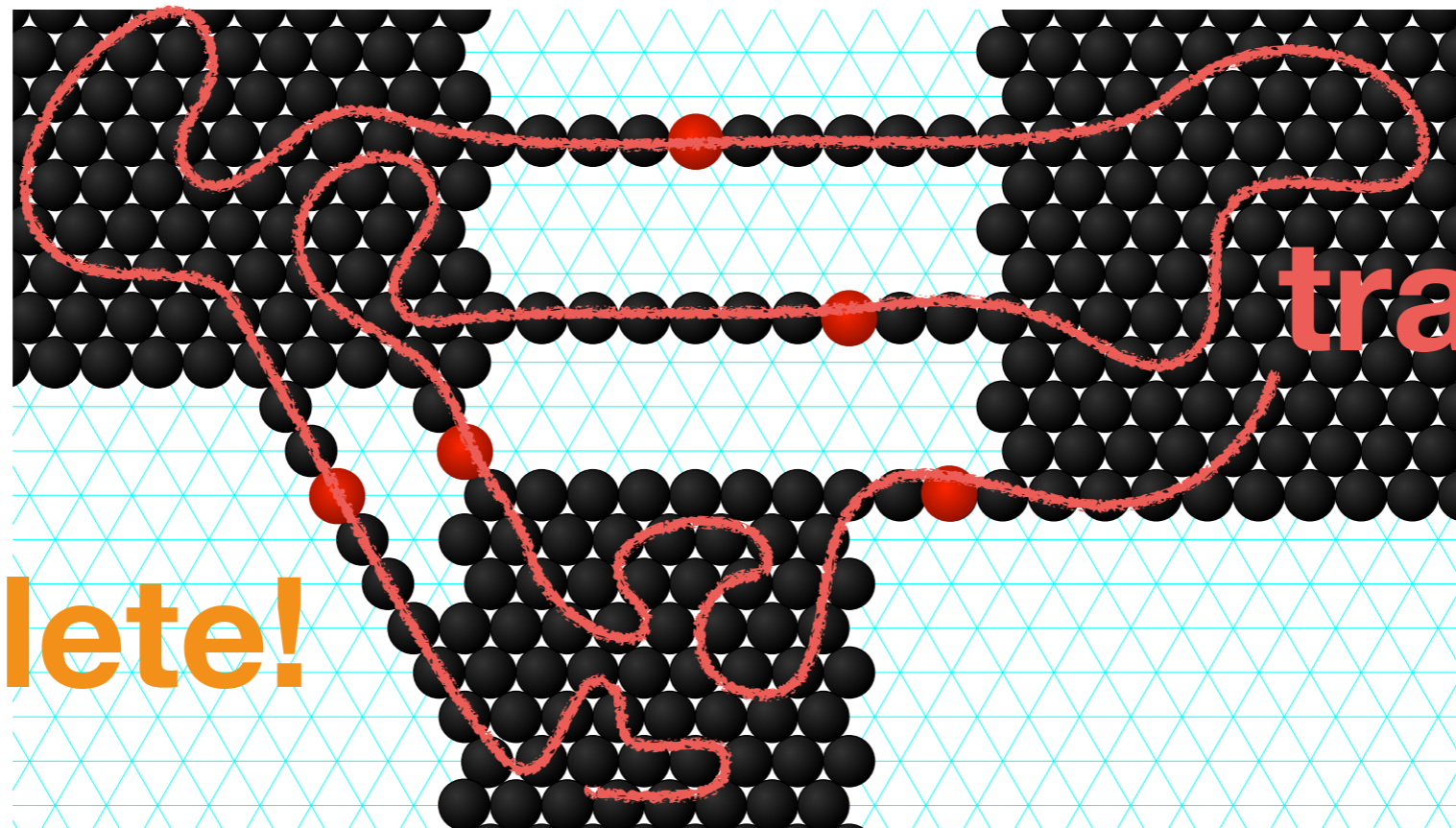
# Example of such molecule



# Trivial fact: Foldable shapes are Hamiltonian



# Fact: Finitely cuttable *infinite* shapes cannot be folded



incomplete!

trapped!

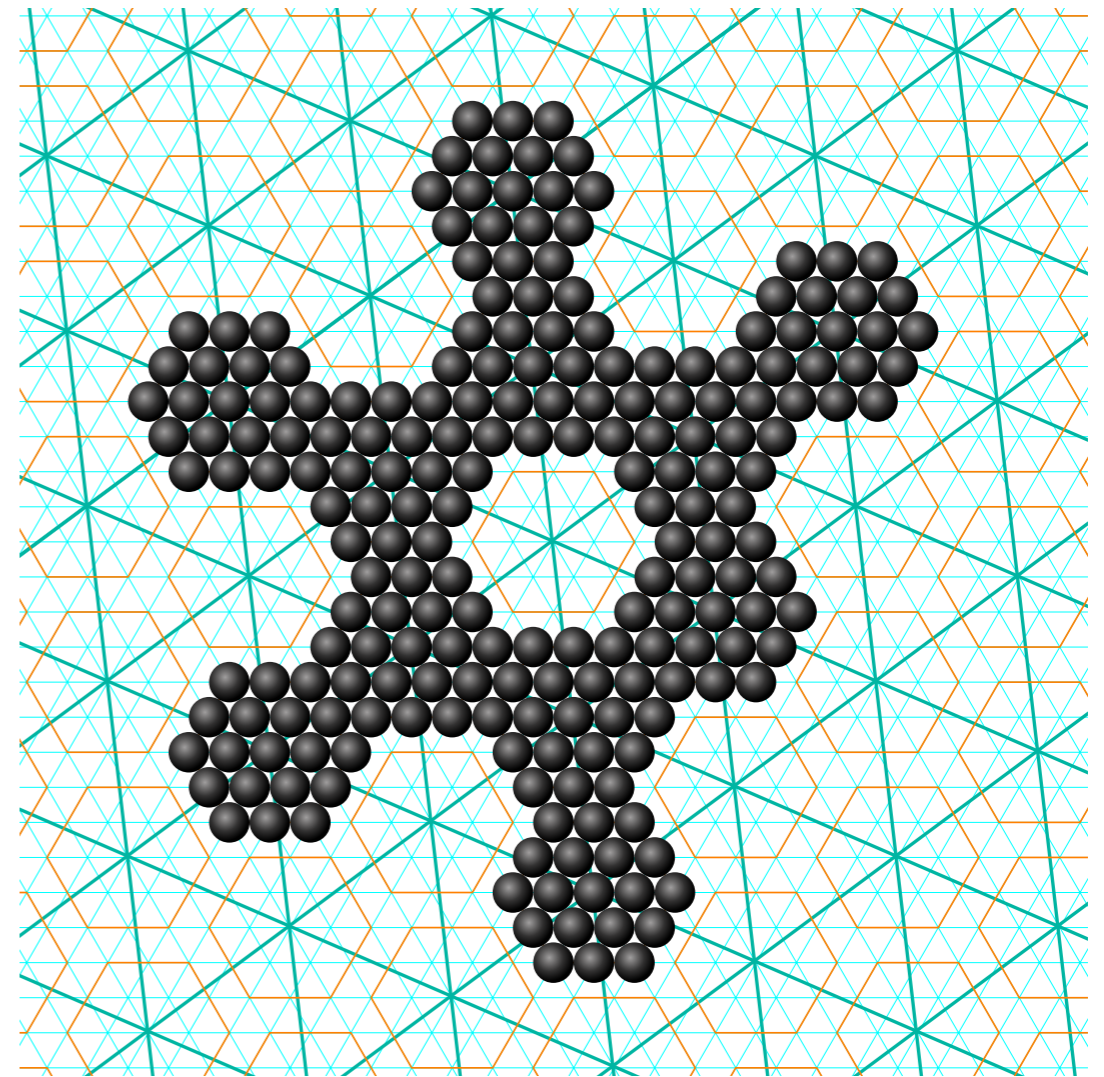
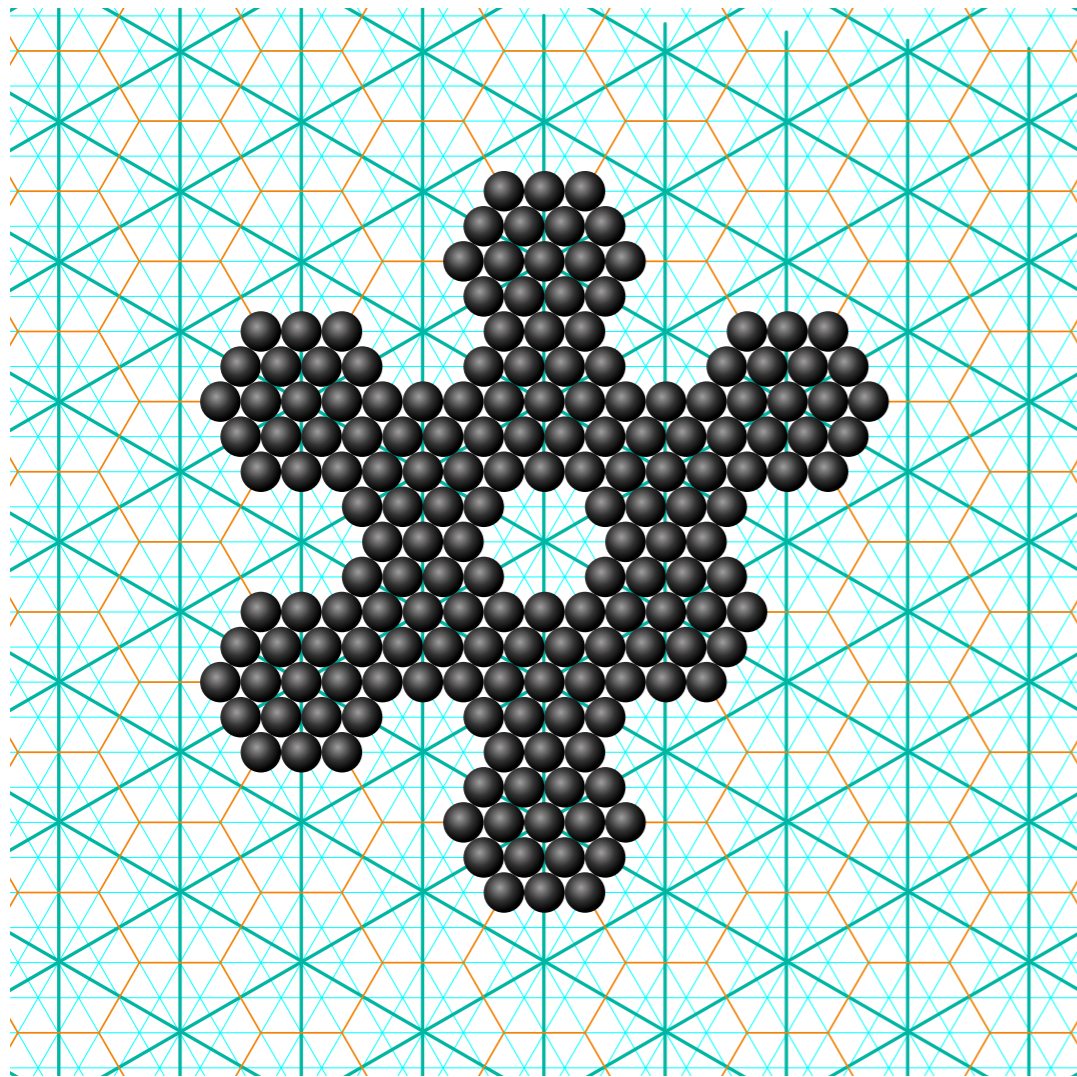
A **finite set of points** cutting the shape into several infinite pieces

***Oritatami systems are thus essentially different from tile assembly systems (aTam)***

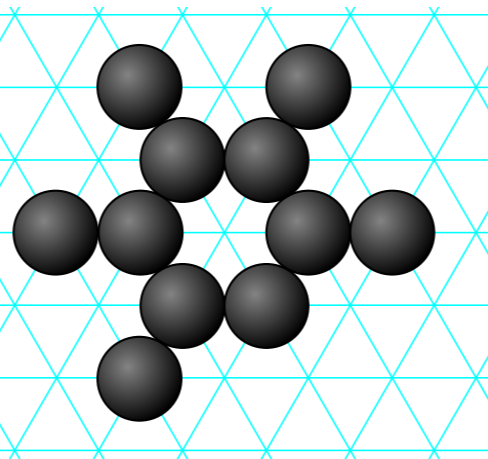
**Consider  
upscaling schemes**



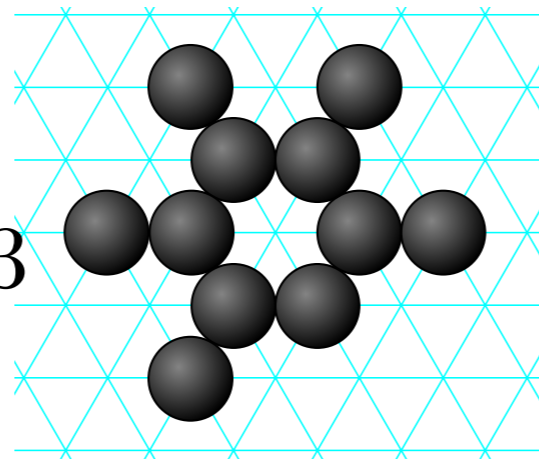
# Upscaling schemes



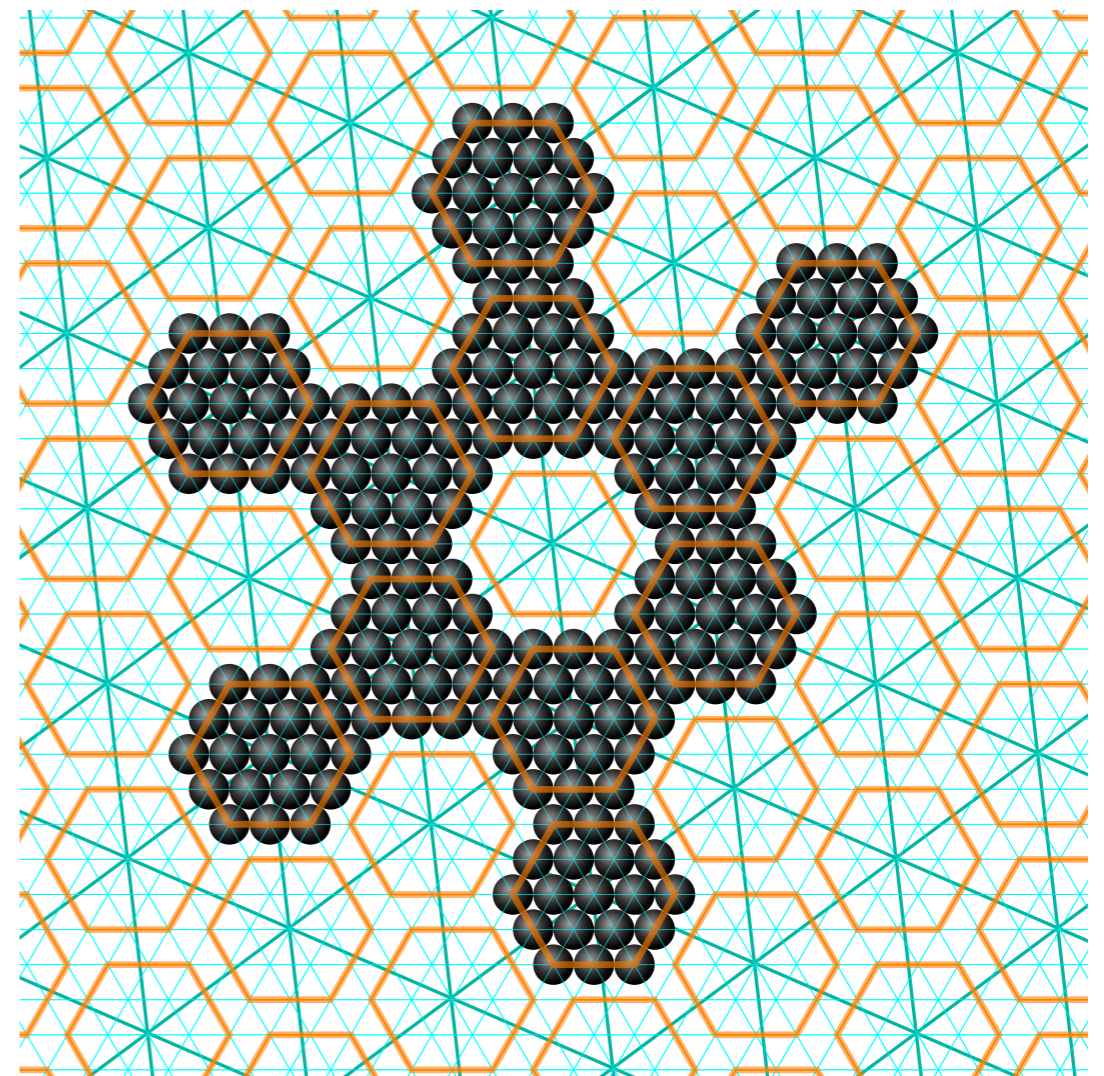
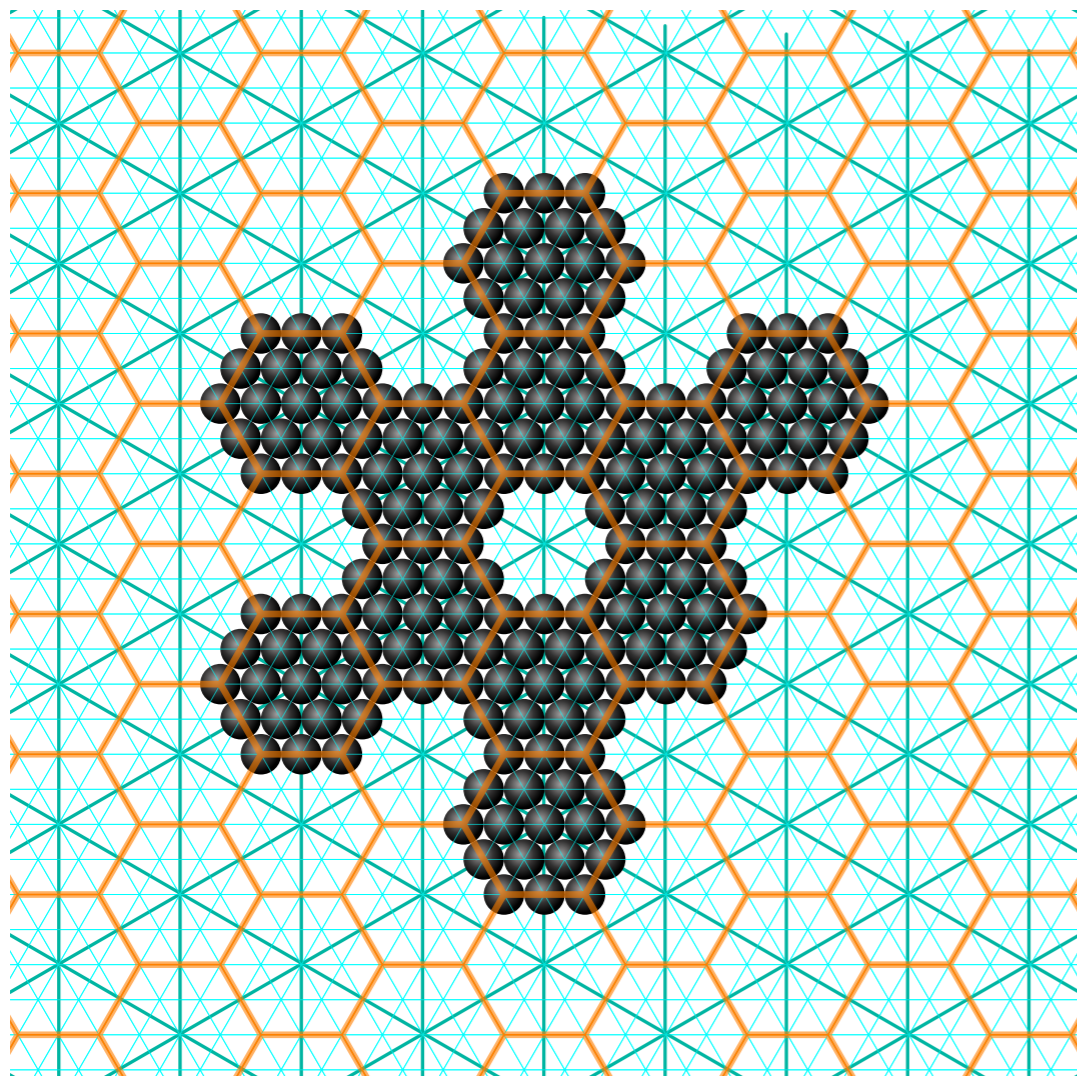
scale  $\mathcal{A}_n, n = 3$



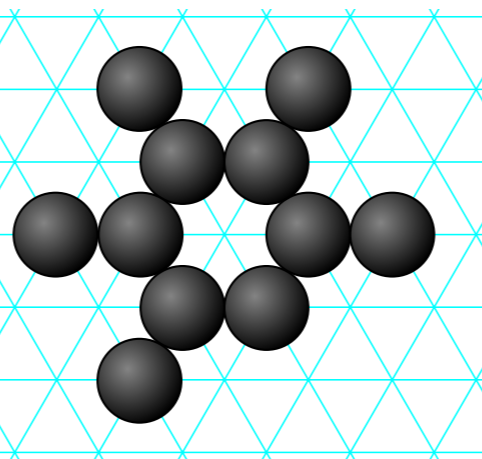
scale  $\mathcal{B}_n, n = 3$



# Upscaling schemes



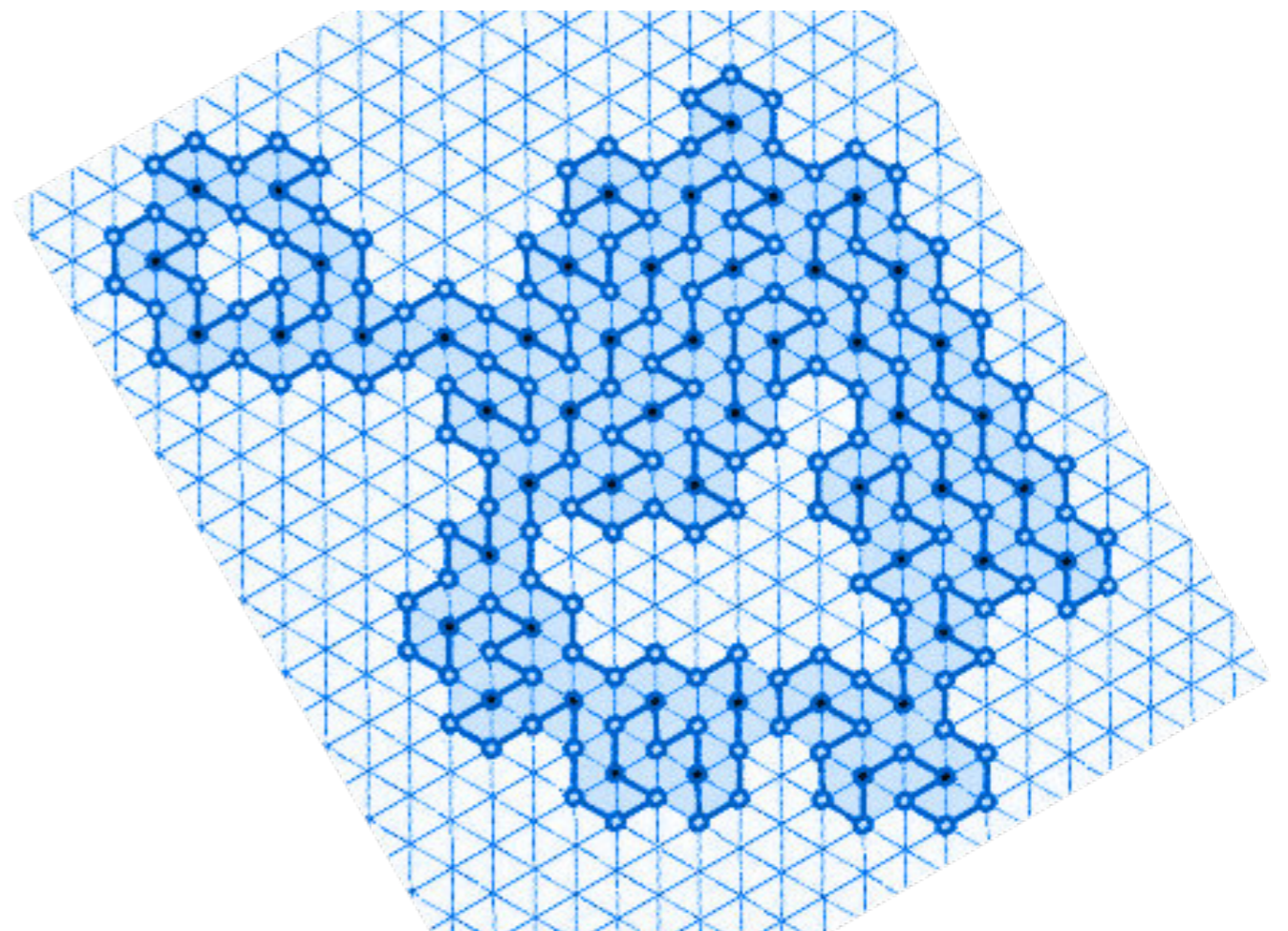
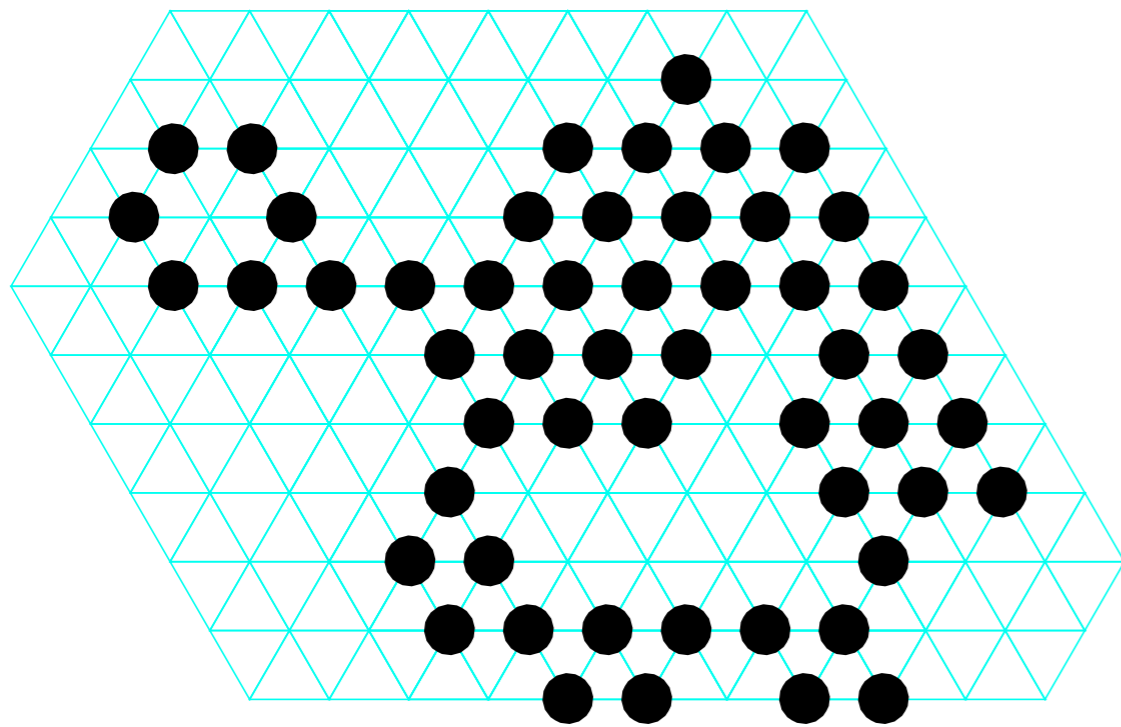
scale  $\mathcal{A}_n, n = 3$



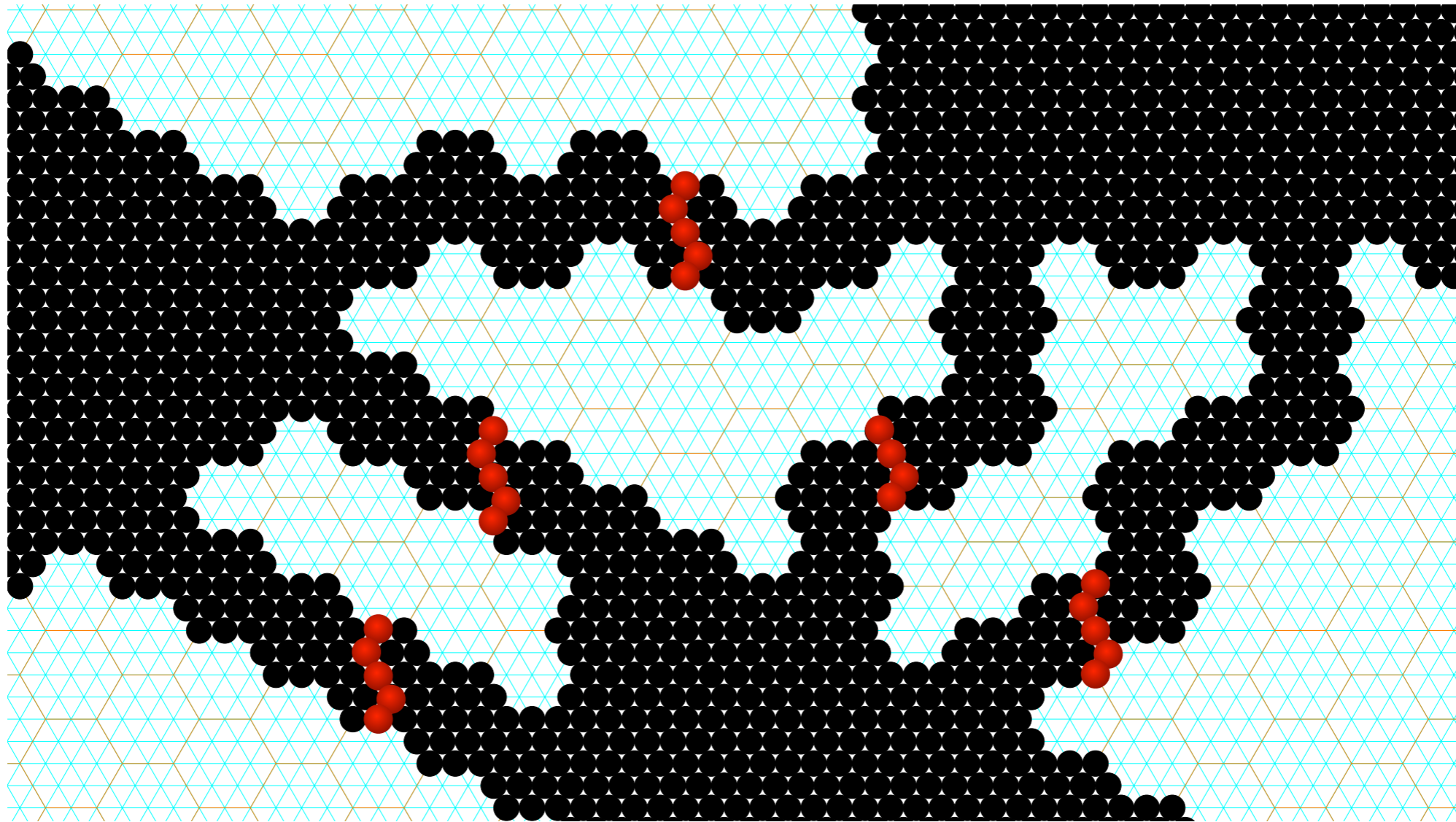
scale  $\mathcal{B}_n, n = 3$

# Finite shapes are Hamiltonian at scale $\mathcal{A}_2$

**Theorem.** There is a quadratic algorithm that computes an Hamiltonian path for any finite shape at scale  $\mathcal{A}_2$



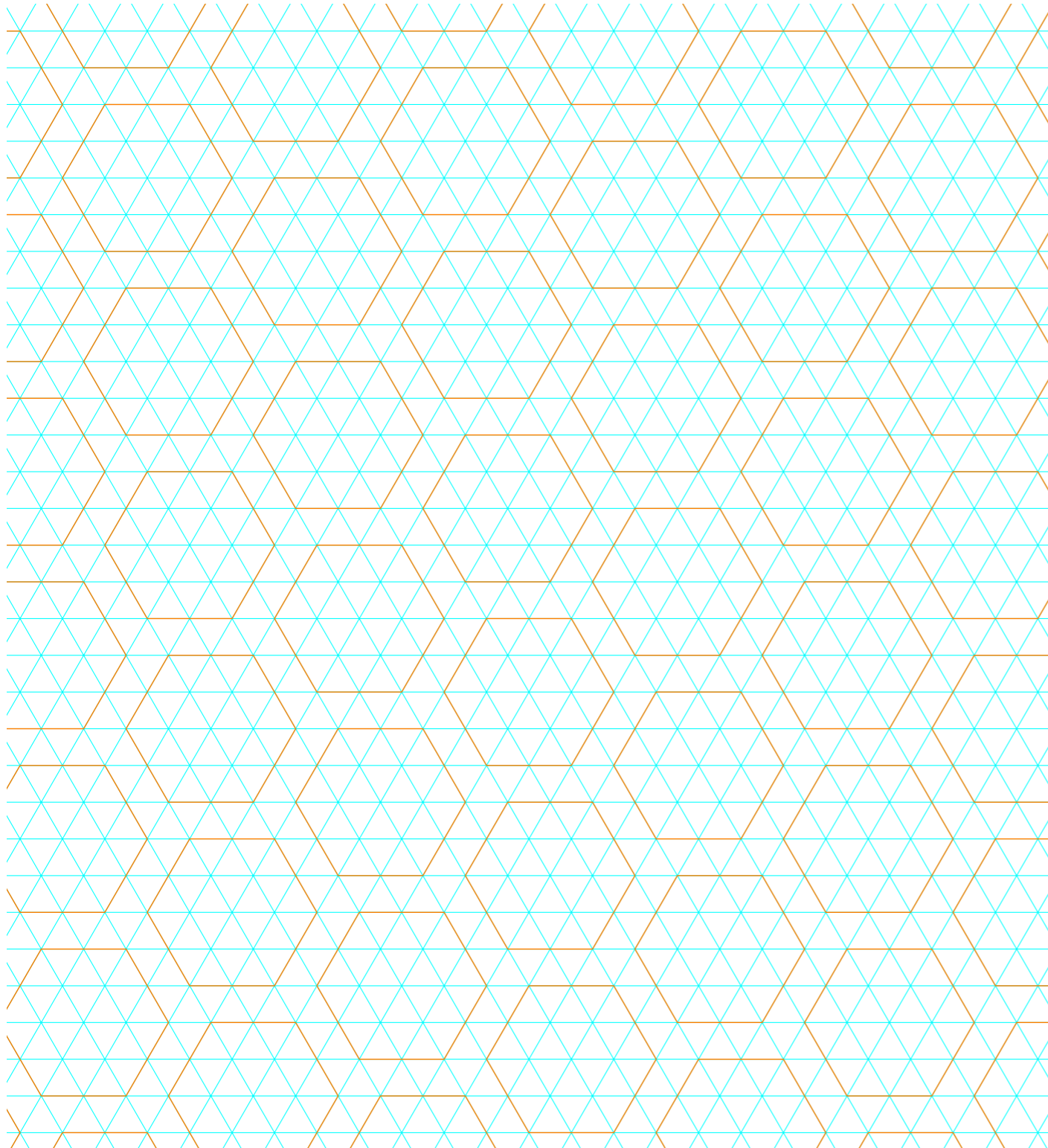
# Upscaling does not help with finitely cuttable infinite shapes



Thus, we focus on **finite shapes**

**Scale**  $\mathcal{B}_n$

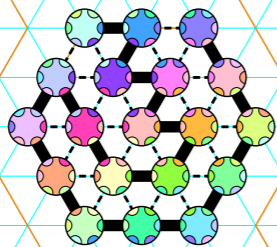
**scale**  $\mathcal{B}_n$



Use a unique pattern



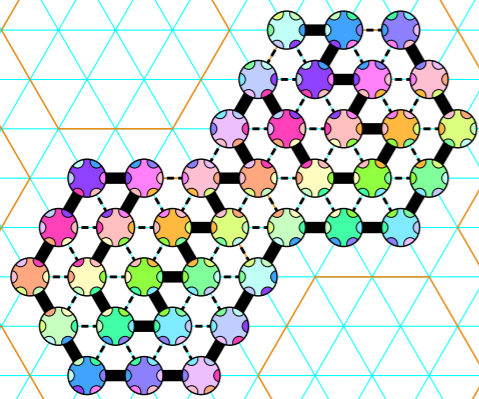
scale  $\mathcal{B}_n$



Use a unique pattern



scale  $\mathcal{B}_n$

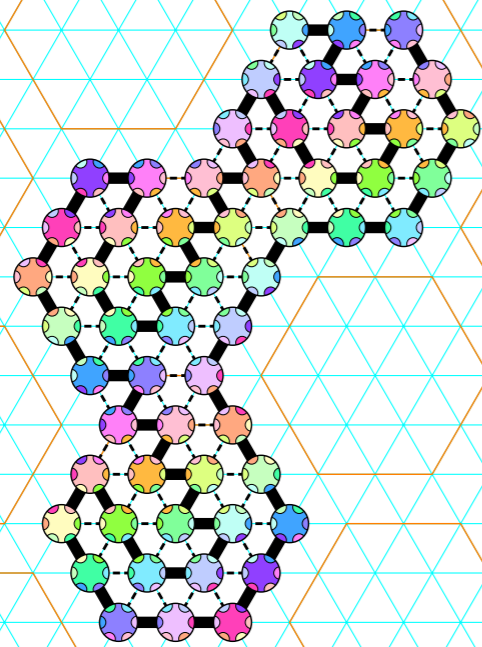


Use a unique pattern





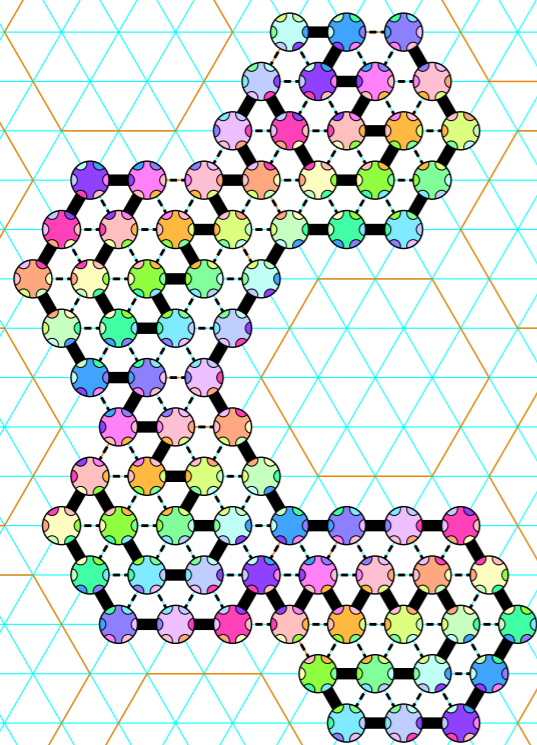
scale  $\mathcal{B}_n$



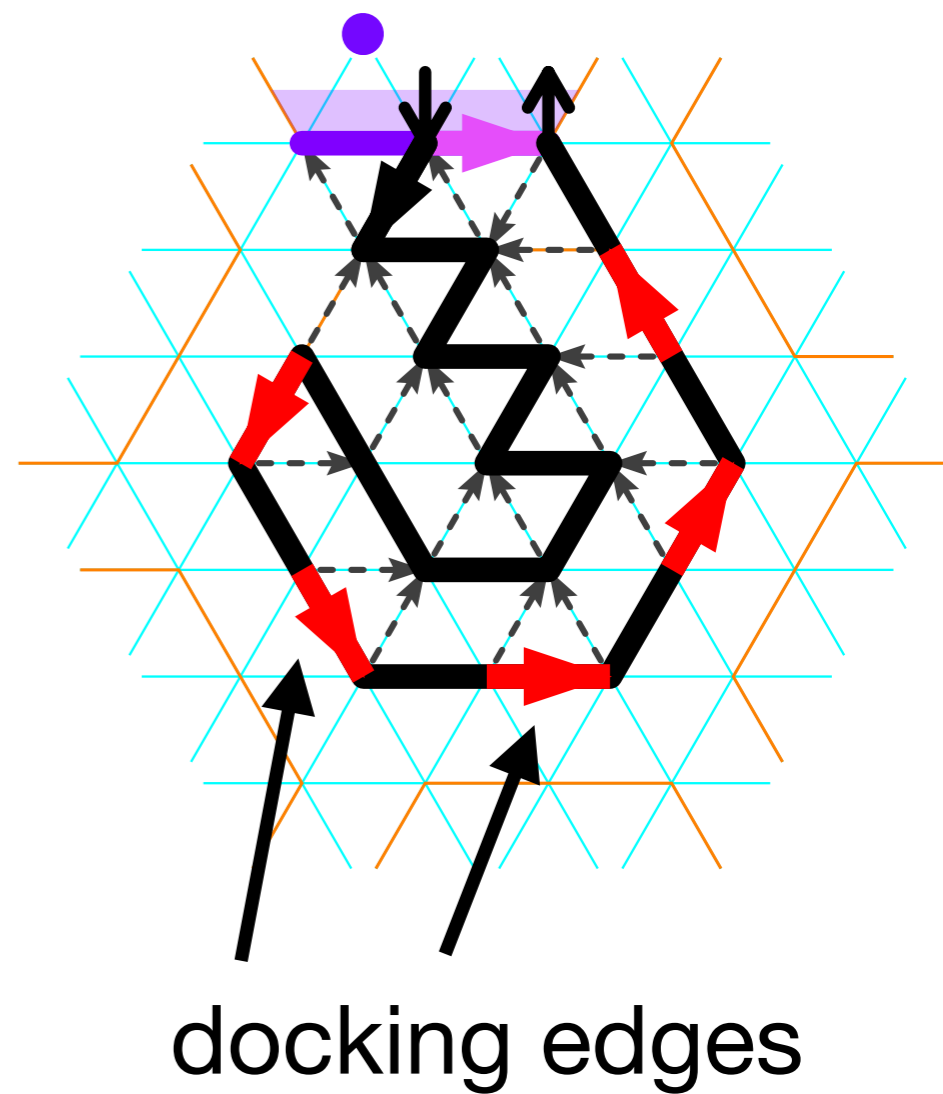
Use a unique pattern



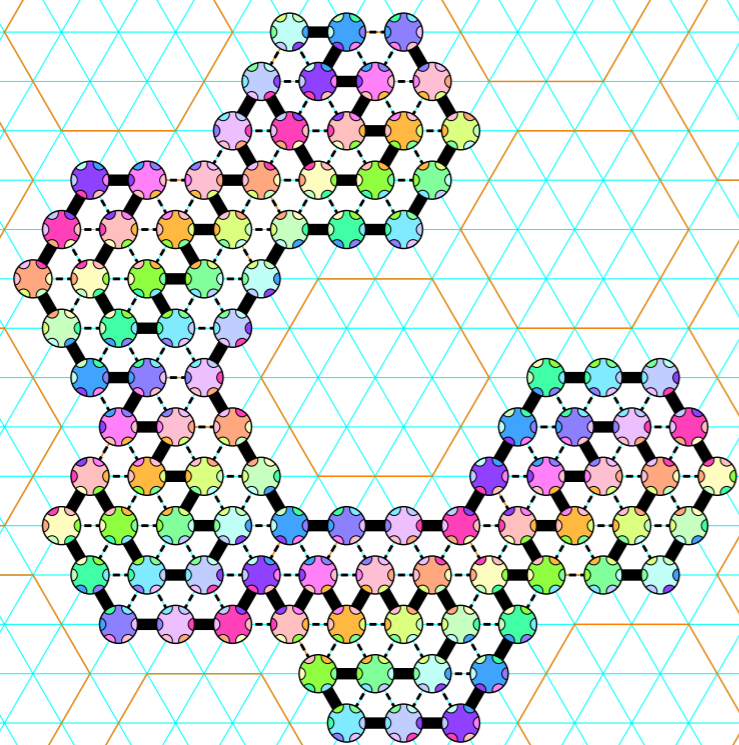
scale  $\mathcal{B}_n$



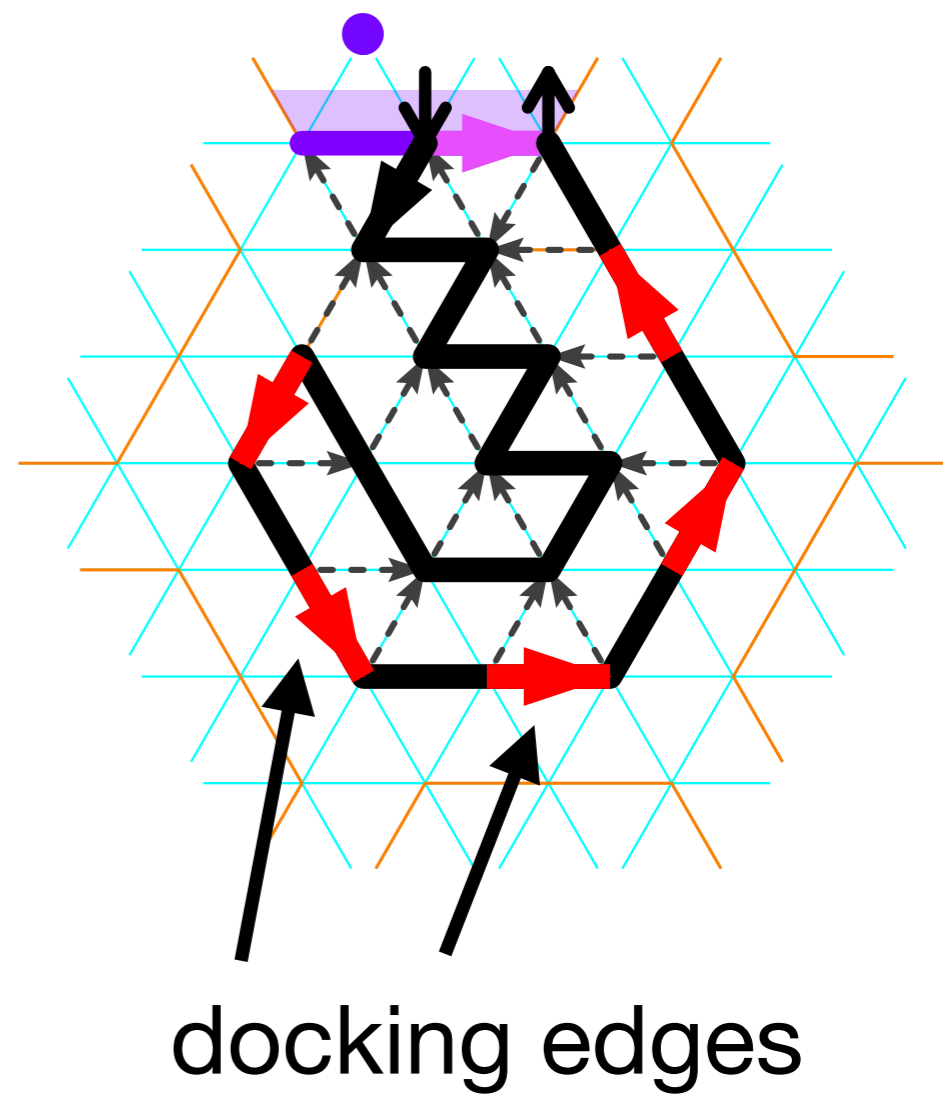
Use a unique pattern



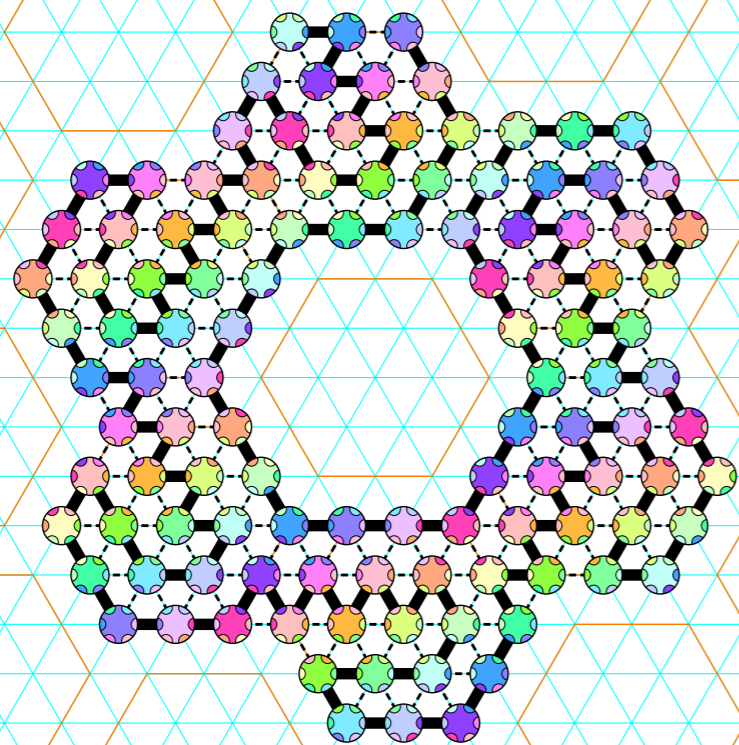
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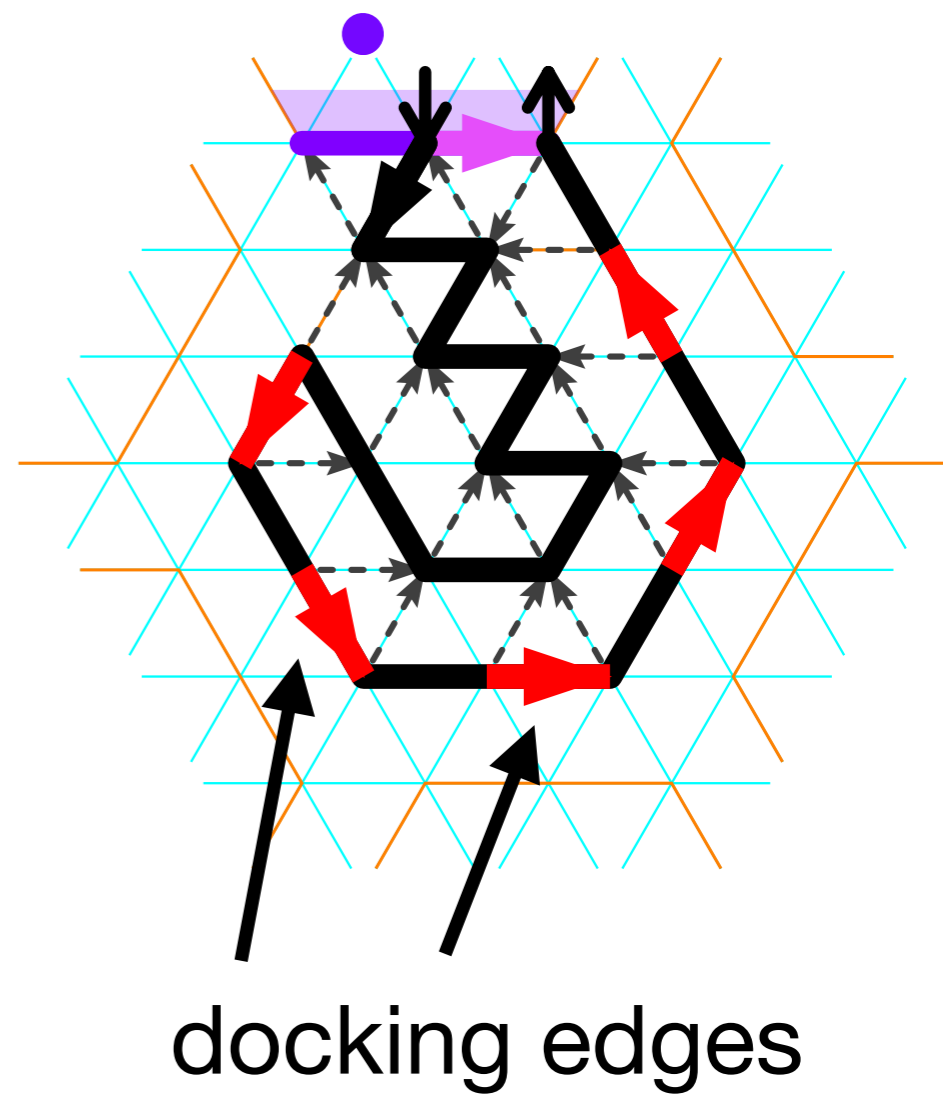
Use a unique pattern



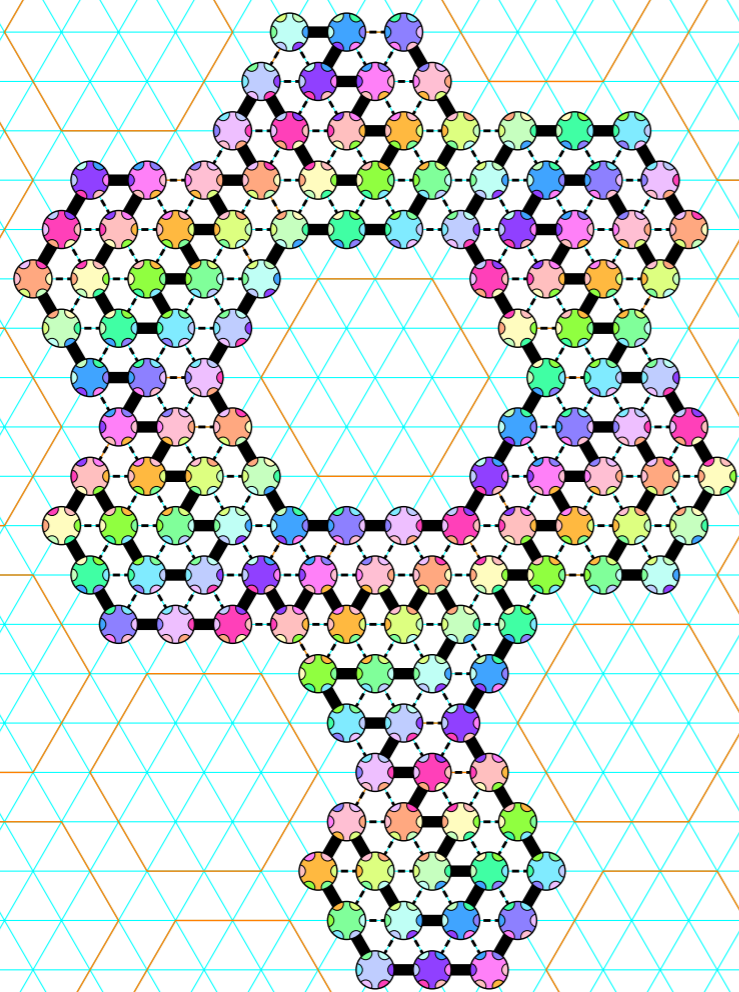
scale  $\mathcal{B}_n$



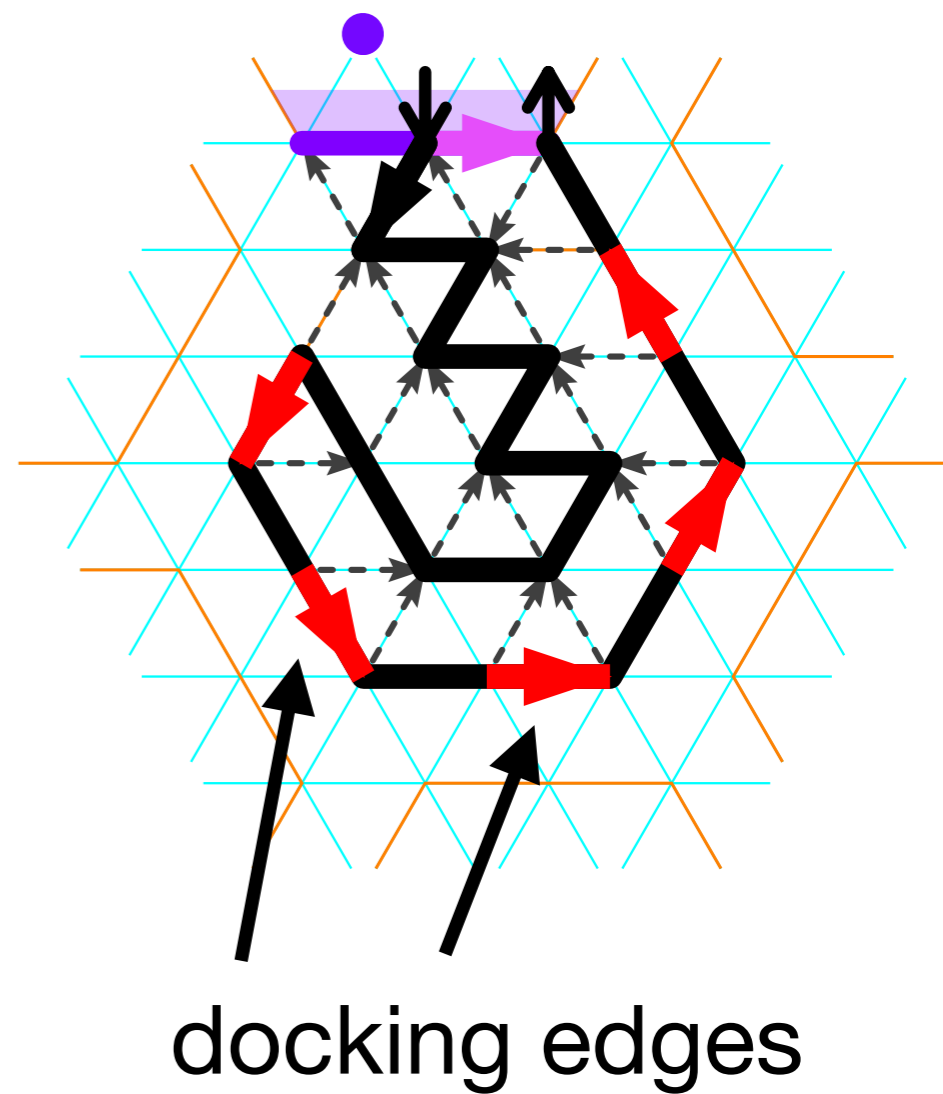
Use a unique pattern



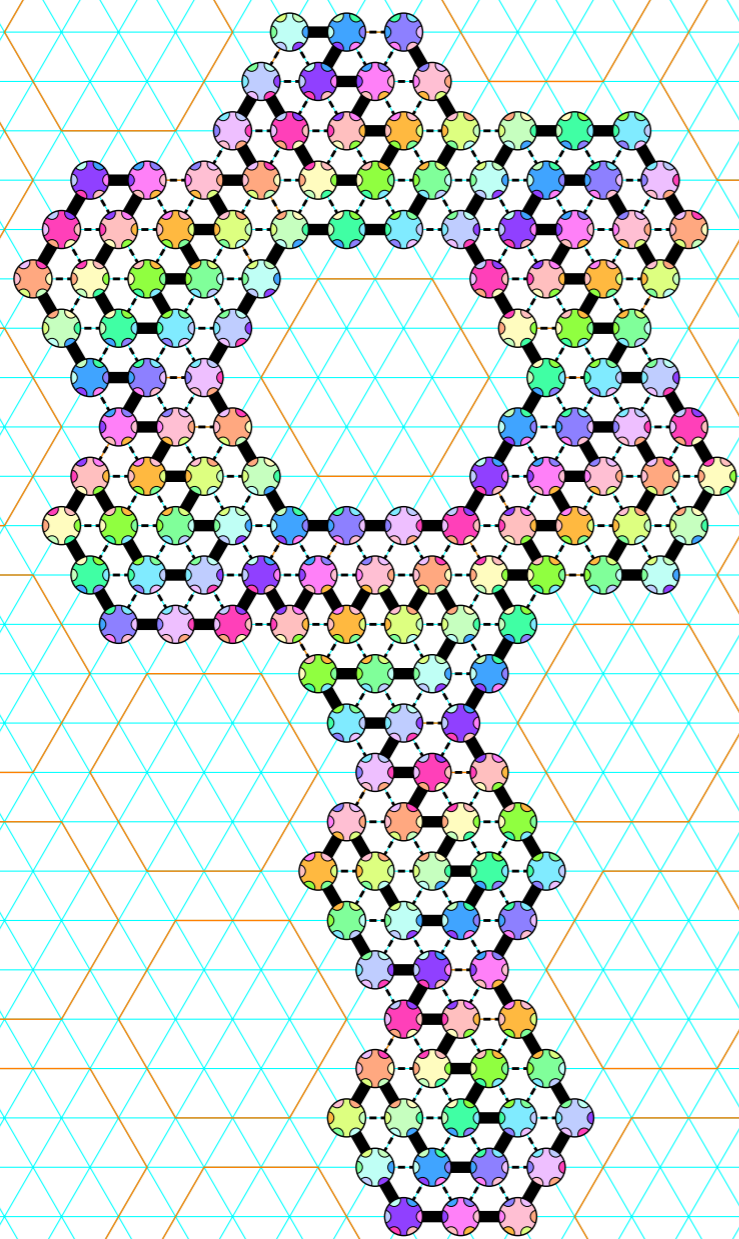
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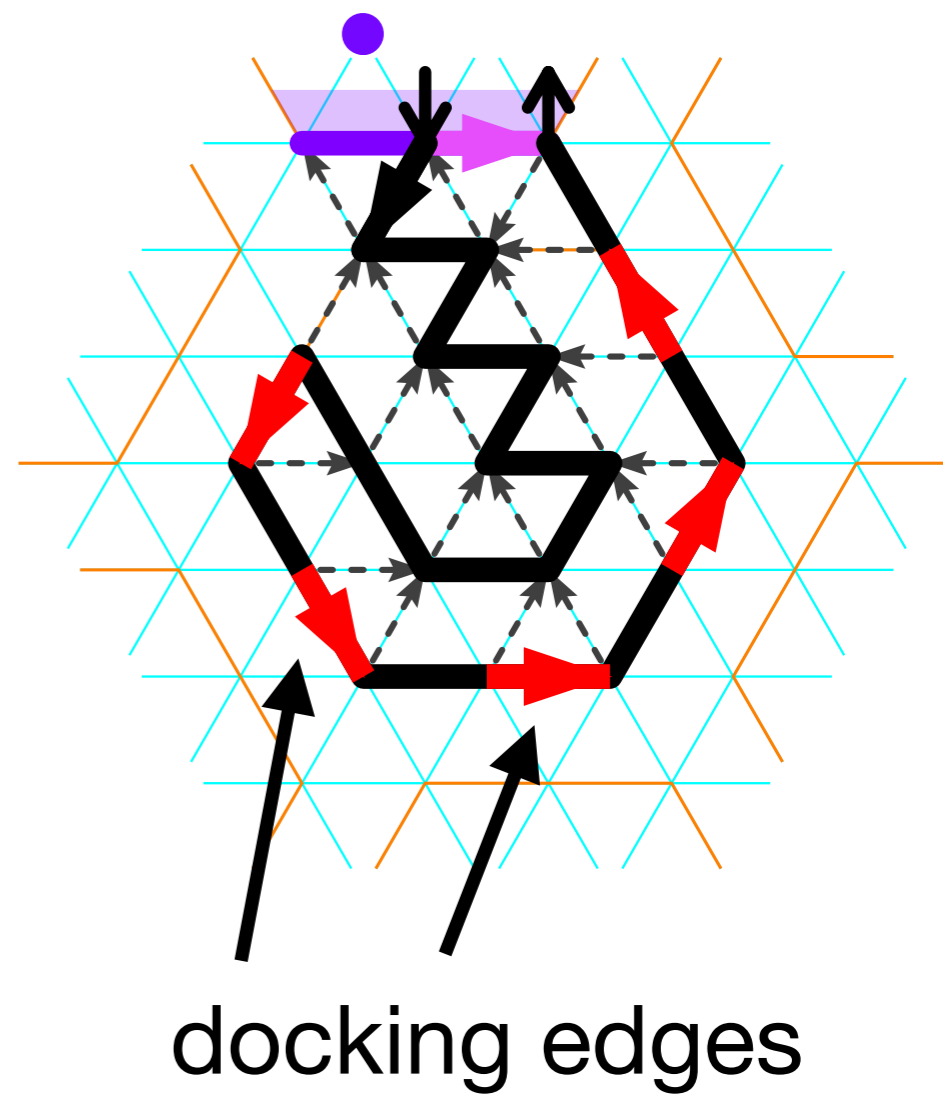
Use a unique pattern



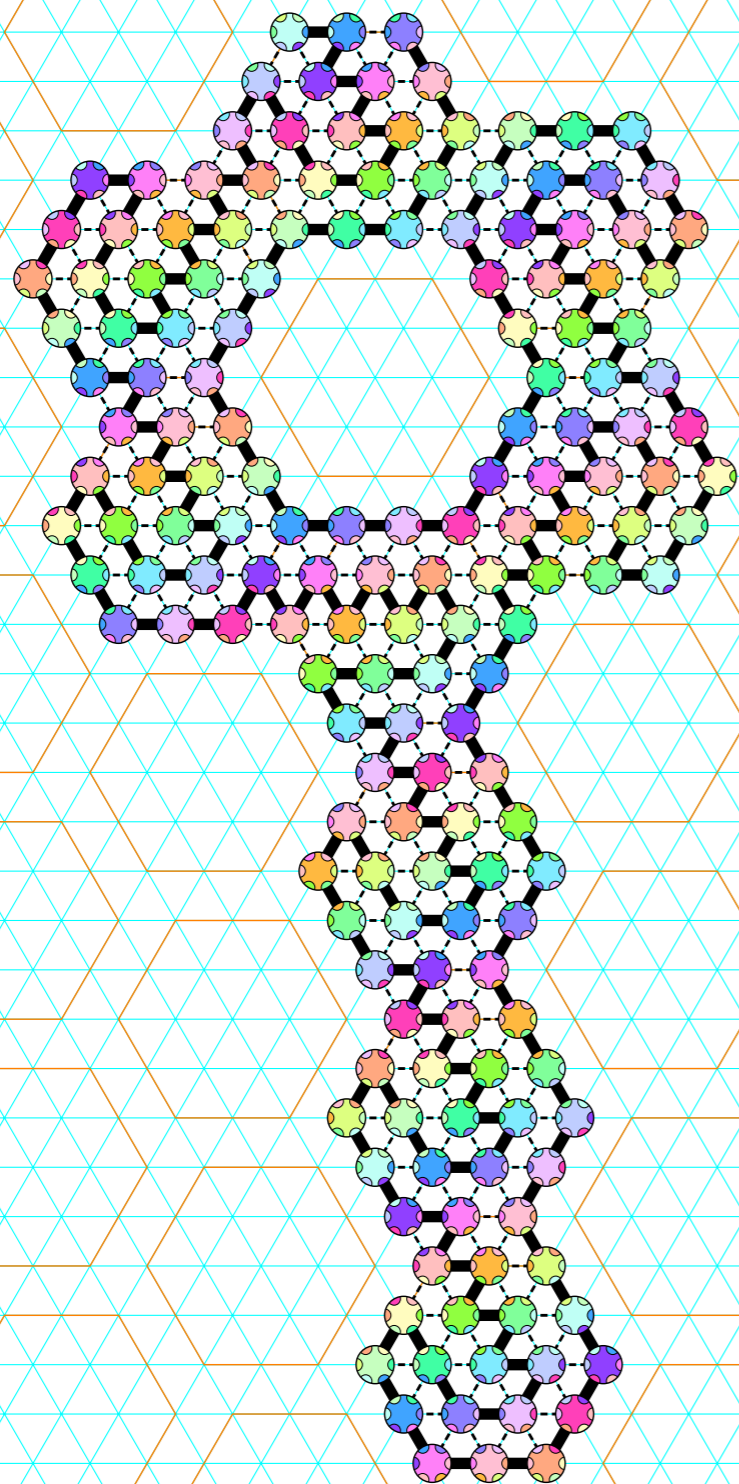
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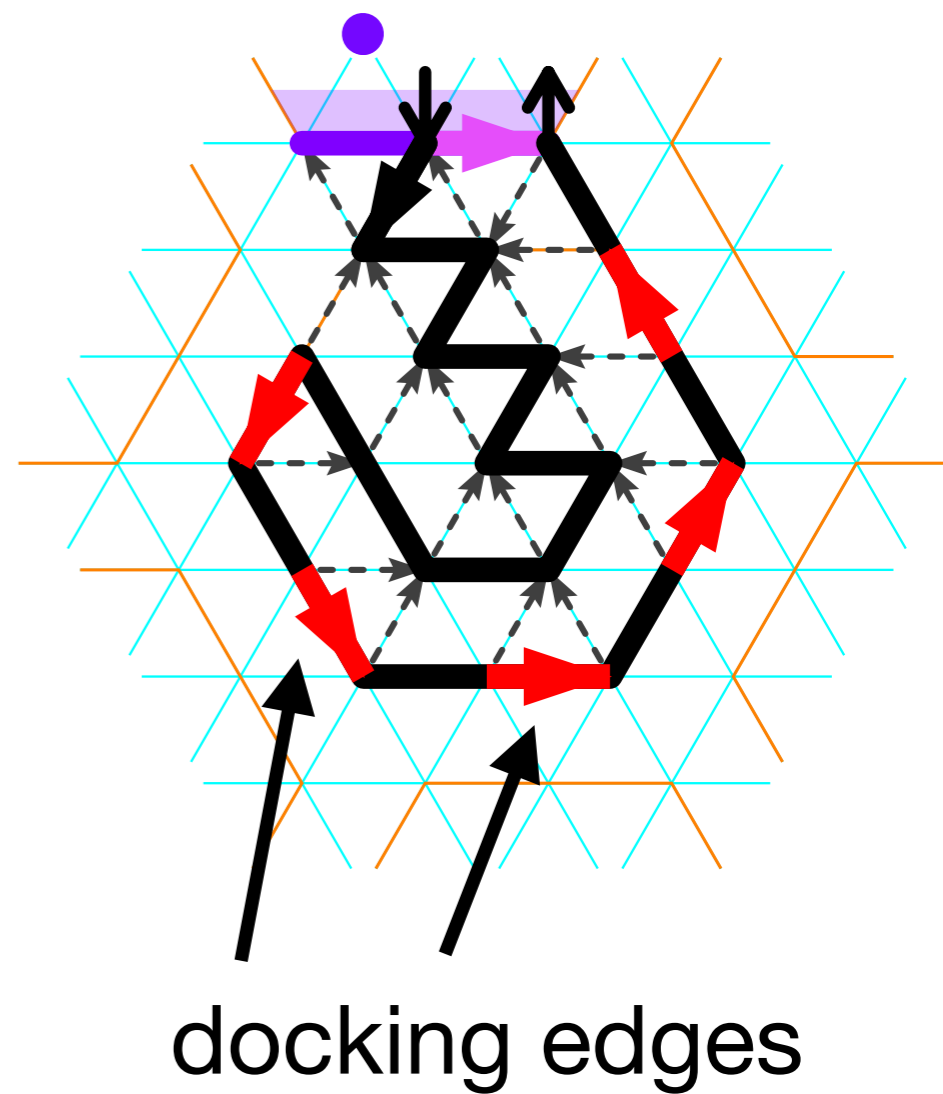
Use a unique pattern



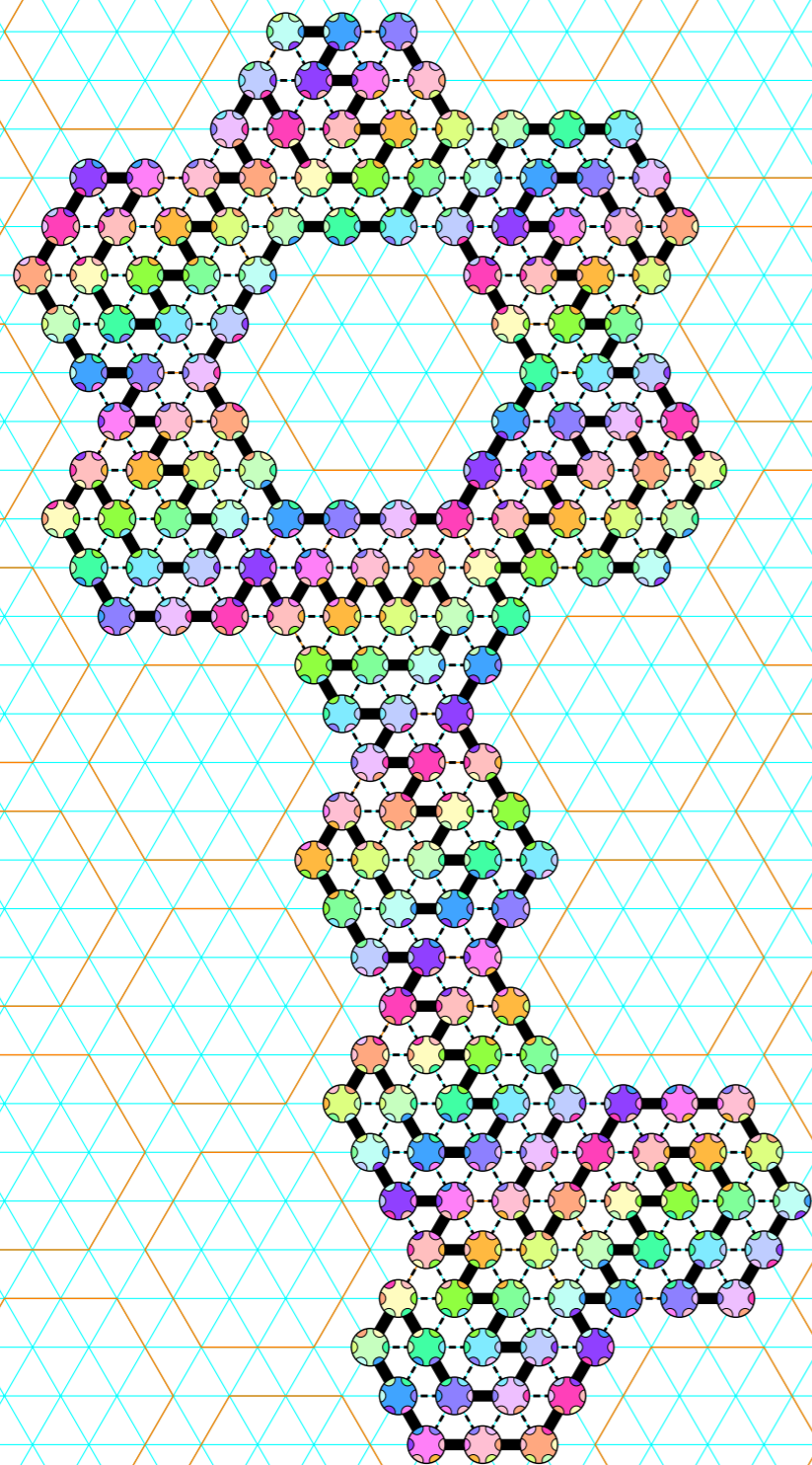
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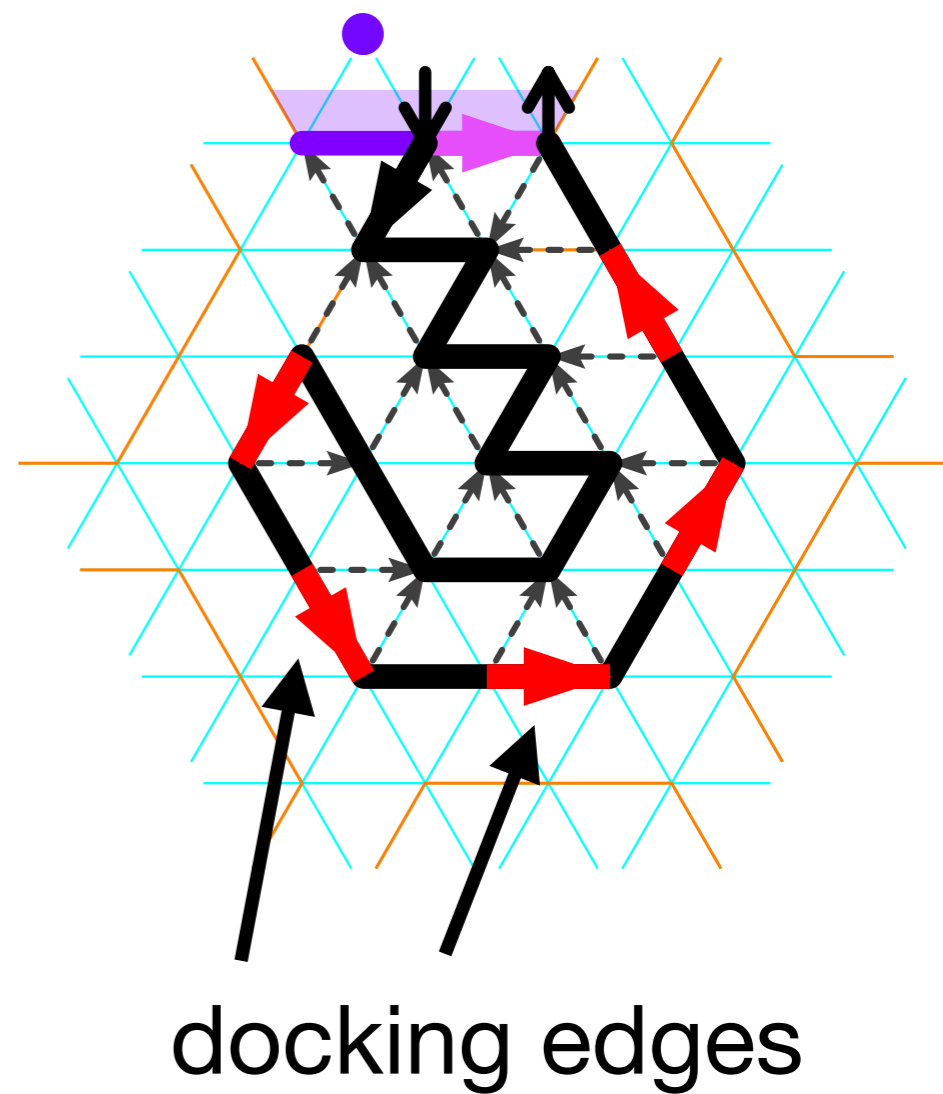
Use a unique pattern



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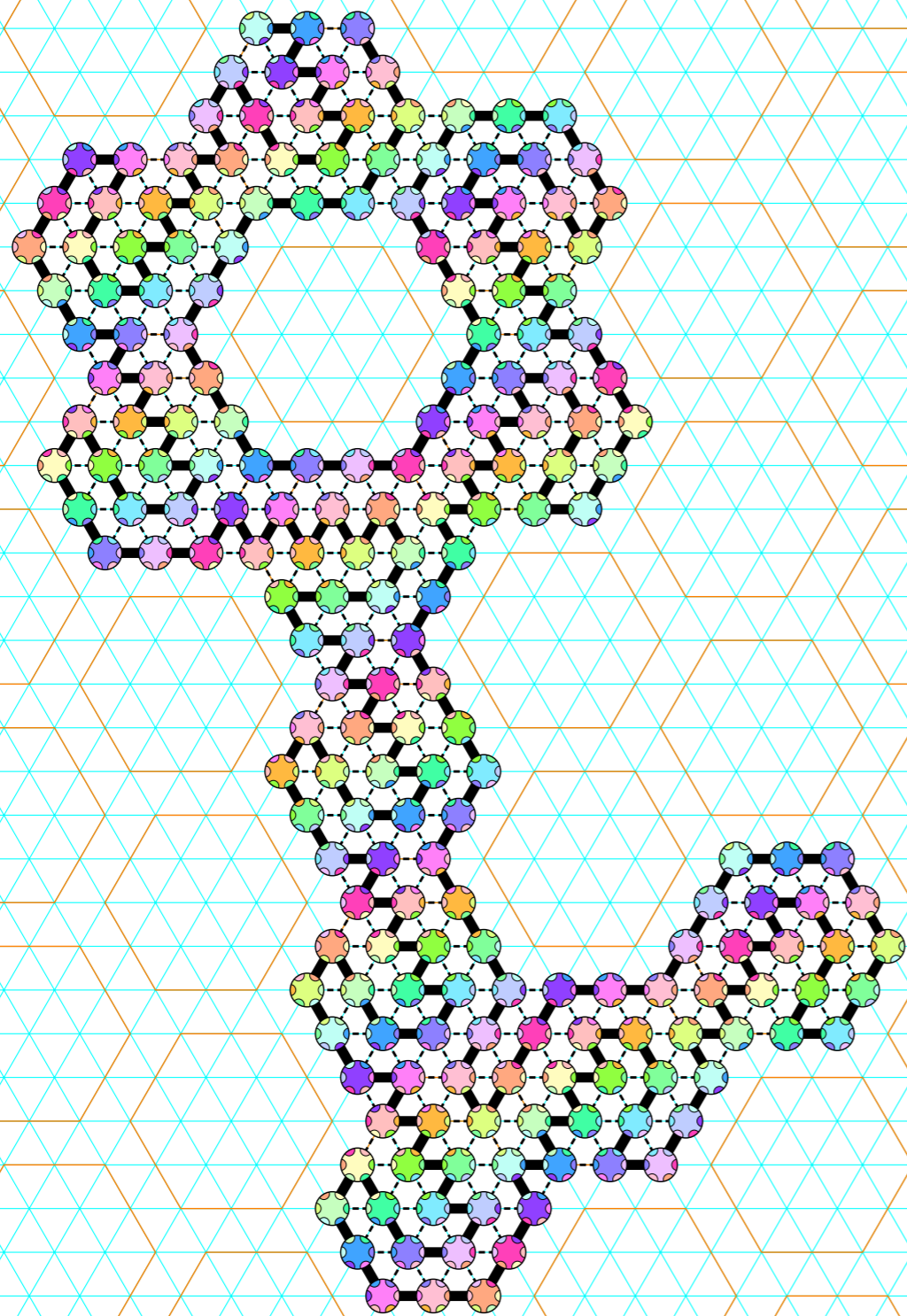


Use a unique pattern





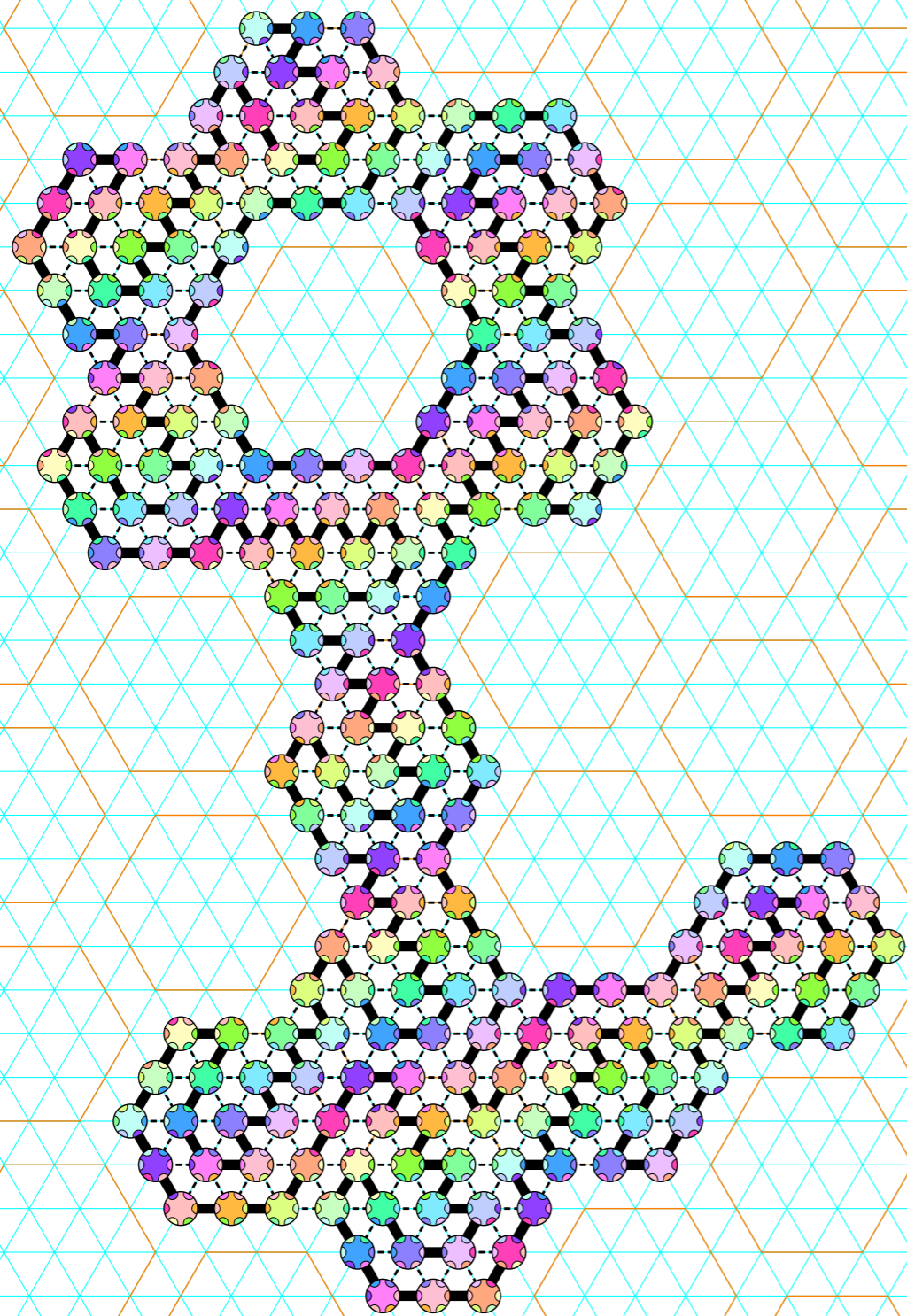
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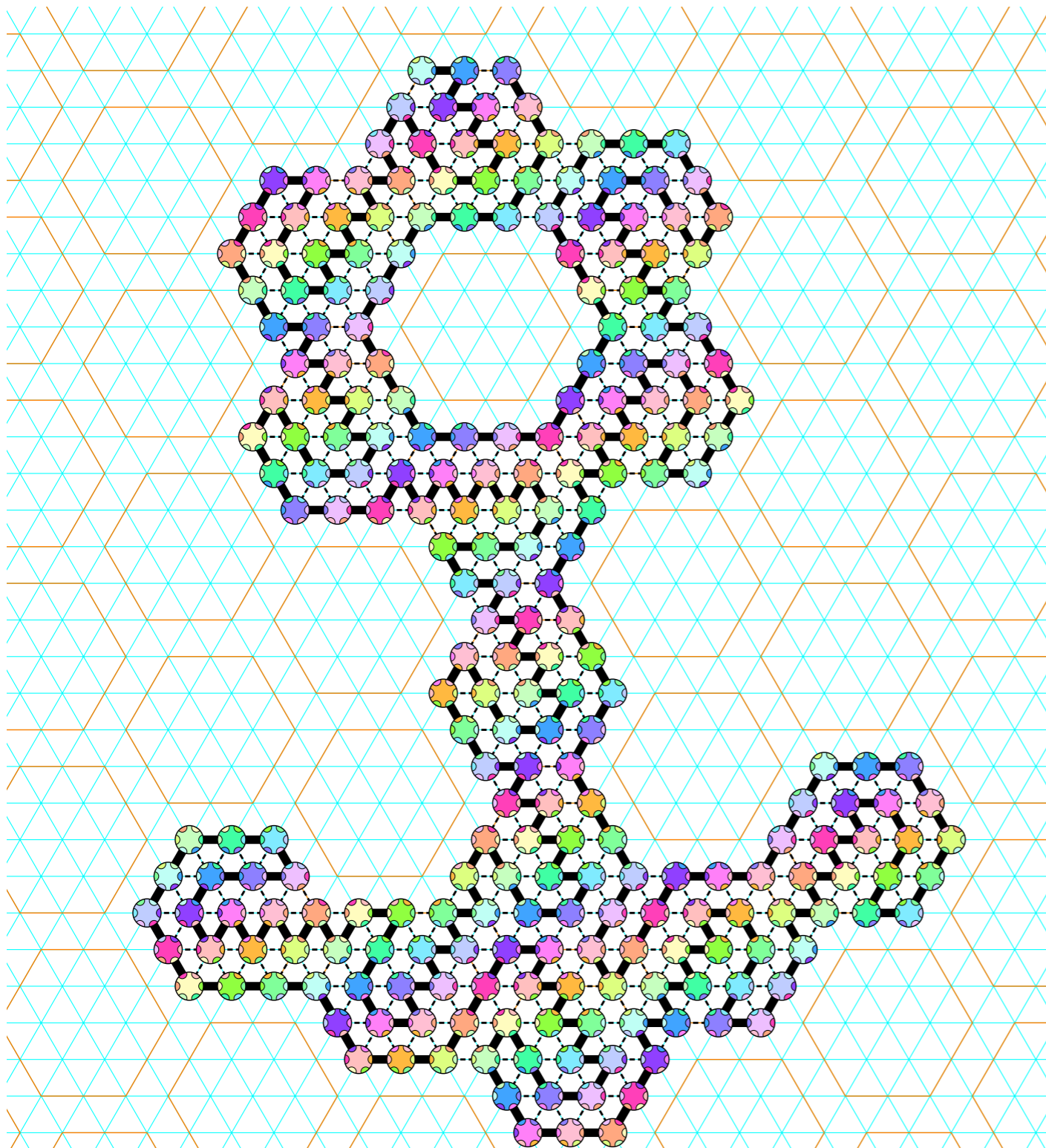
scale  $\mathcal{B}_n$



Use a unique pattern



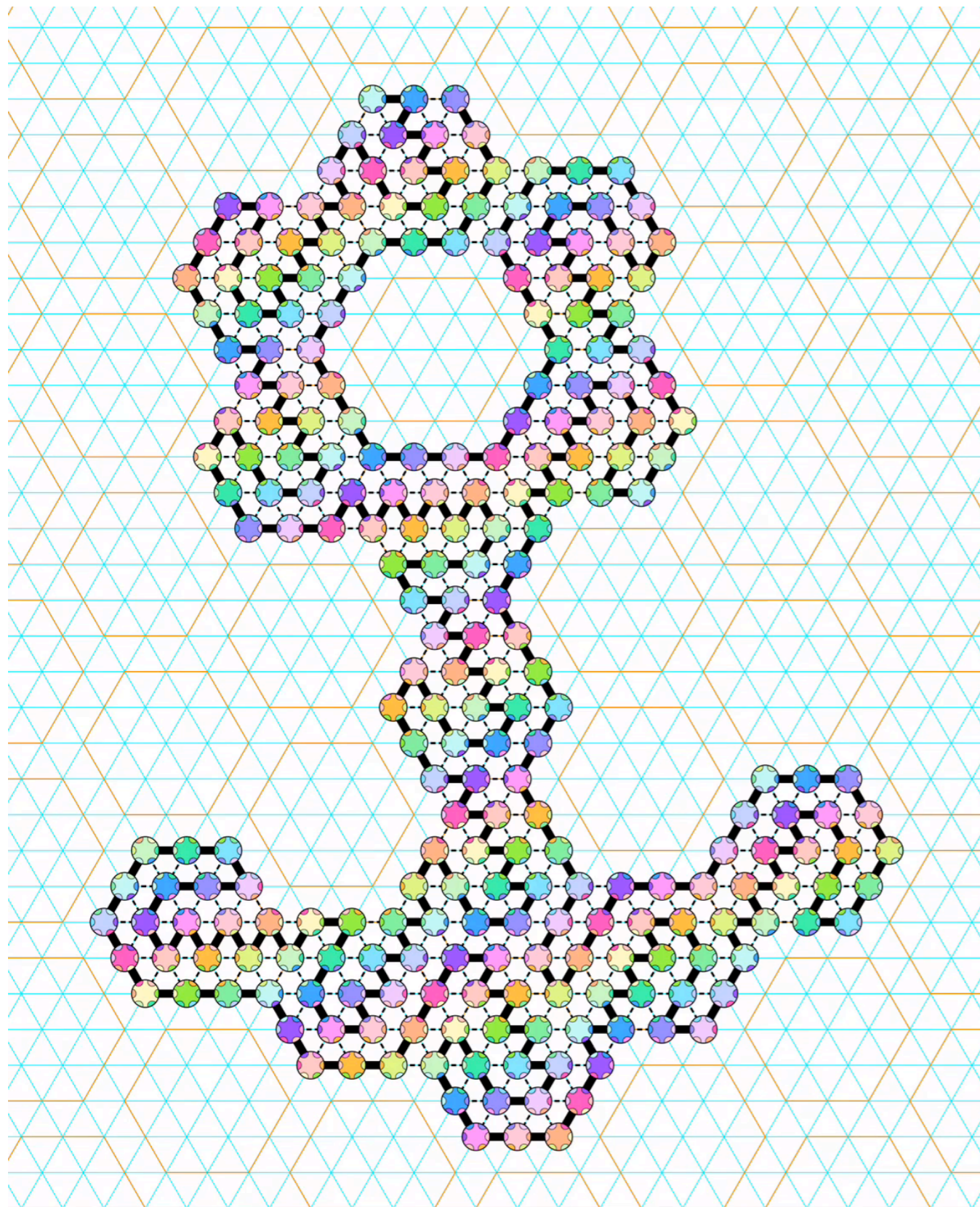
scale  $\mathcal{B}_n$



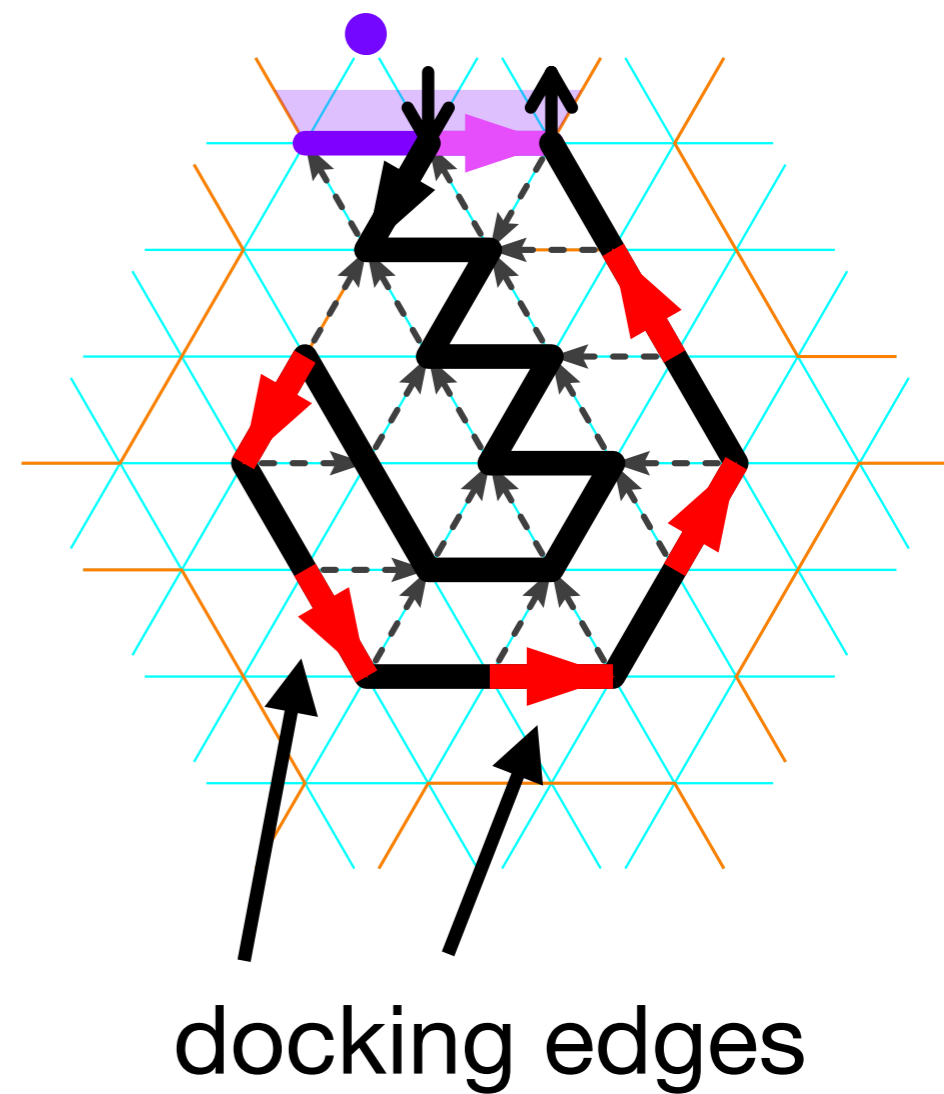
Use a unique pattern



scale  $\mathcal{B}_n$



Use a unique pattern



# scale $\mathcal{B}_n$

Use a unique pattern

**Theorem.** All finite shapes can be folded at scale  $\mathcal{B}_n$  for  $n \geq 3$

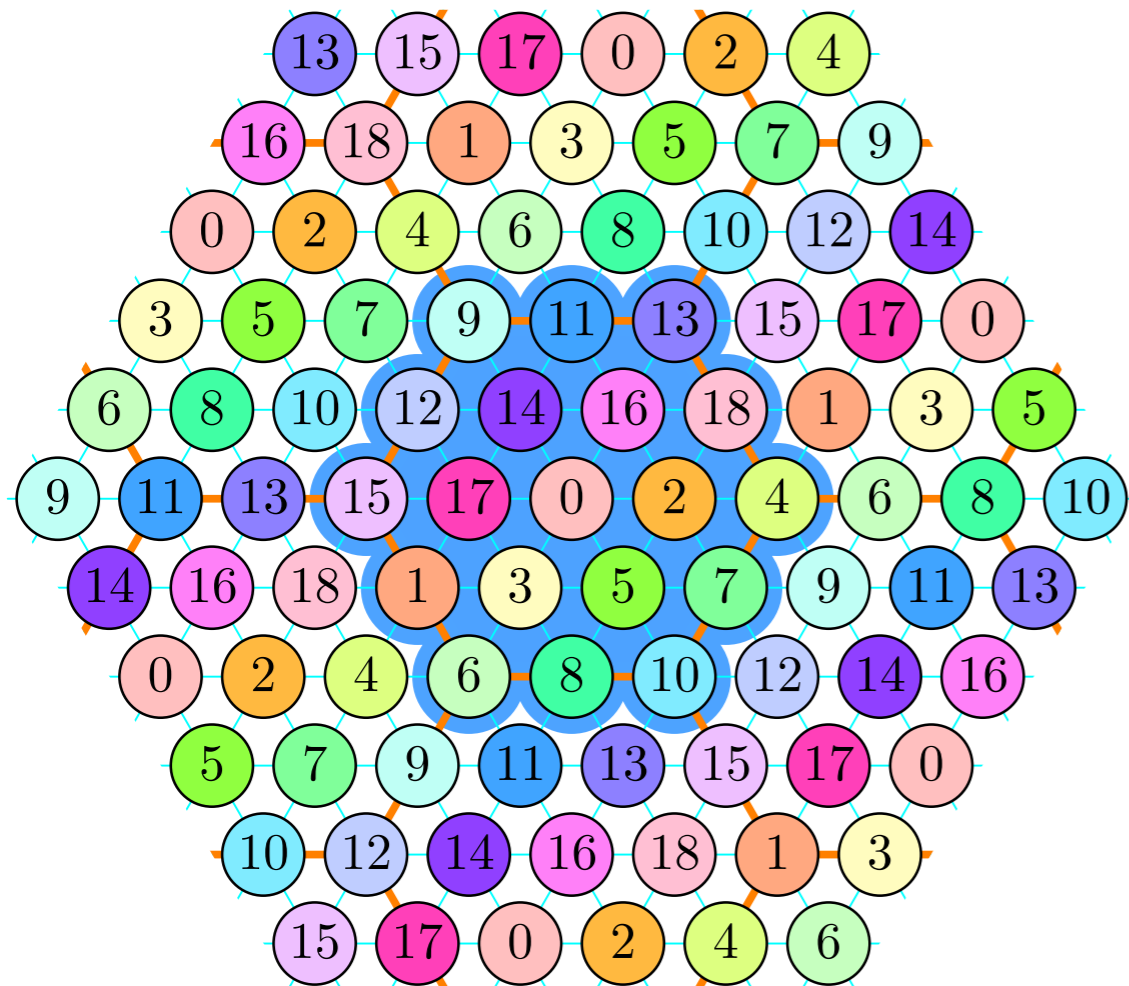
**Proof.** By induction:

For **all red edges**, the corresponding **three purple positions** are filled before.



**How many bead  
types are needed?**

# Affine coloring of hexagons



**Theorem.** Let  $H_n$  be the hexagon of radius  $n$ ,

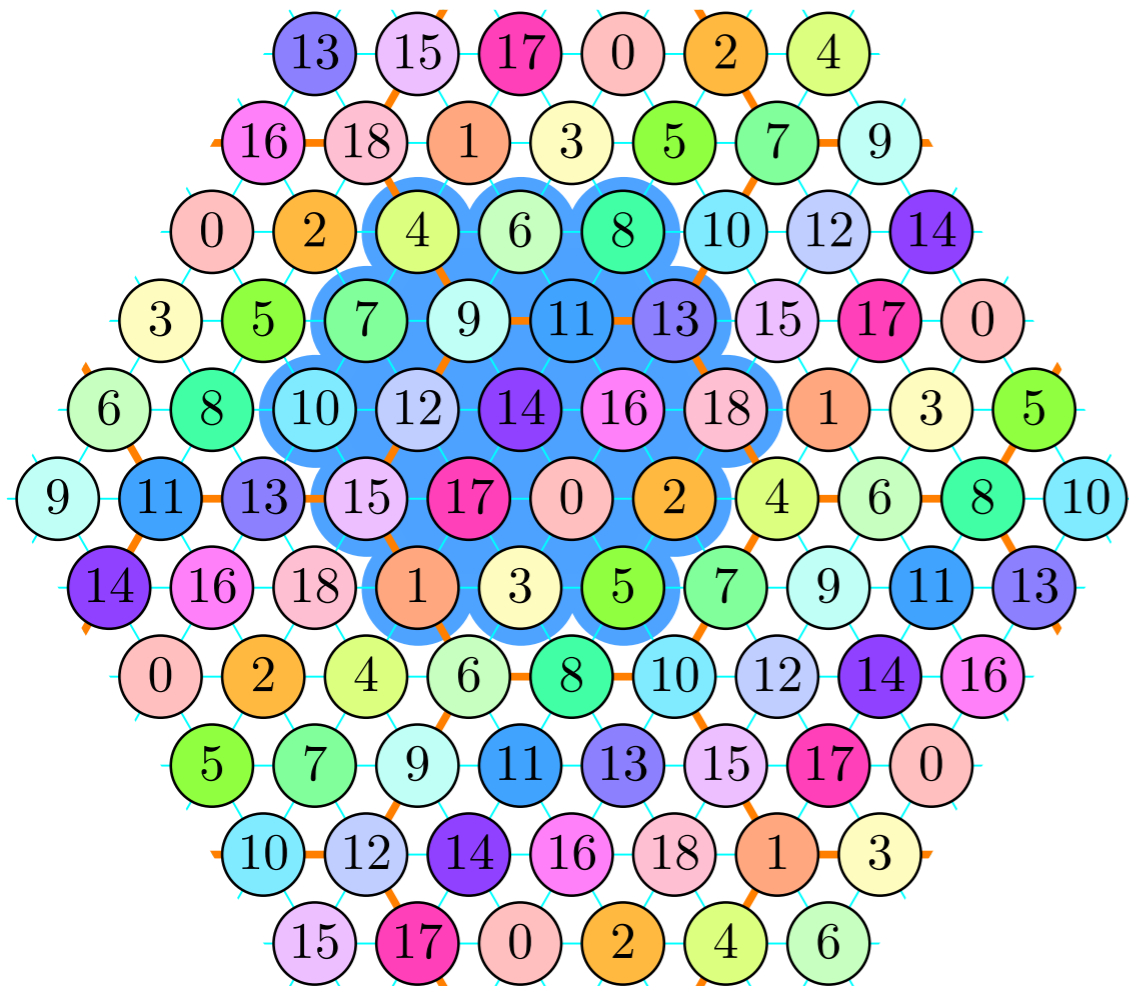
$$c(i,j) = ni + (n+1)j \pmod{|H_n|}$$

is a proper coloring of  $H_n$

**Corollary 1.** As it is affine, it is a proper coloring of *any* translation of  $H_n$

**Corollary 2.** Furthermore, the colors of the neighbors of a given node are fixed translations modulo  $|H_n|$  of its own color

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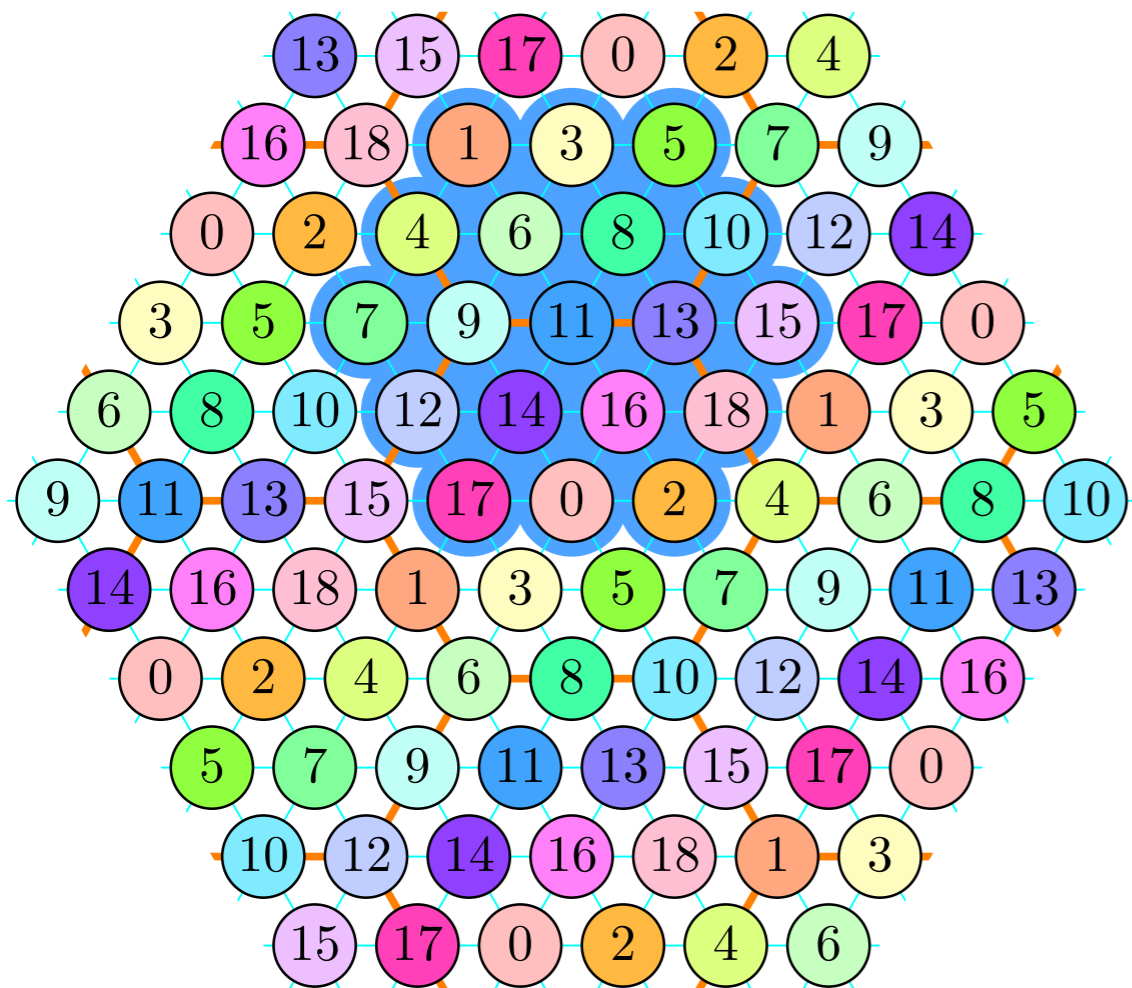
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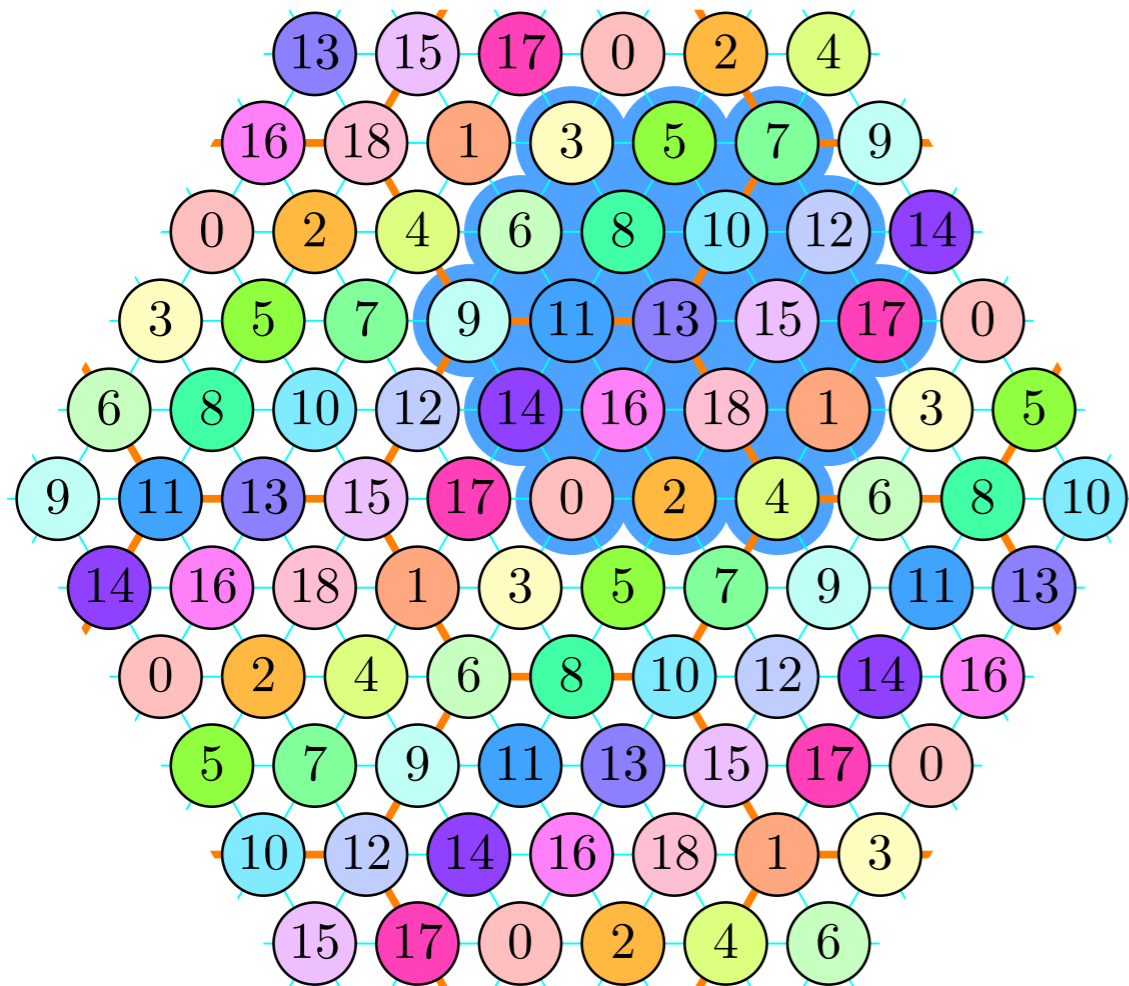
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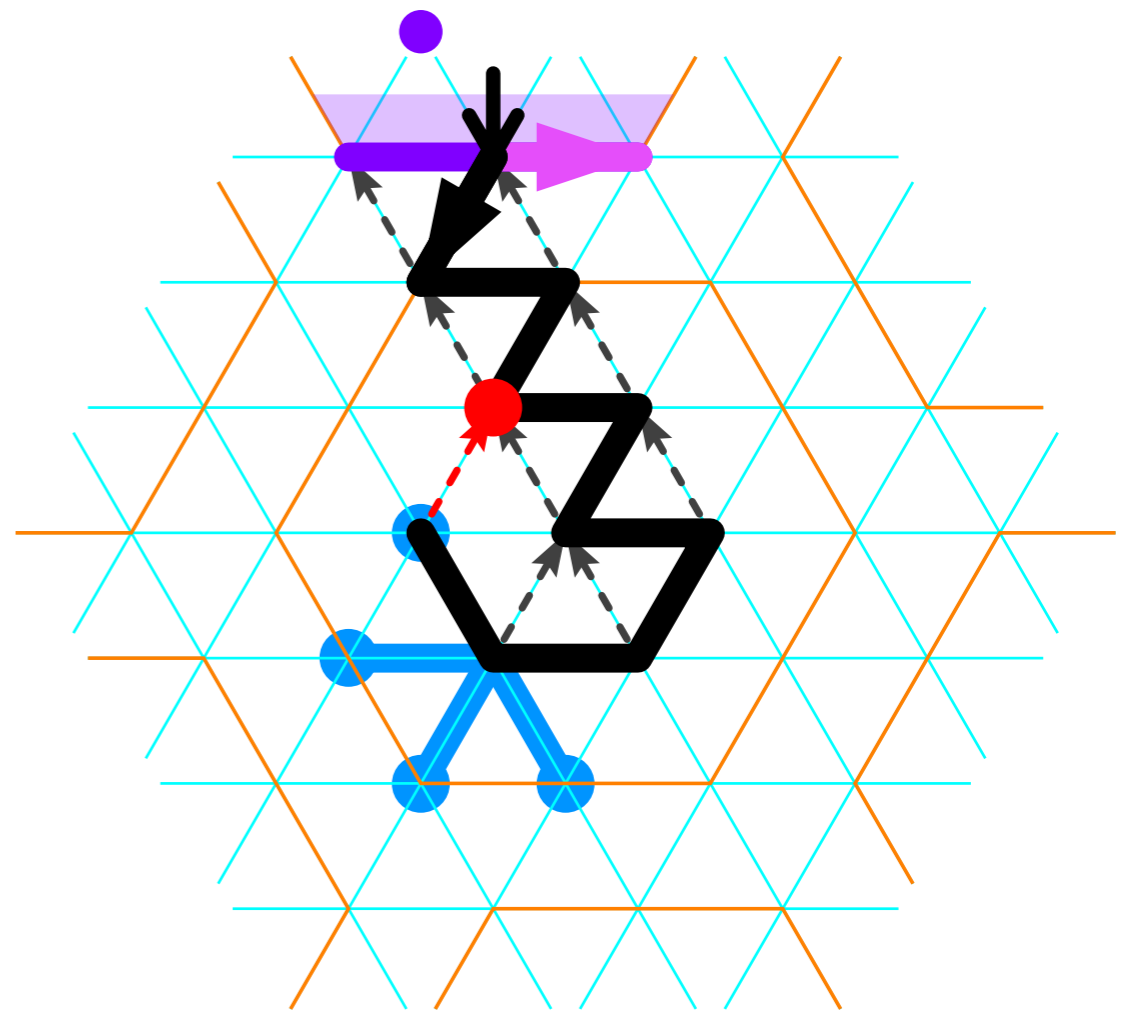
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# Tight oritatami Systems

An oritatami system is *tight* if:

- delay  $\delta = 1$
- every bead destination has a **tight neighbor**, i.e. such that there is only **one available position** next to it

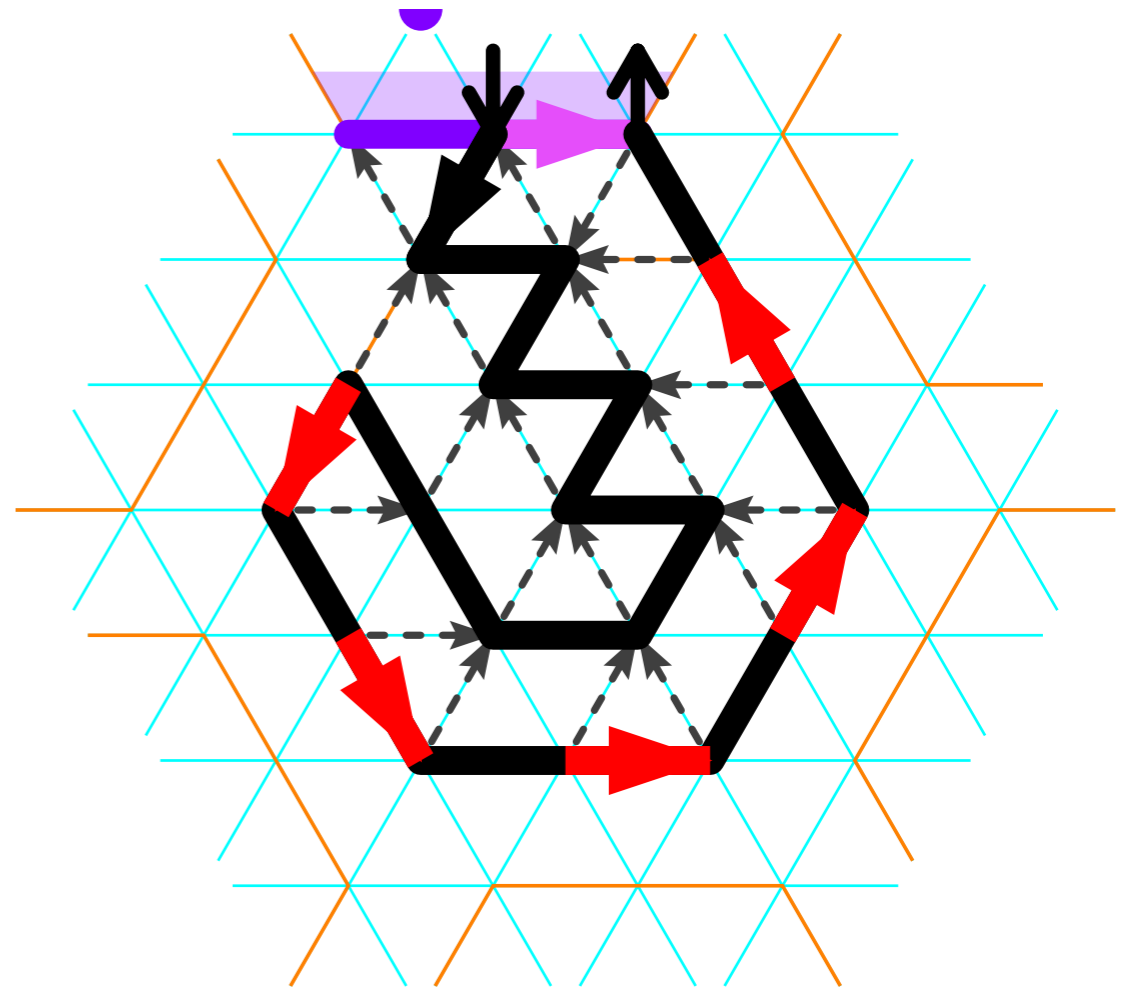


*For tight oritatami system, each bead's position is uniquely determined by whom it is attracted to*

# Tight oritatami Systems

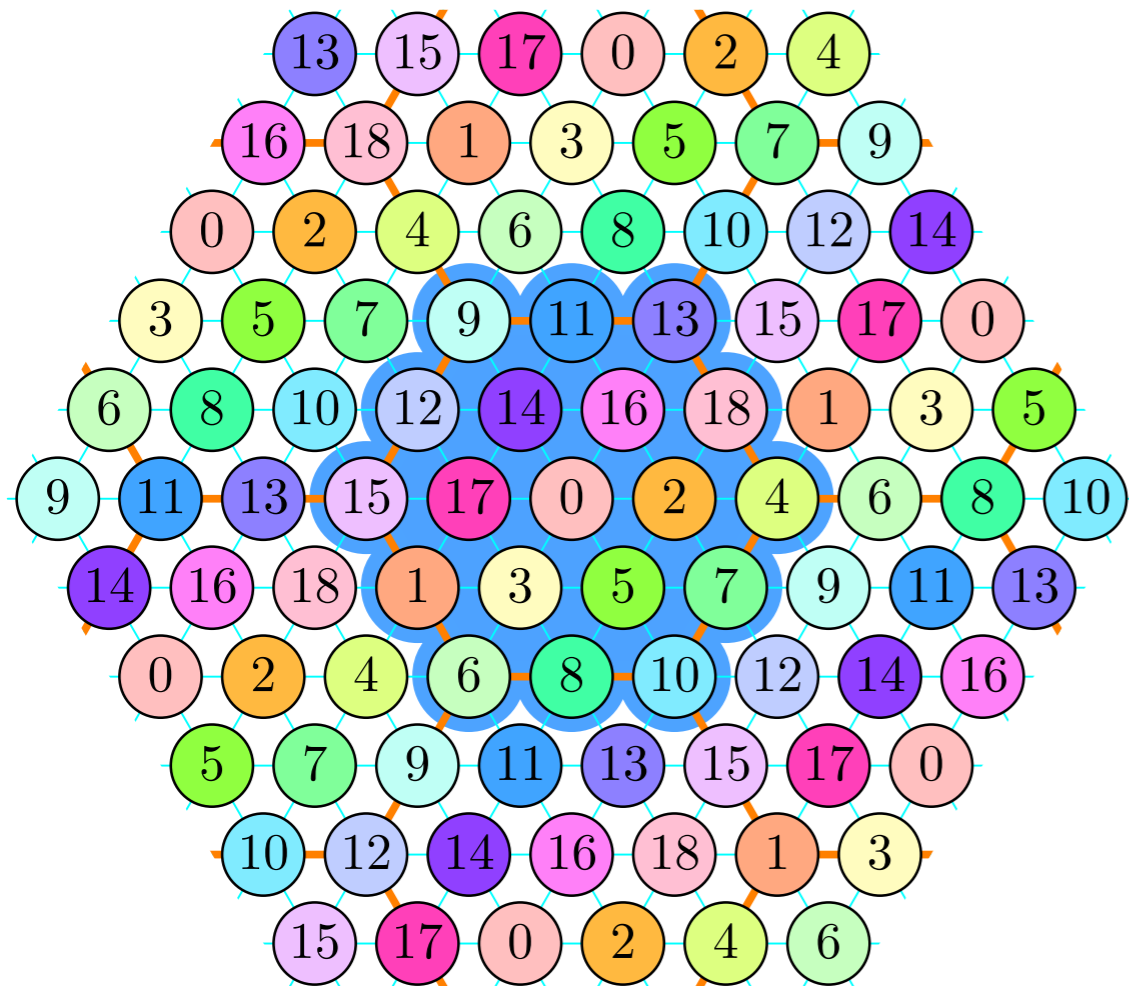
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# 19 bead types are enough for tight oritatami systems



Each bead located at  $(i, j)$  receives bead type:

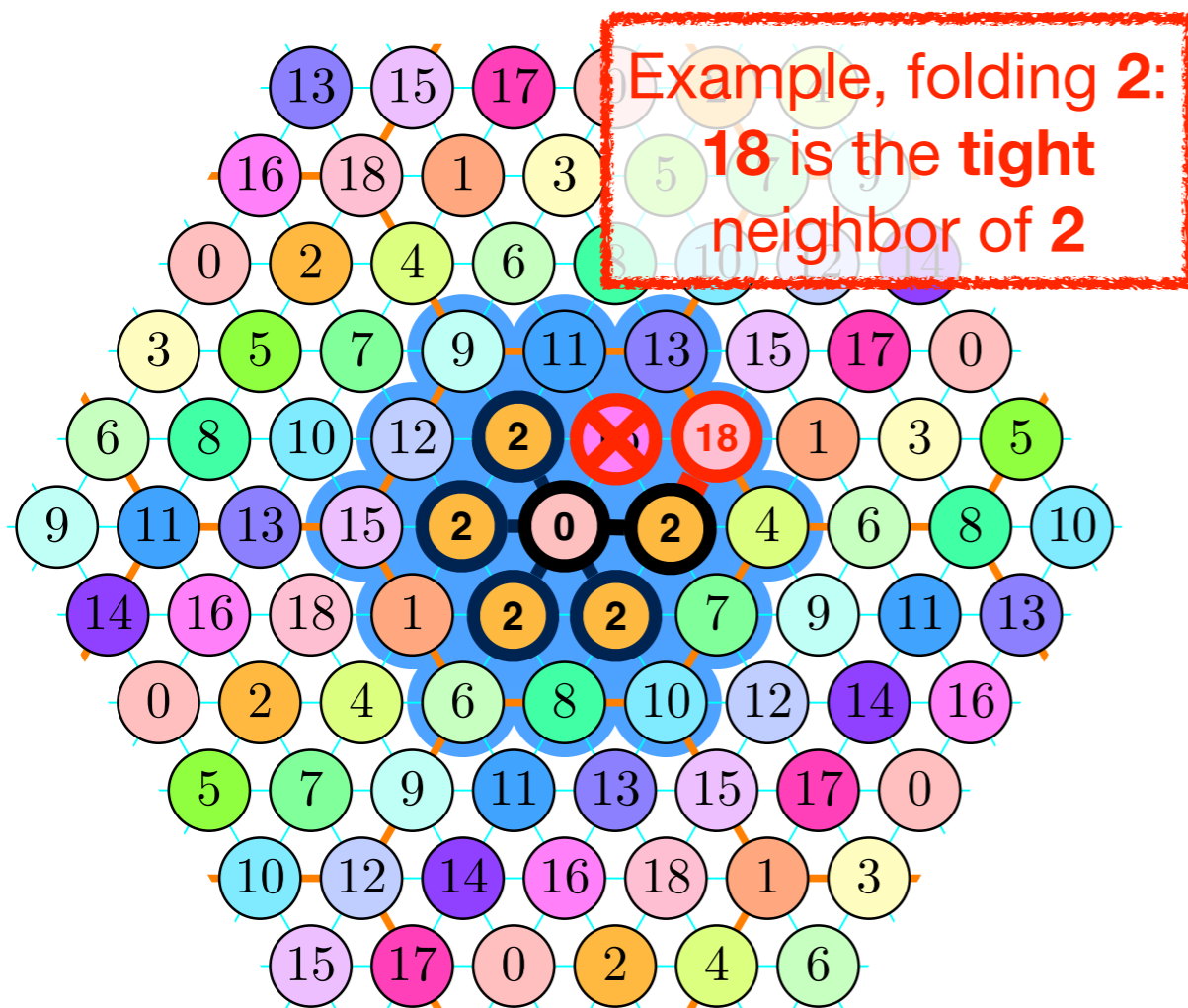
$$c(i, j)$$

and  $c \heartsuit c'$  iff

$$c' = c + \Delta c(d) \pmod{19}$$

***For tight oritatami system, each bead's position is fully determined by whom it is attracted to***

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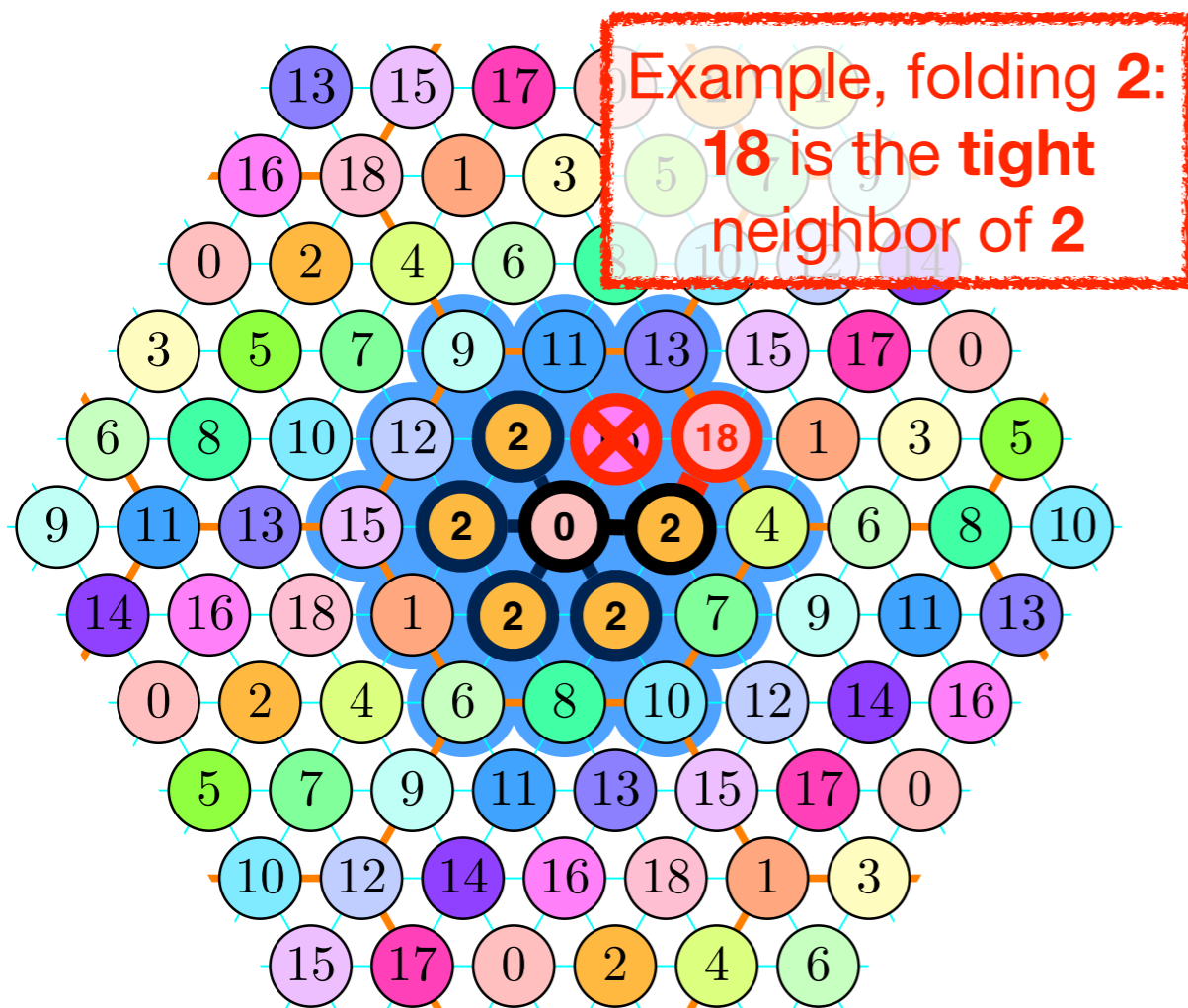
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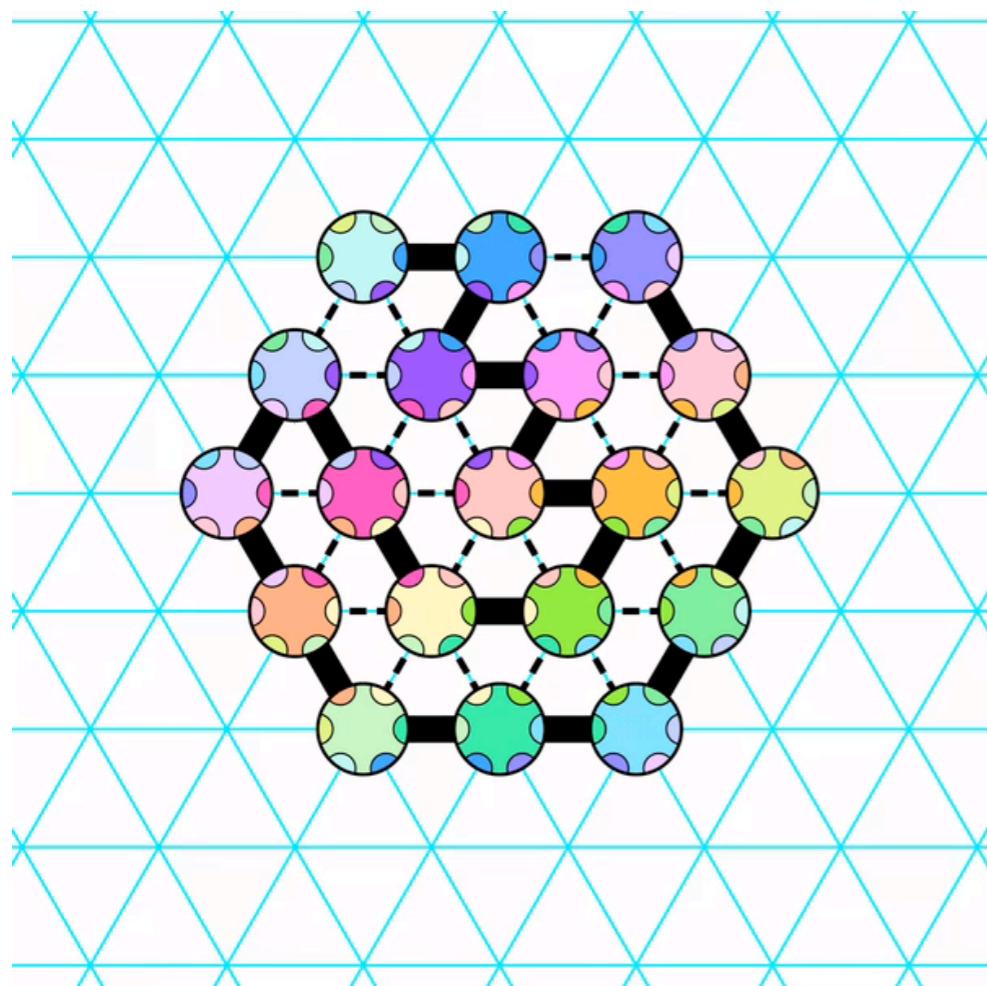
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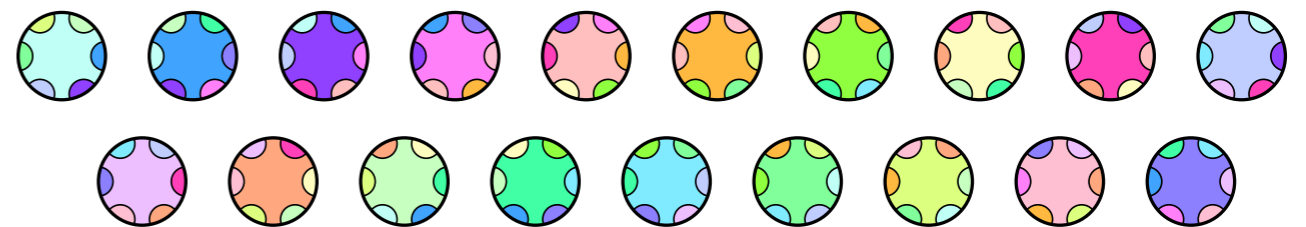


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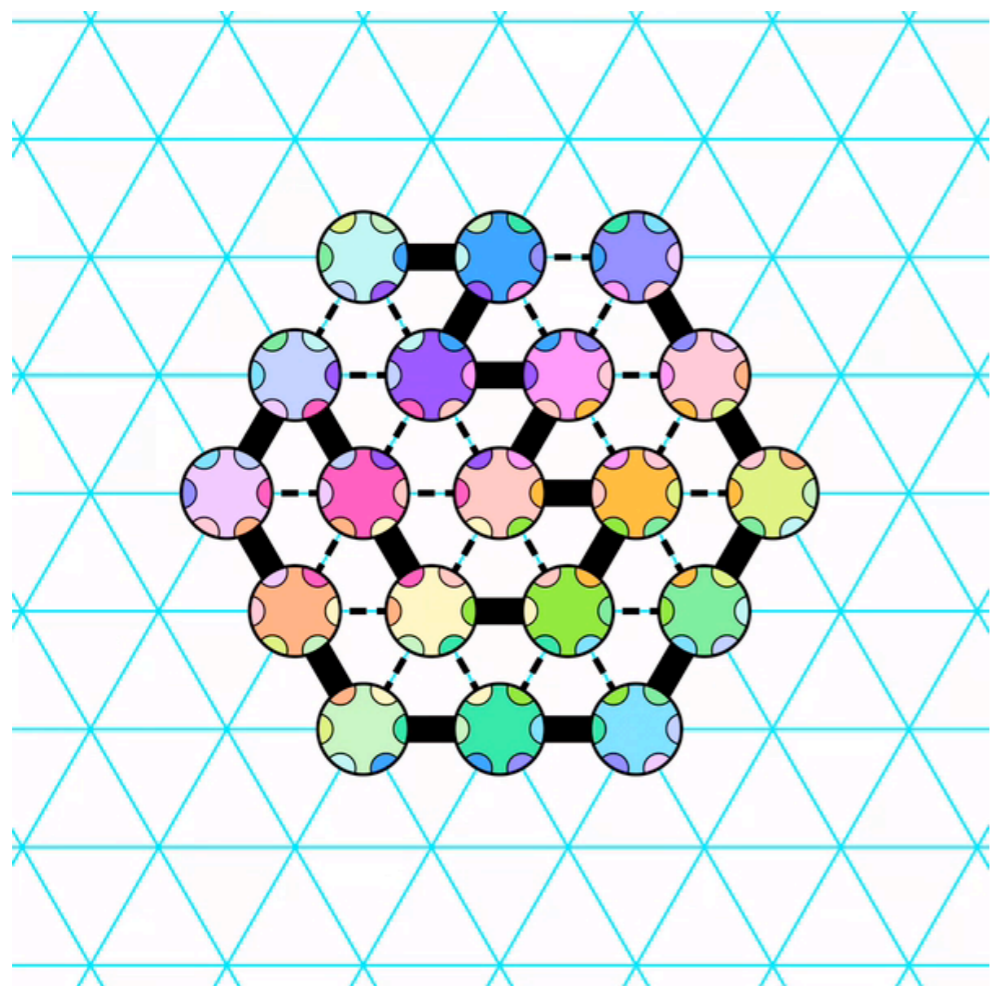
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# 19 bead types are enough for tight oritatami systems

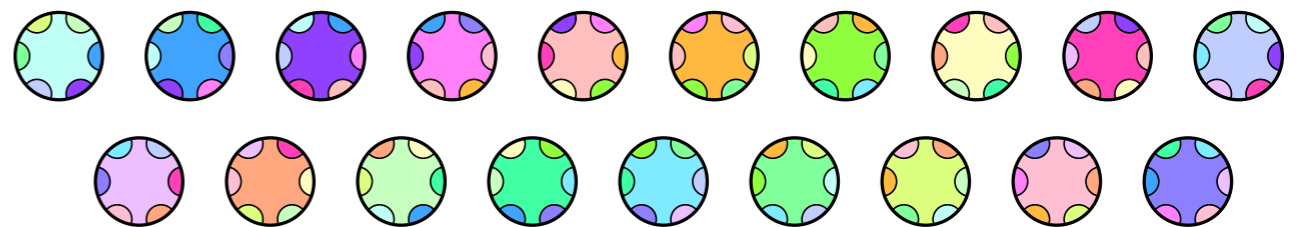


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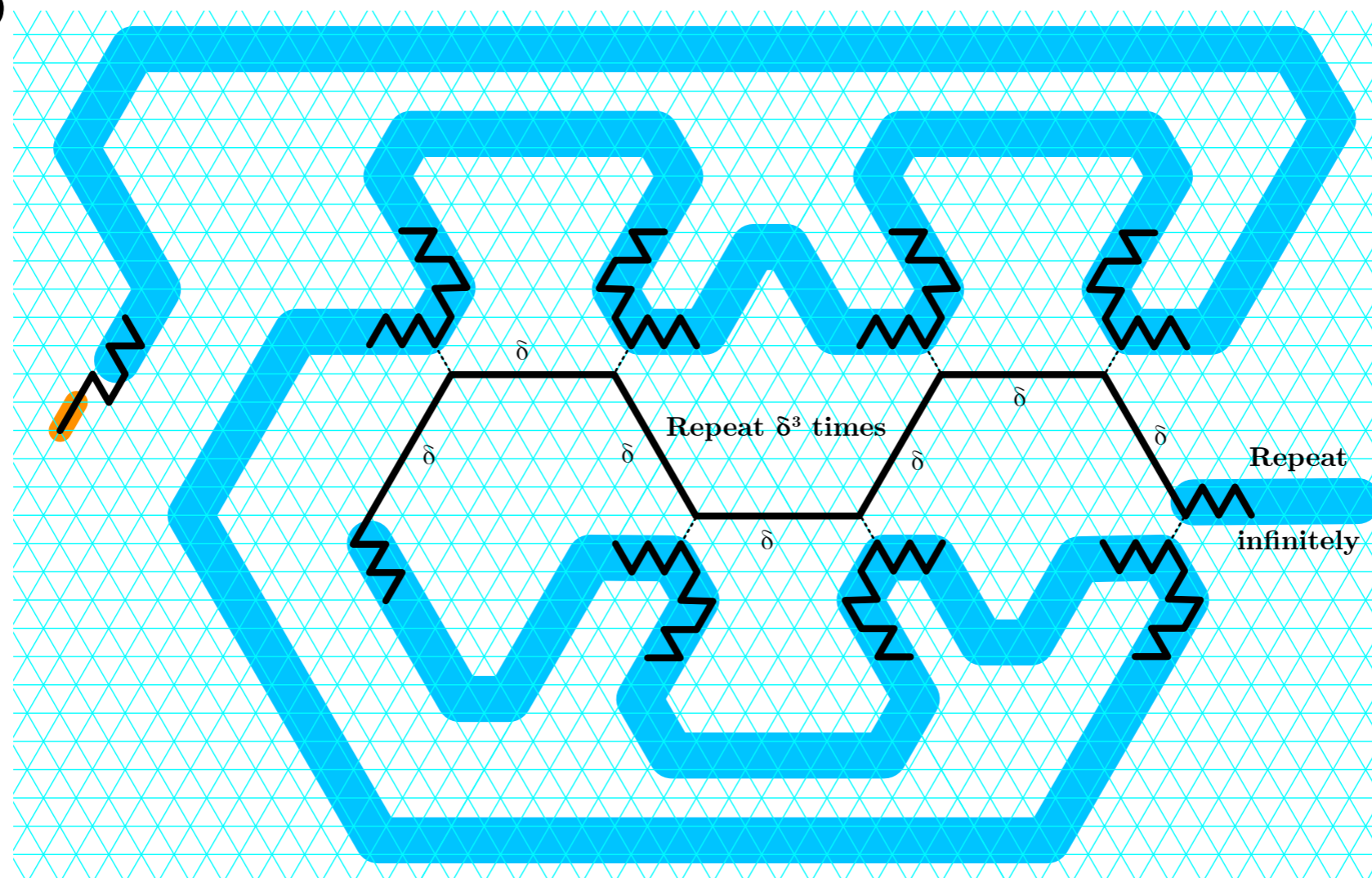
$$c' = c + \Delta c(d) \pmod{19}$$



**Theorem.** There is a **constant-time incremental** algorithm that outputs a tight oritatami system using **19 bead types** that folds any finite shape at scale  $\mathcal{B}_n \geq 3$  from a **seed of size 3**

# Would increasing the delay instead of upscaling help?

**Theorem.** For any delay  $\delta$ , there is an infinite shape that cannot be folded by no oritatami system with delay  $\delta$



# **Turedo: building nanobots with oritatomami**

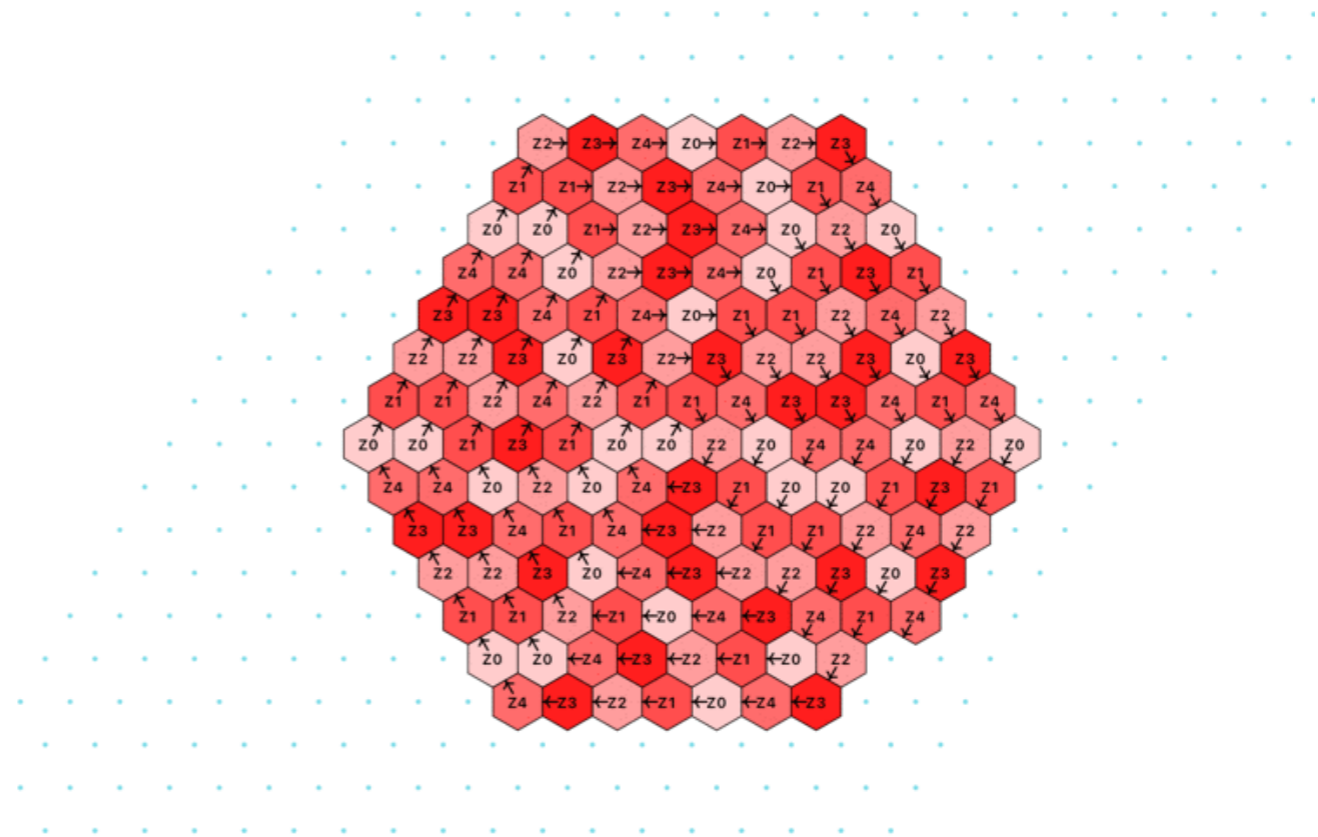
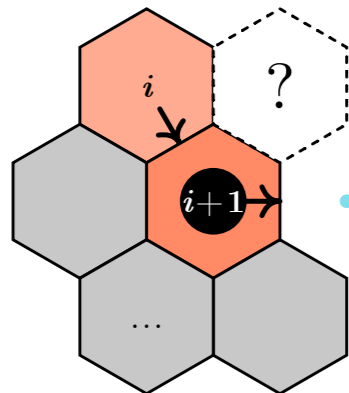
[Pchelina, S., Seki and Theyssier, *STACS* 2022]

# Turedos

A finite automata follows a **self-avoiding path**, moving and **writing** a state according to a **uniform local rule**

**A clockwise walker**

The rule:

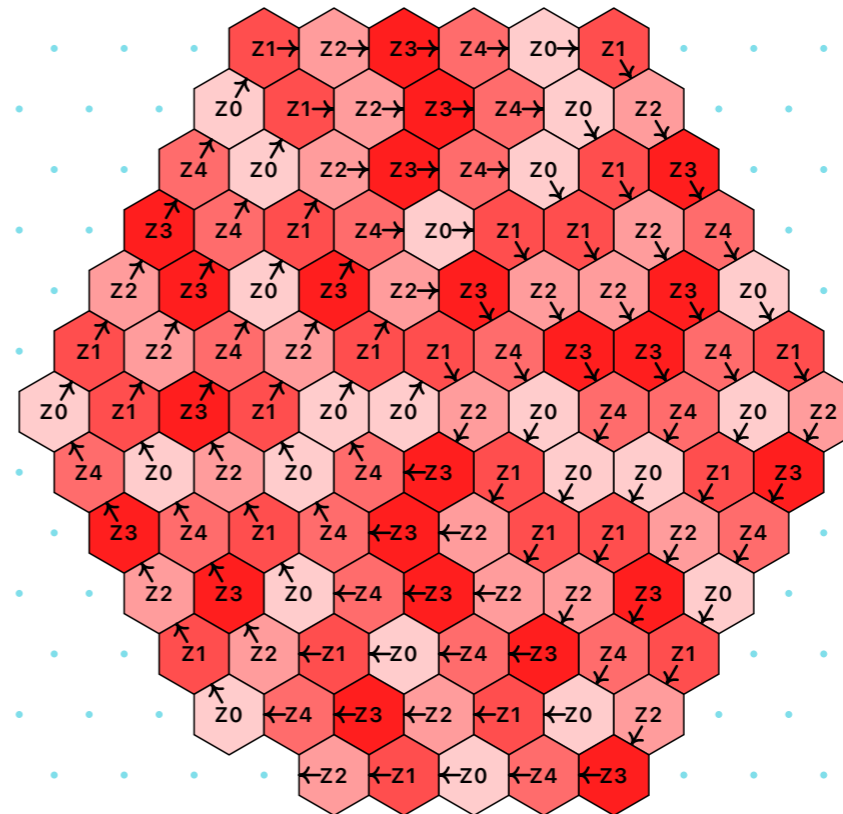
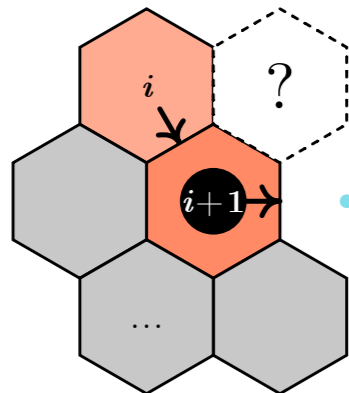


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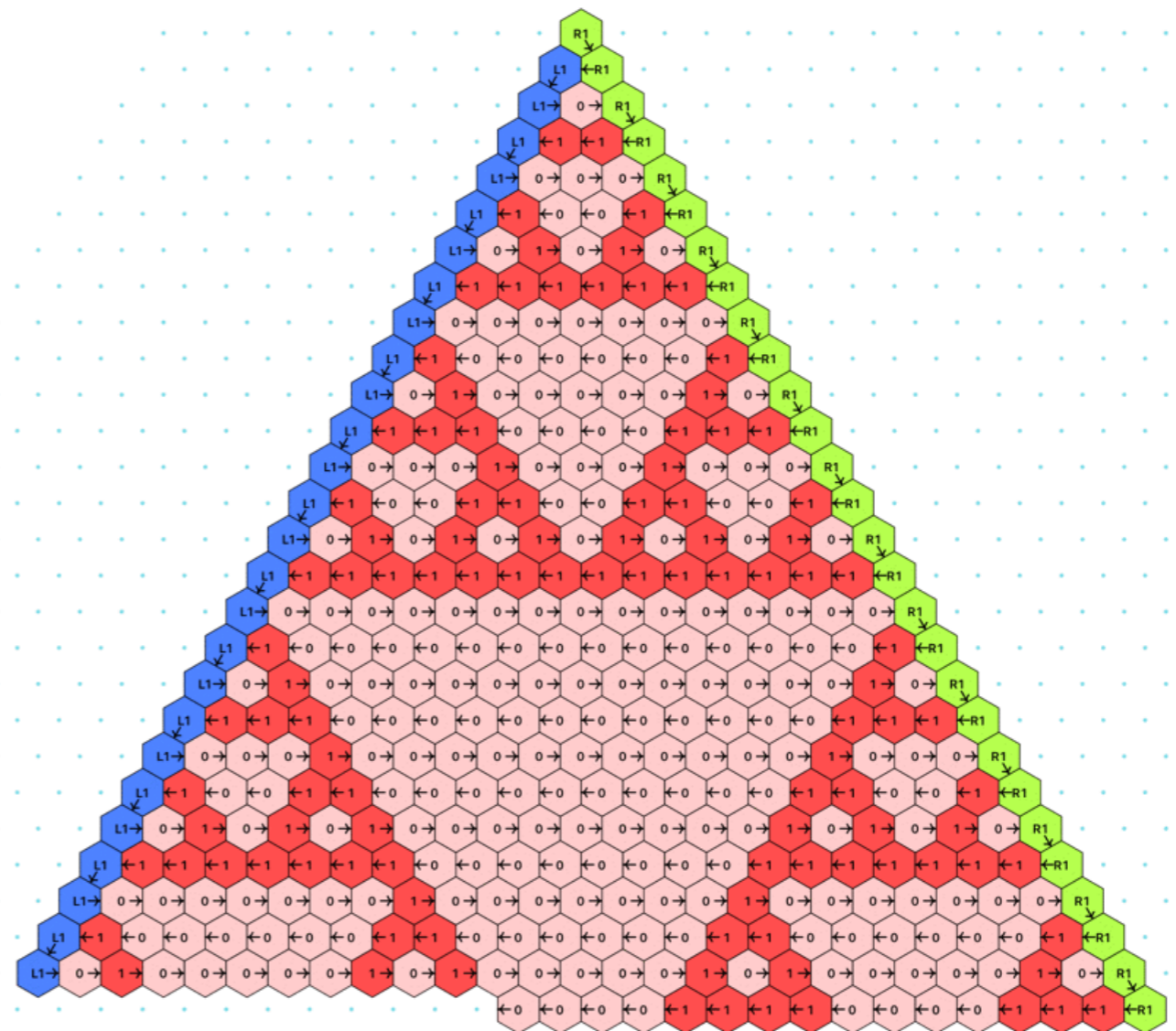
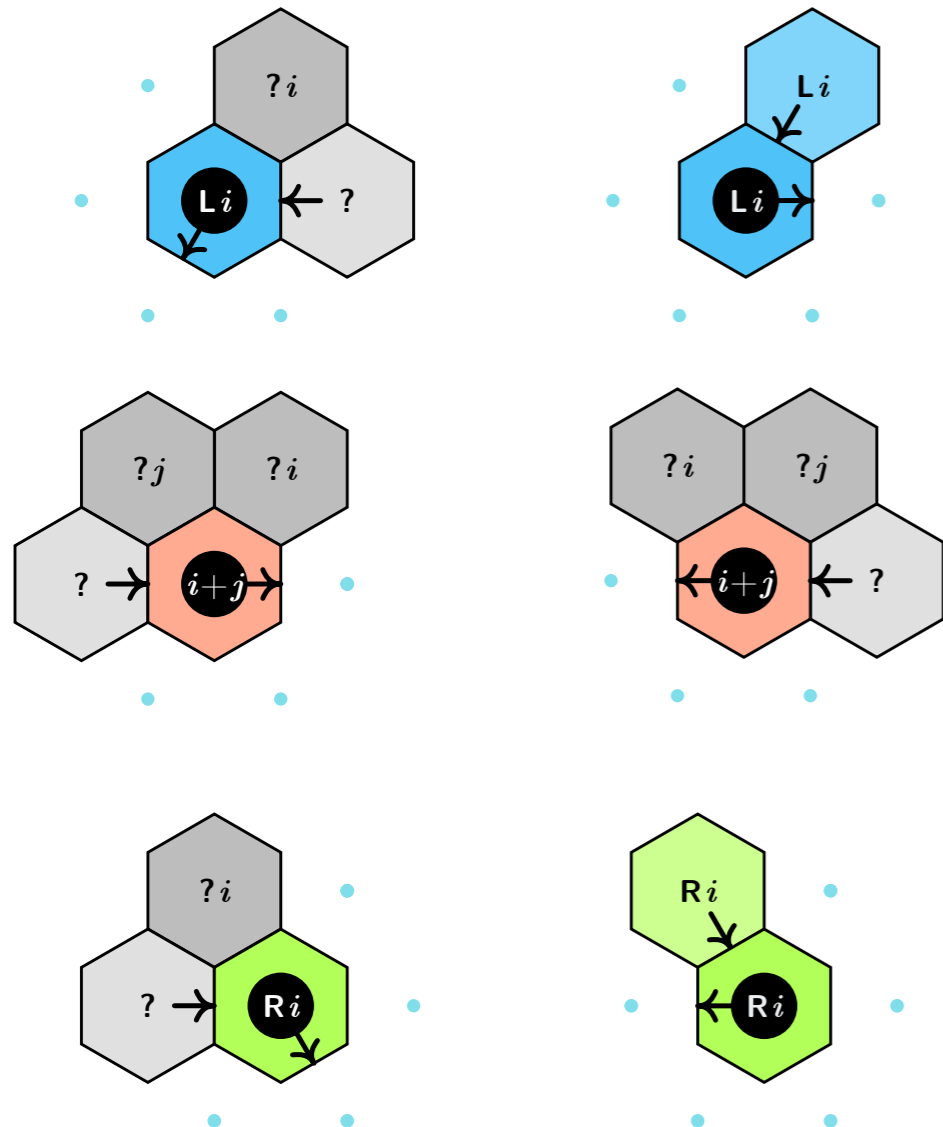


# Radius-1 Turedos

## implement cellular automata

### Left/Right Swiping

The rule:

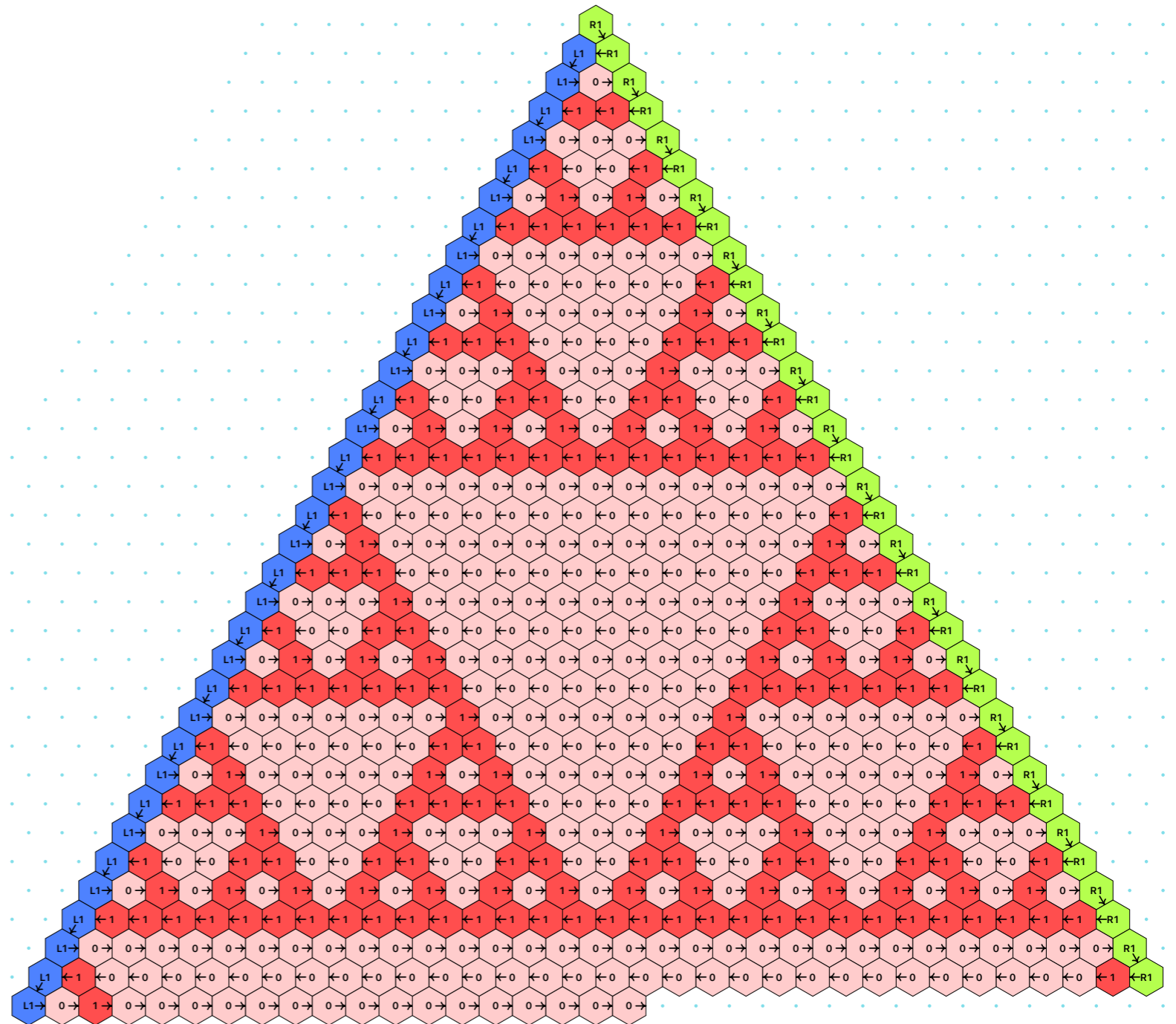
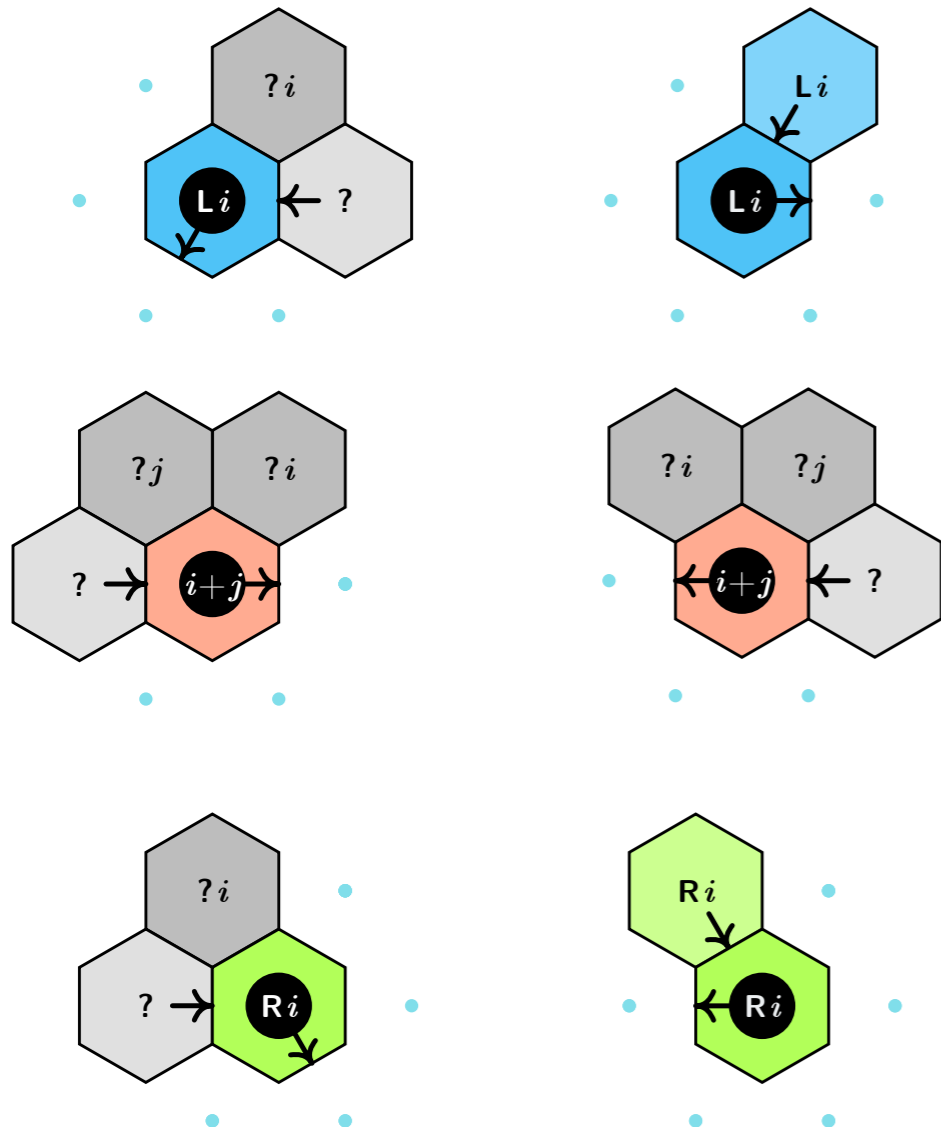


# Radius-1 Turedos

## implement cellular automata

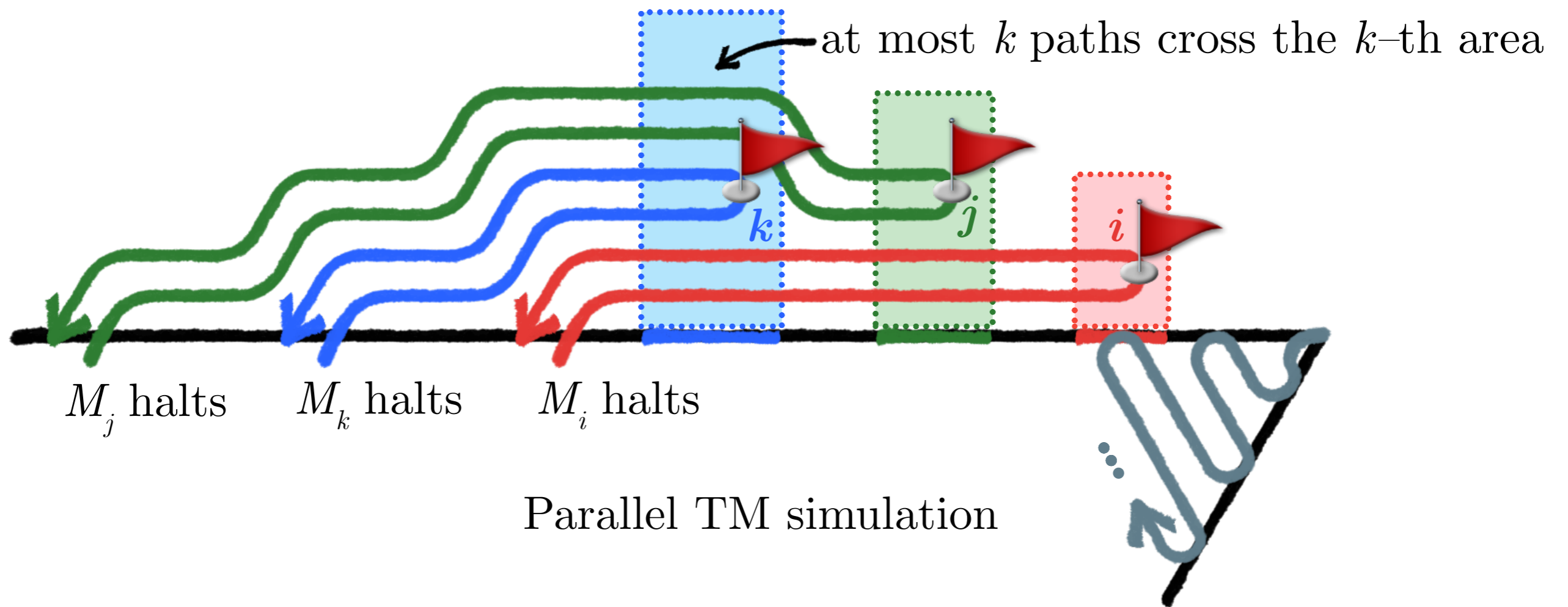
### Left/Right Swiping

The rule:



# Theorem 1.

## Radius-1 turedos doodle uncomputably



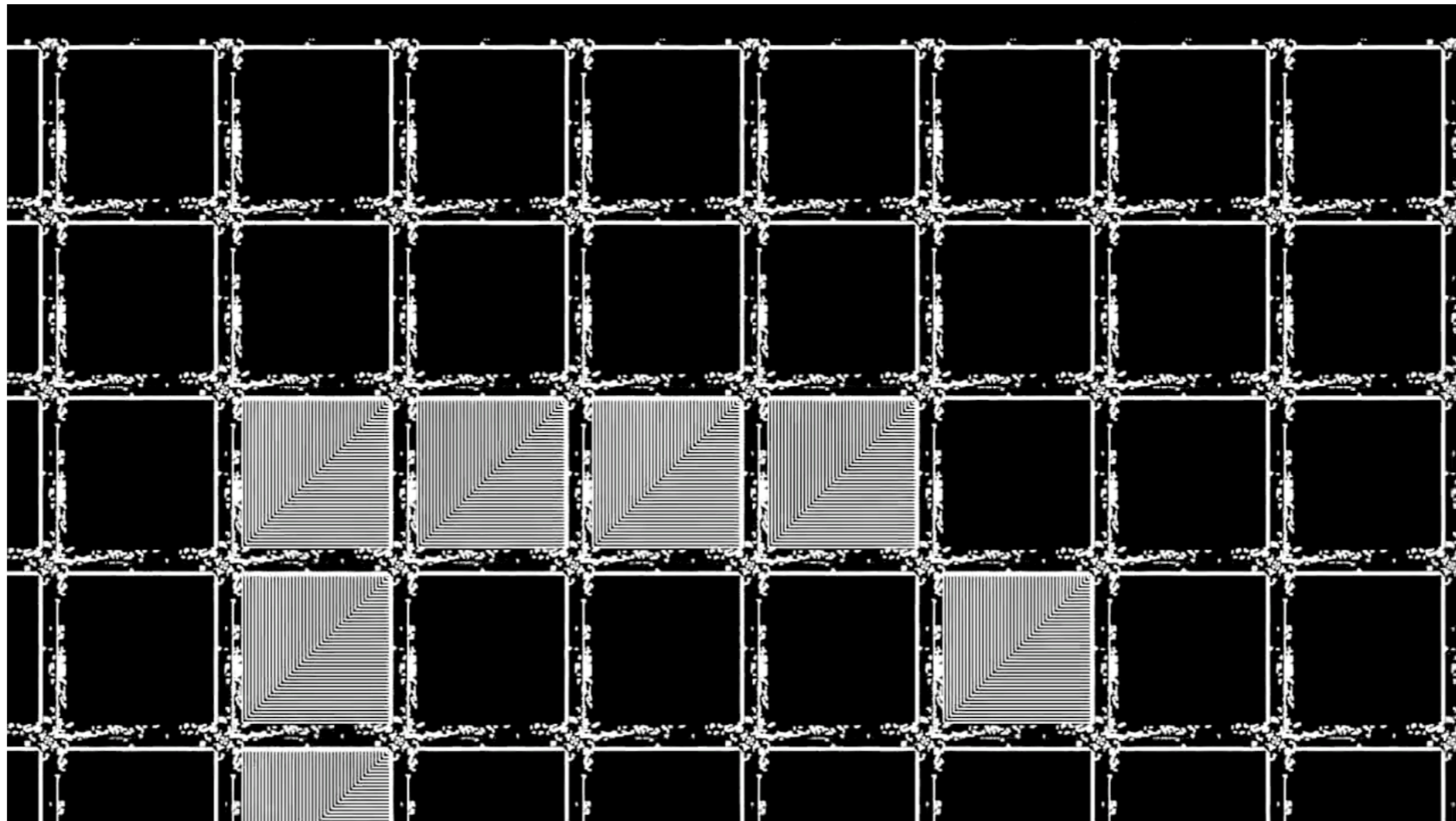




**Delay-3 Oritatami systems simulate  
radius-1 Turedos intrinsically**

# Intrinsic simulation

- Linear time & scape rescaling

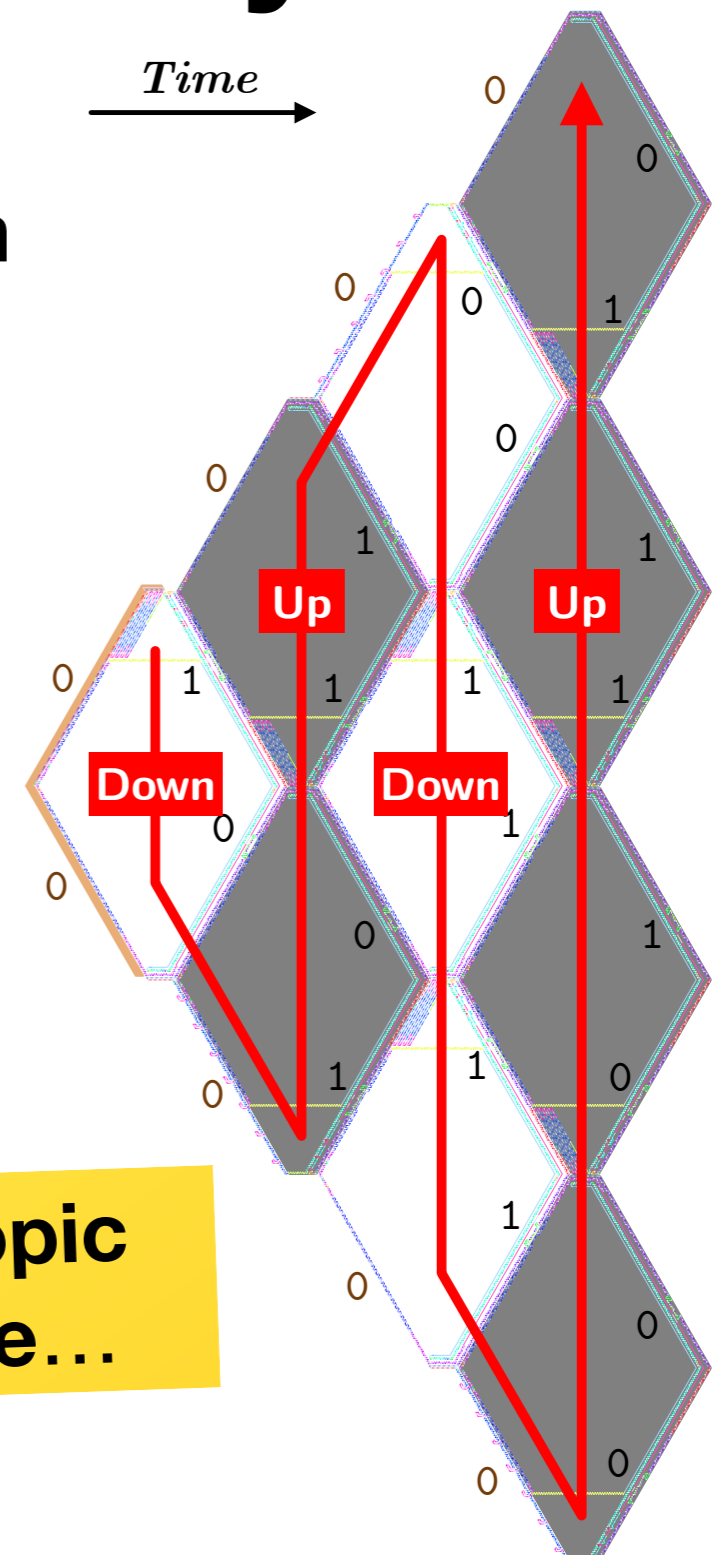
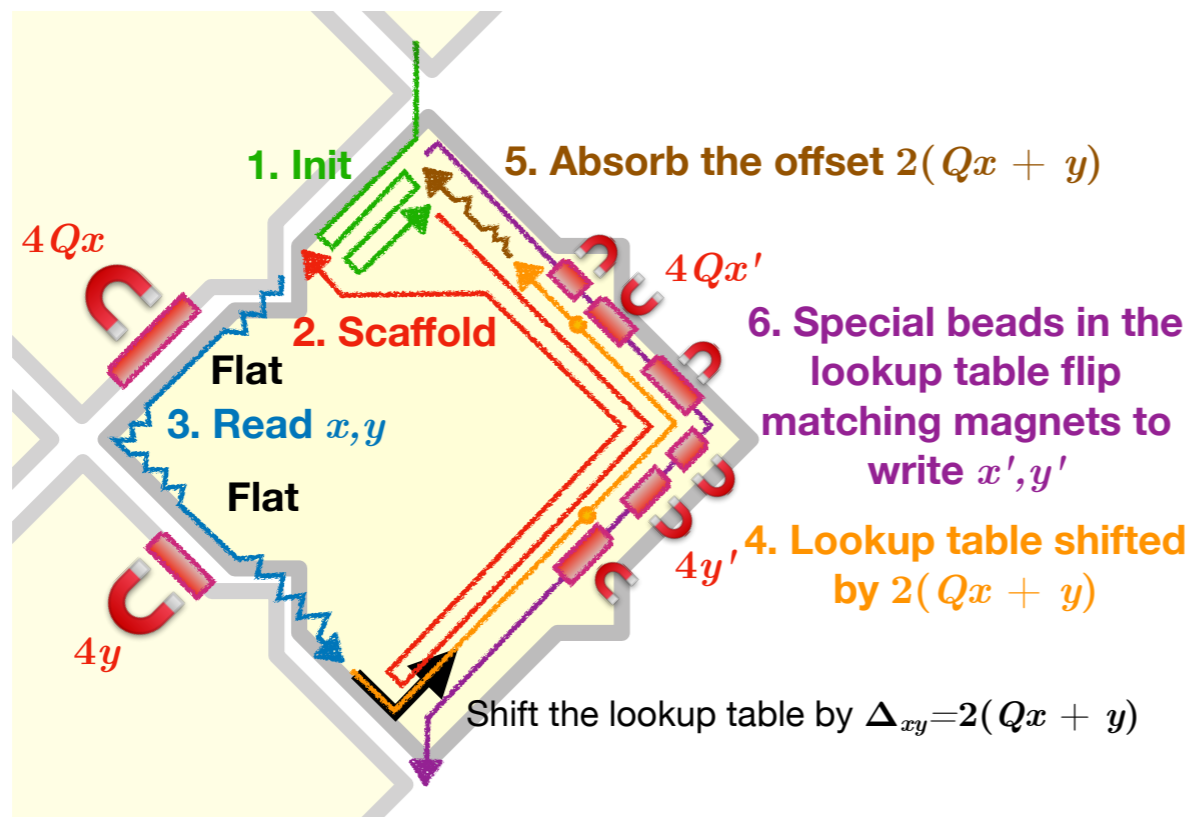


*Brice Due 2006*

The Game of Life self-simulating itself intrinsically:  
*Smaller cells simulate macro-cells*

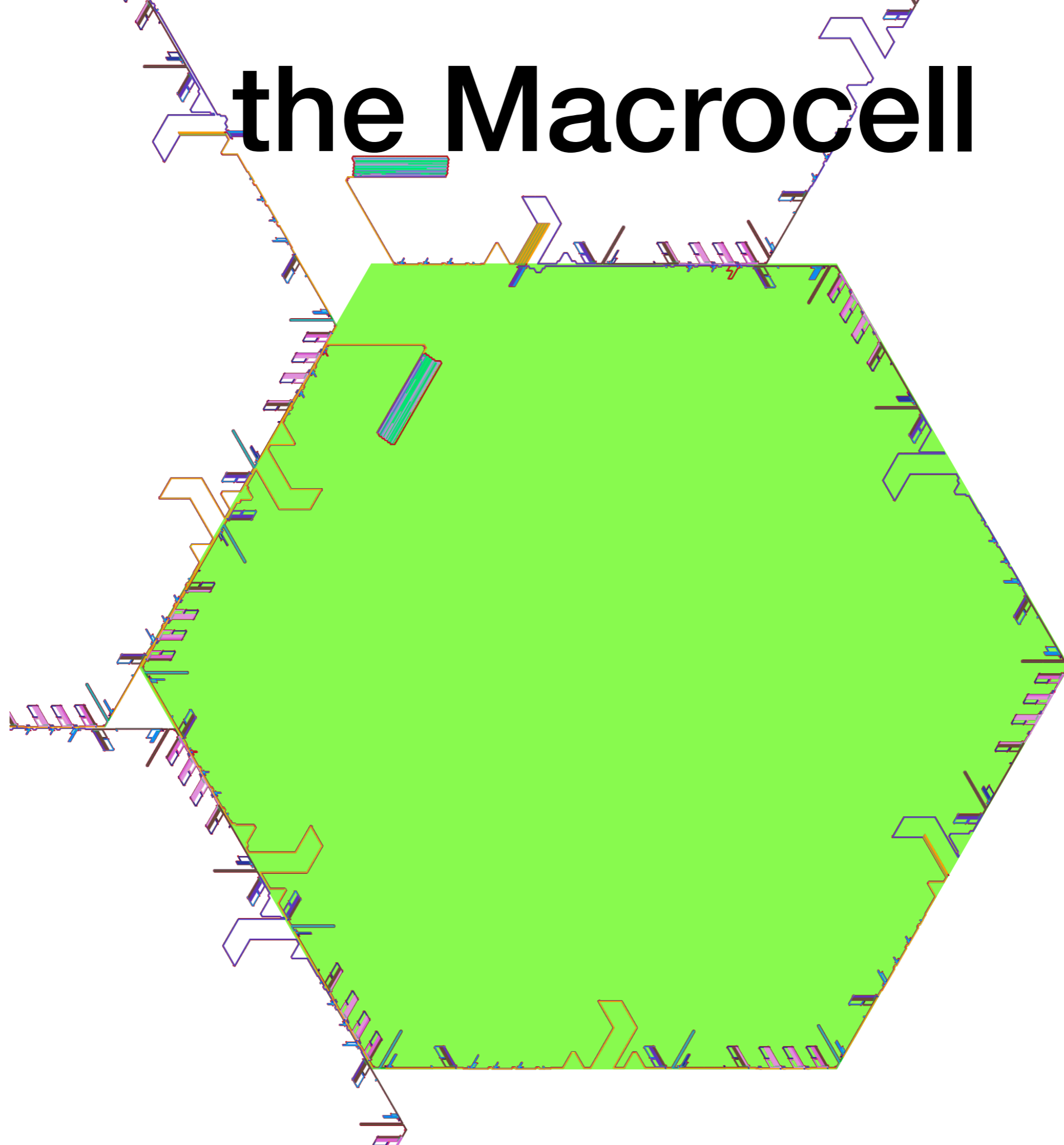
# Oritatami systems simulate 1D CA intrinsically

- **Previous work.** [PSSU, 2020]  
1D Cellular automata intrinsic simulation

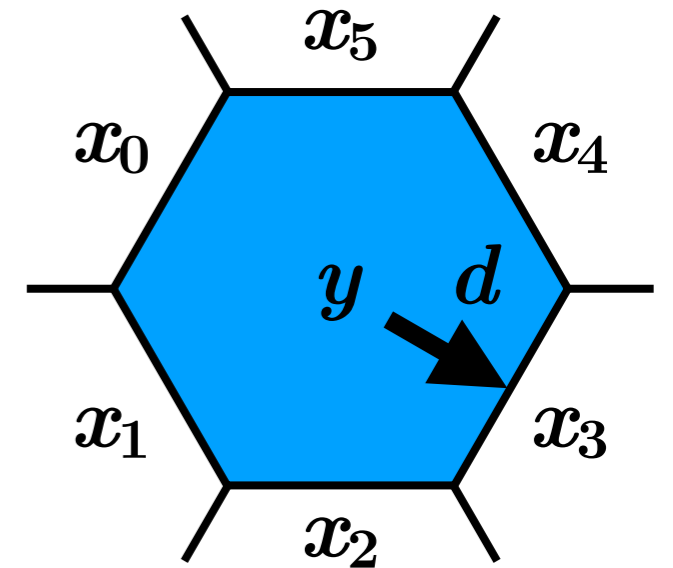


**2 Problems. Macrocells must be isotropic**  
We need to **exit from an arbitrary side...**

# the Macrocell



# Bit-weighted encoding for Turedos



- **Turedo**

$Q = 2^q - 1$  states and the empty state  $\perp$

Transition function:

$$F : (Q \cup \{\perp\})^6 \rightarrow Q \times \{\leftarrow, \nearrow, \nearrow, \rightarrow, \searrow, \swarrow\}$$

$$(x_0, \dots, x_5) \mapsto (y, d)$$

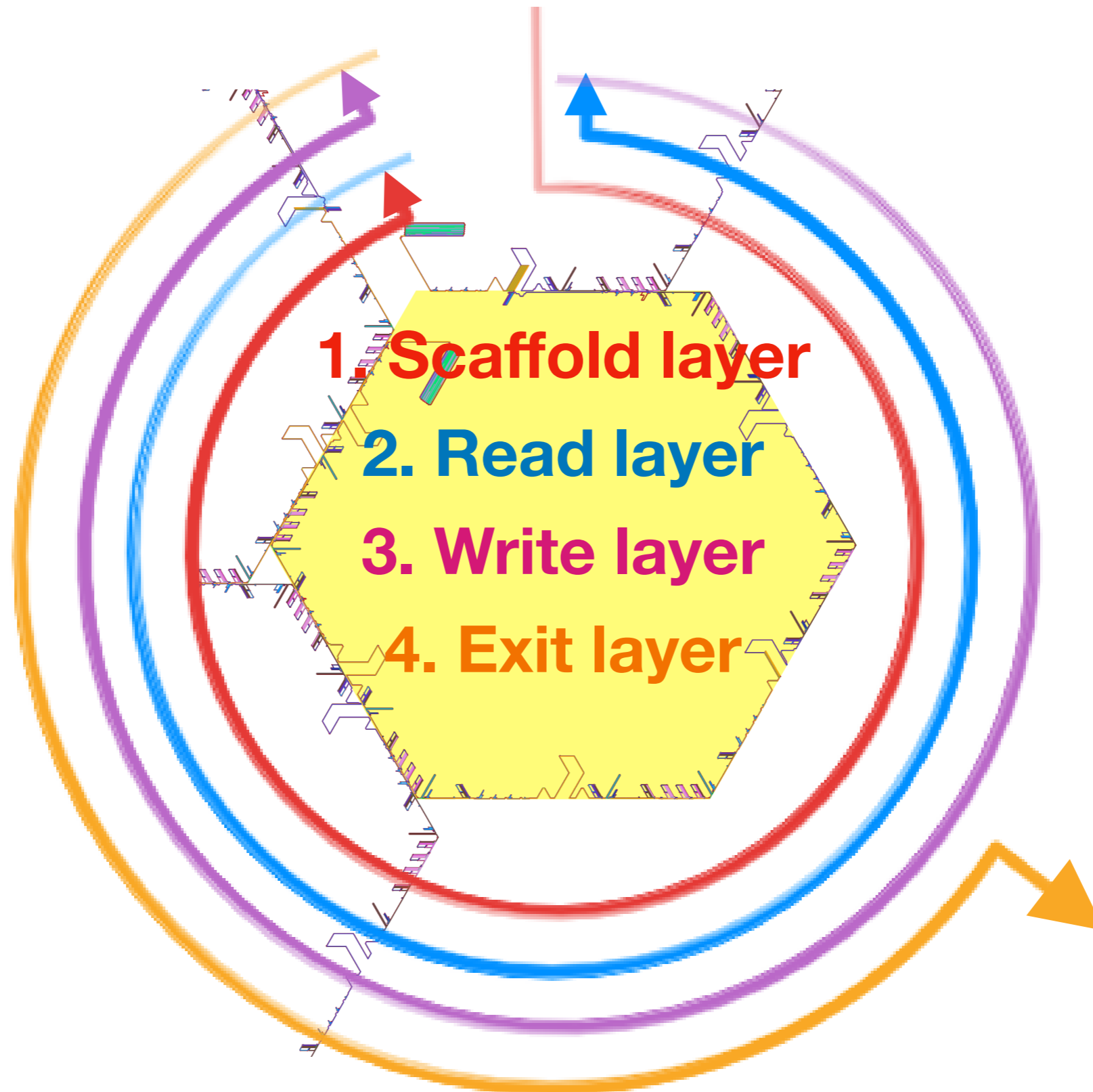
- **Bit-weight encoding**

$w_{ij}$  = weight of the  $j$ -th bit  $x_{ij}$  of  $x_i$

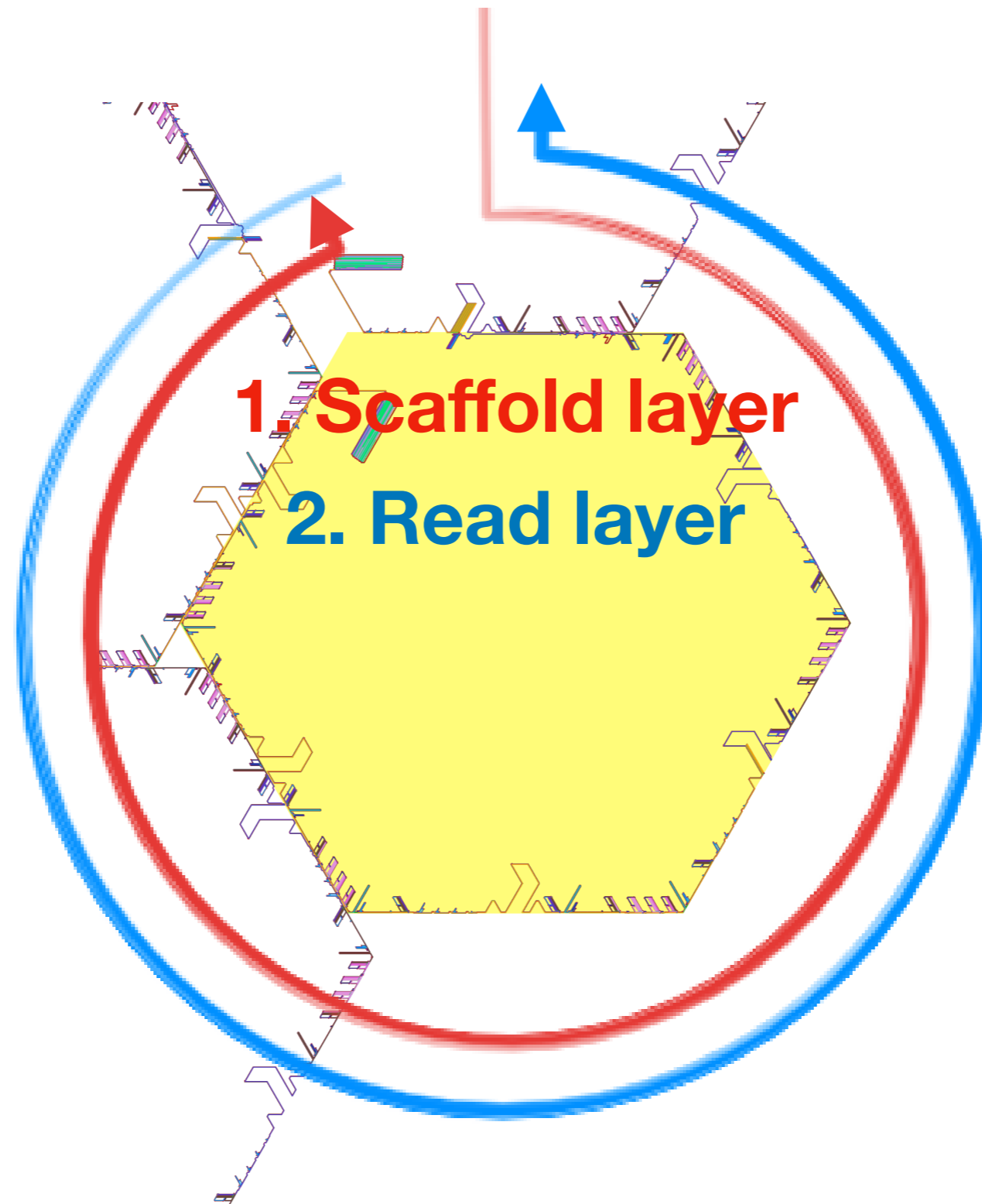
$$F(x) = \Phi(w(x)) \text{ where } w(x) = \sum_{ij} w_{ij} x_{ij}$$

- $w_{ij} = 2^{qi+j}$  works for all  $F$

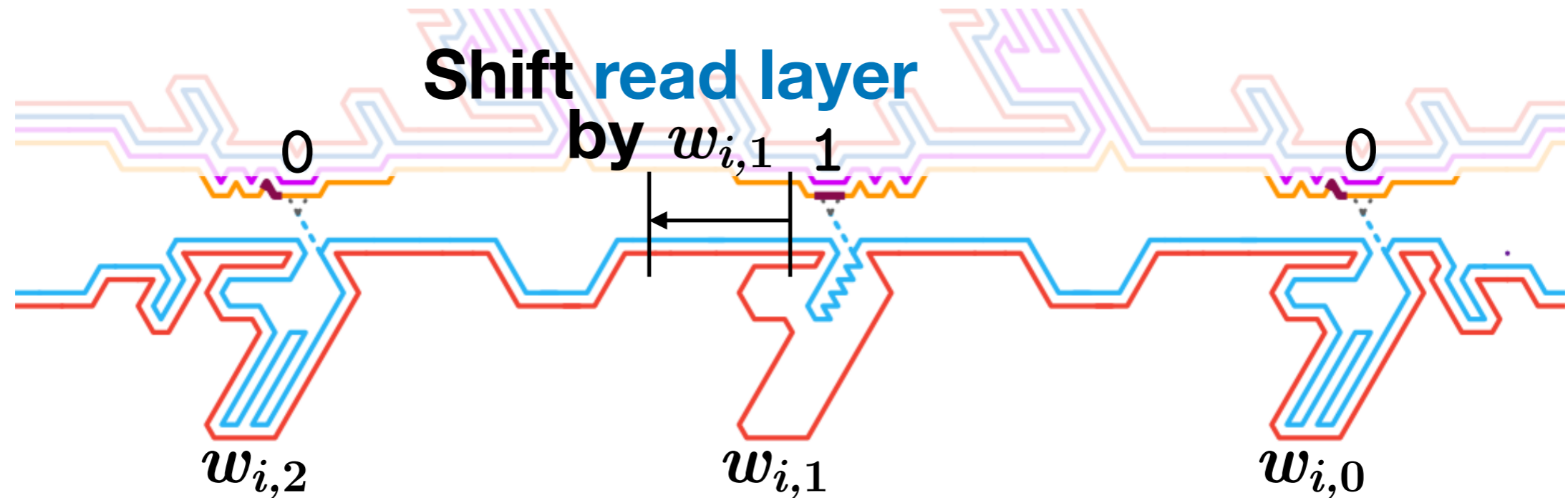
# the Macrocell



# the Read layer



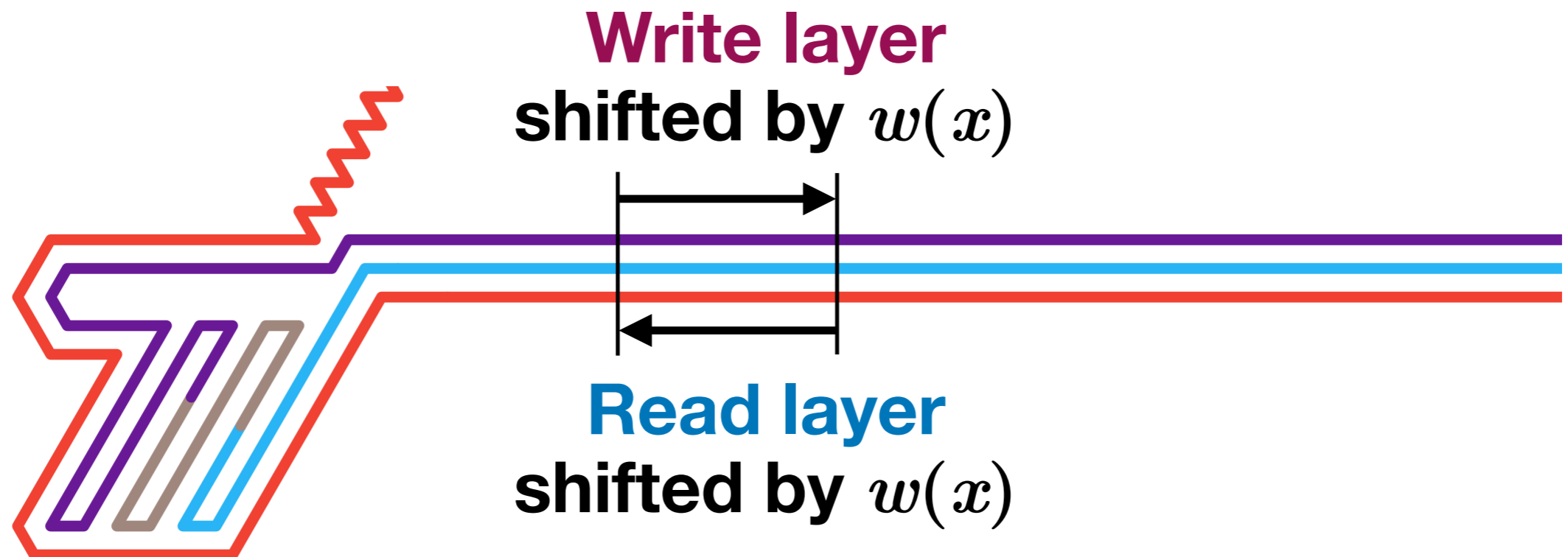
# Reading. Reading pockets



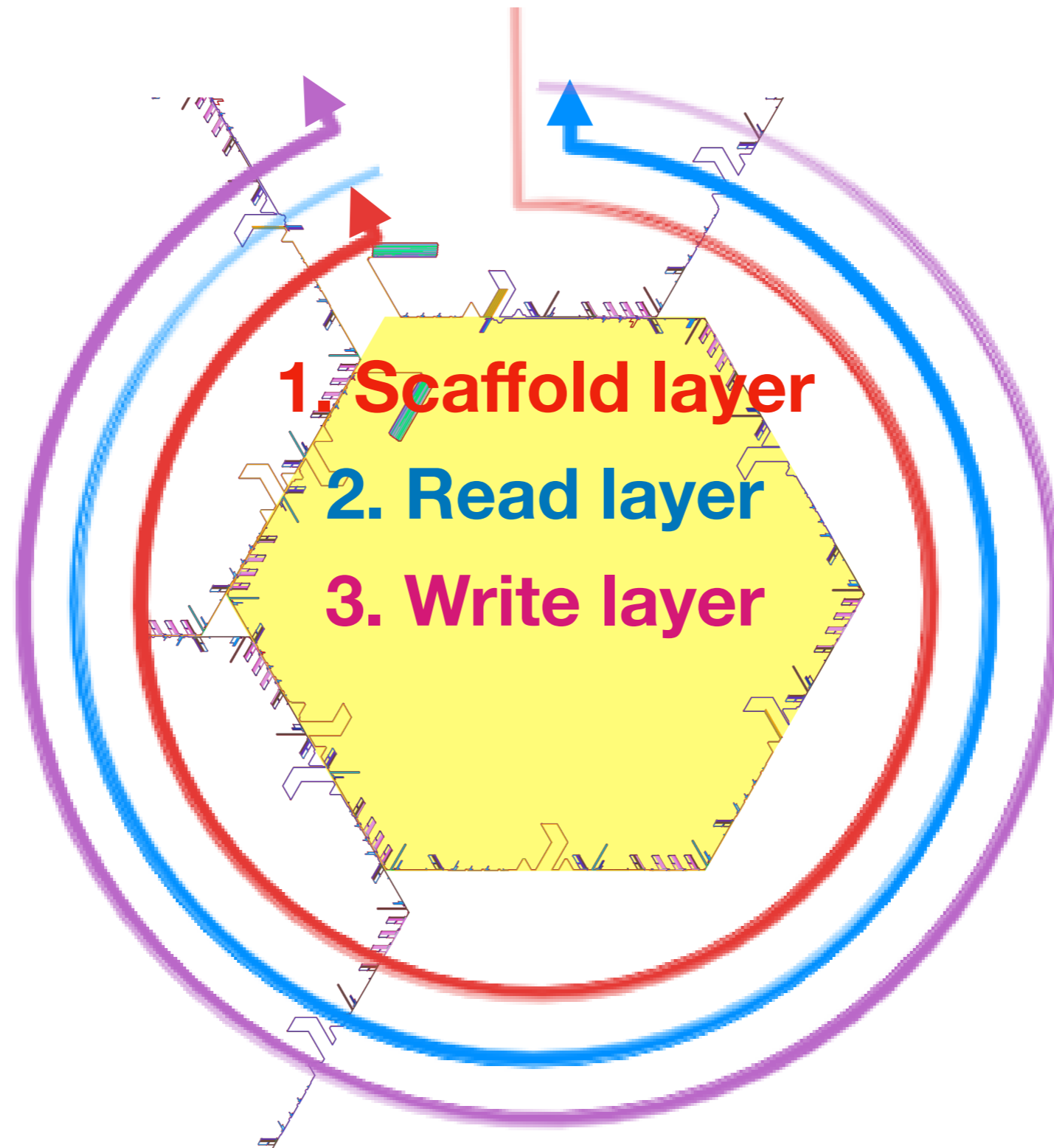
- If  $j$ -th bit = 1, then Shift +=  $w_{ij}$
- ⇒ Shift on  $i$ -th side =  $\sum_j w_{ij} x_{ij} = w(x_i)$
- ⇒ **Total Shift on all side =  $w(x)$**



# Uturn pocket. Read to write

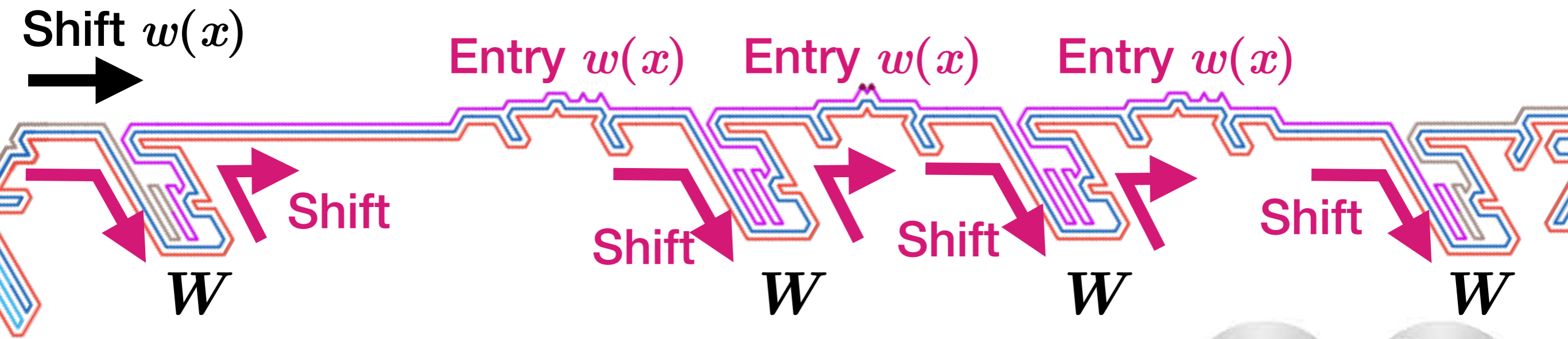


# the Macrocell



# Writing. Shift pushes the transition table to the right

bits 0 and 1 fold differently



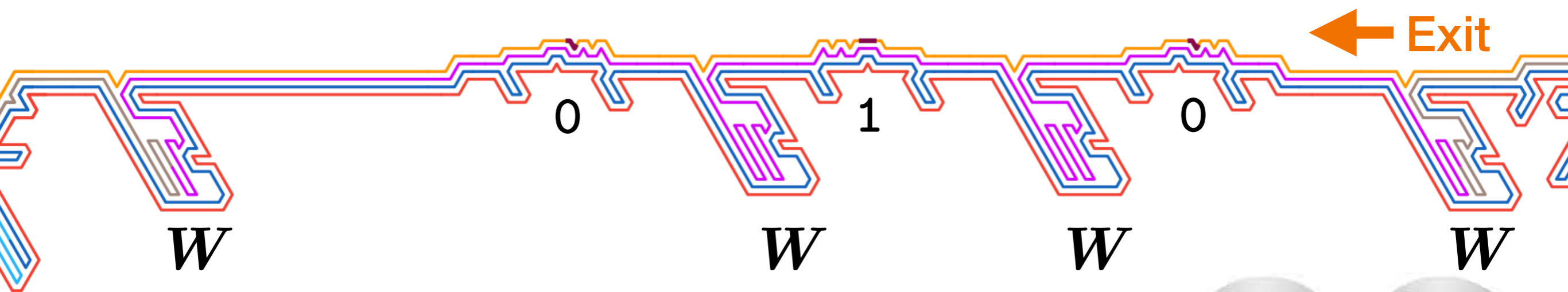
The pockets hide the  $W = \sum_{ij} w_{ij}$   
unused entries in the transition table



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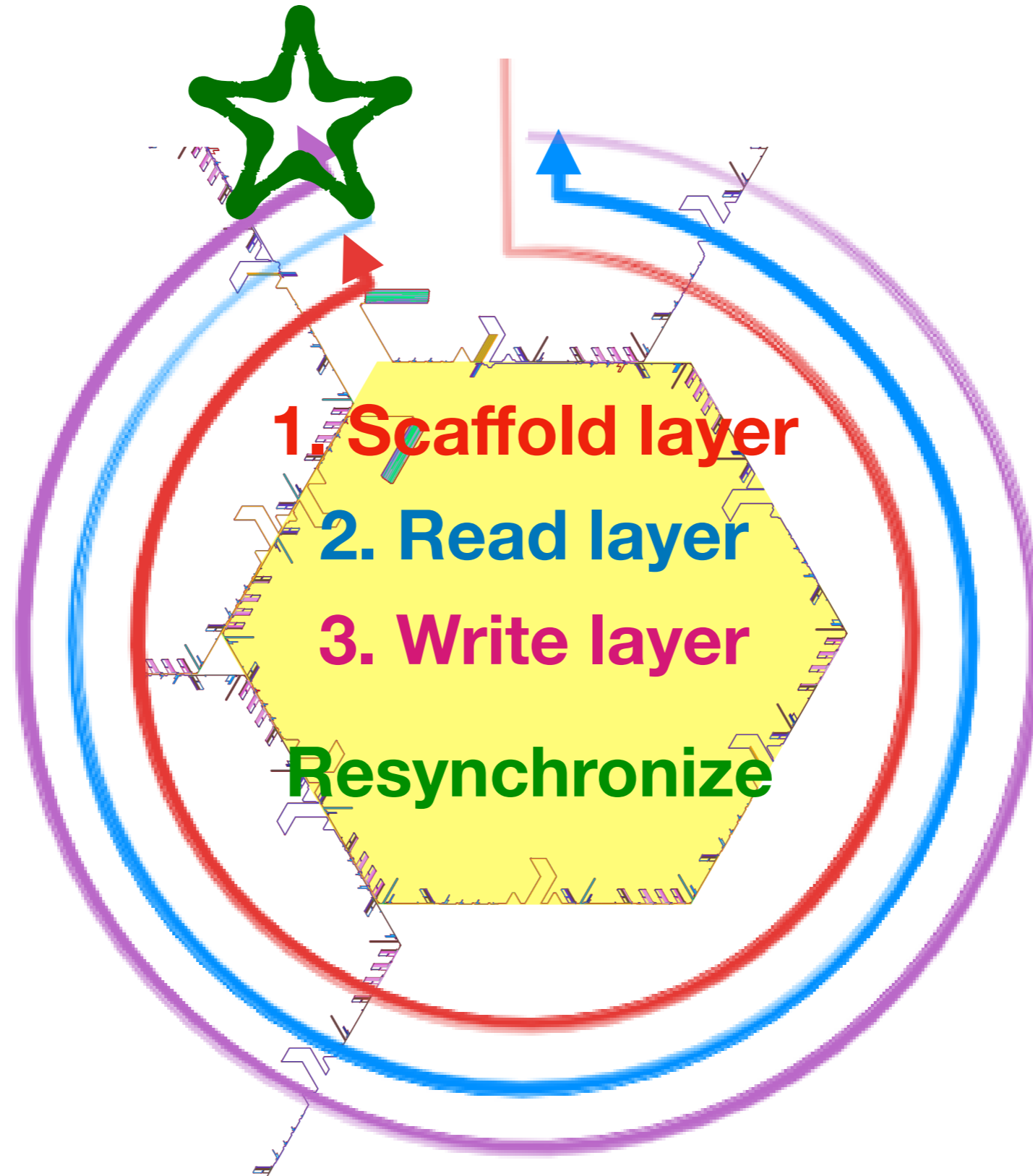
⇒ the exit layer shows or hide the special beads



The pockets hide the  $W = \sum_{ij} w_{ij}$   
unused entries in the transition table

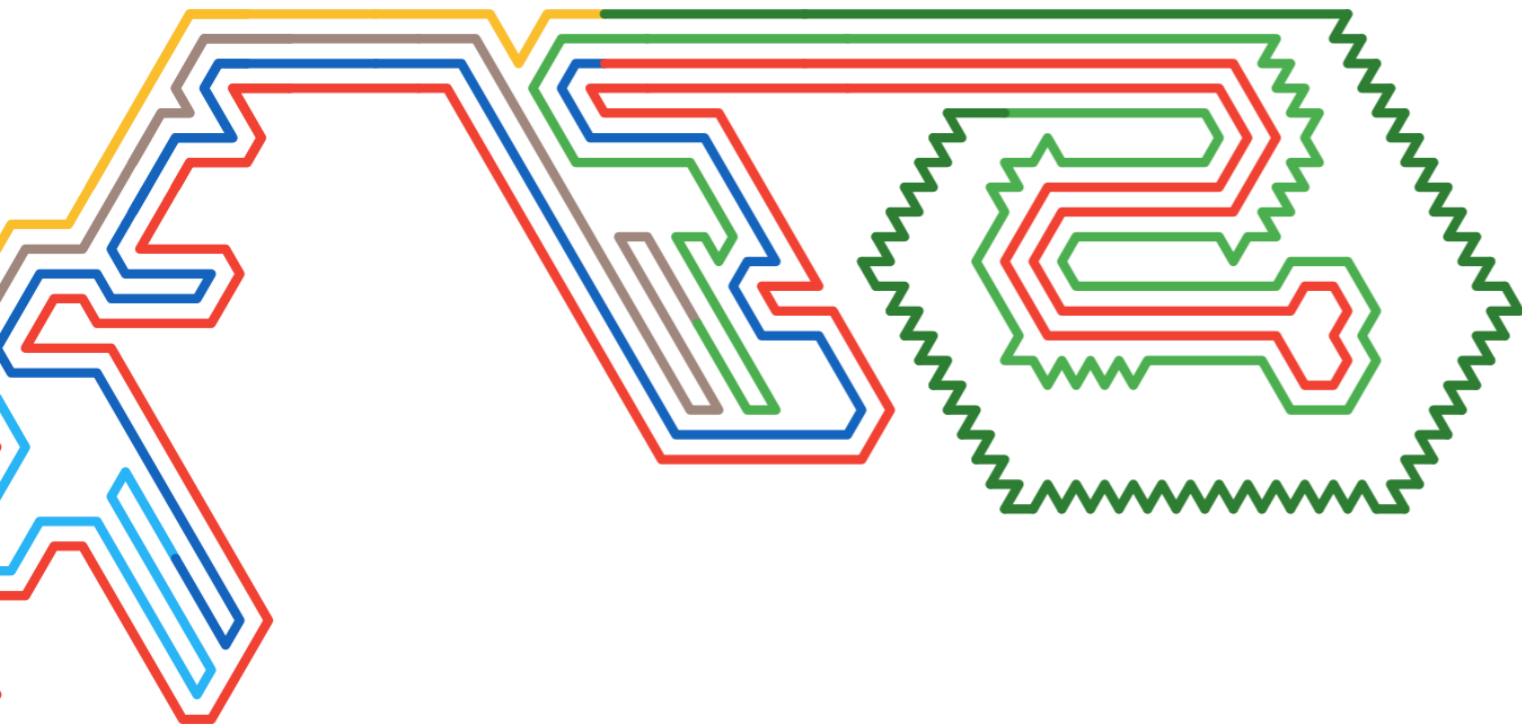


# the Macrocell

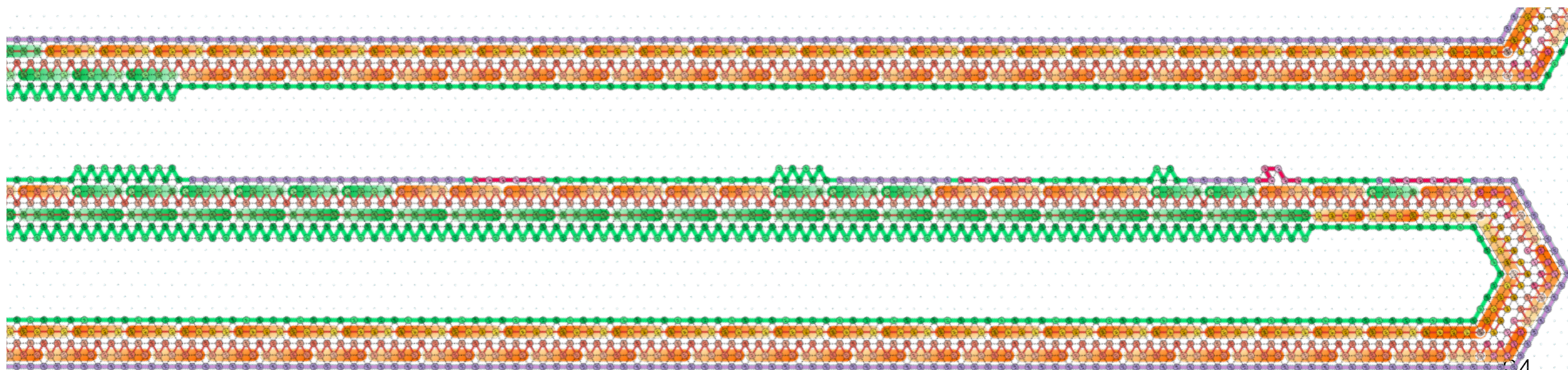


# Resynchronizing.

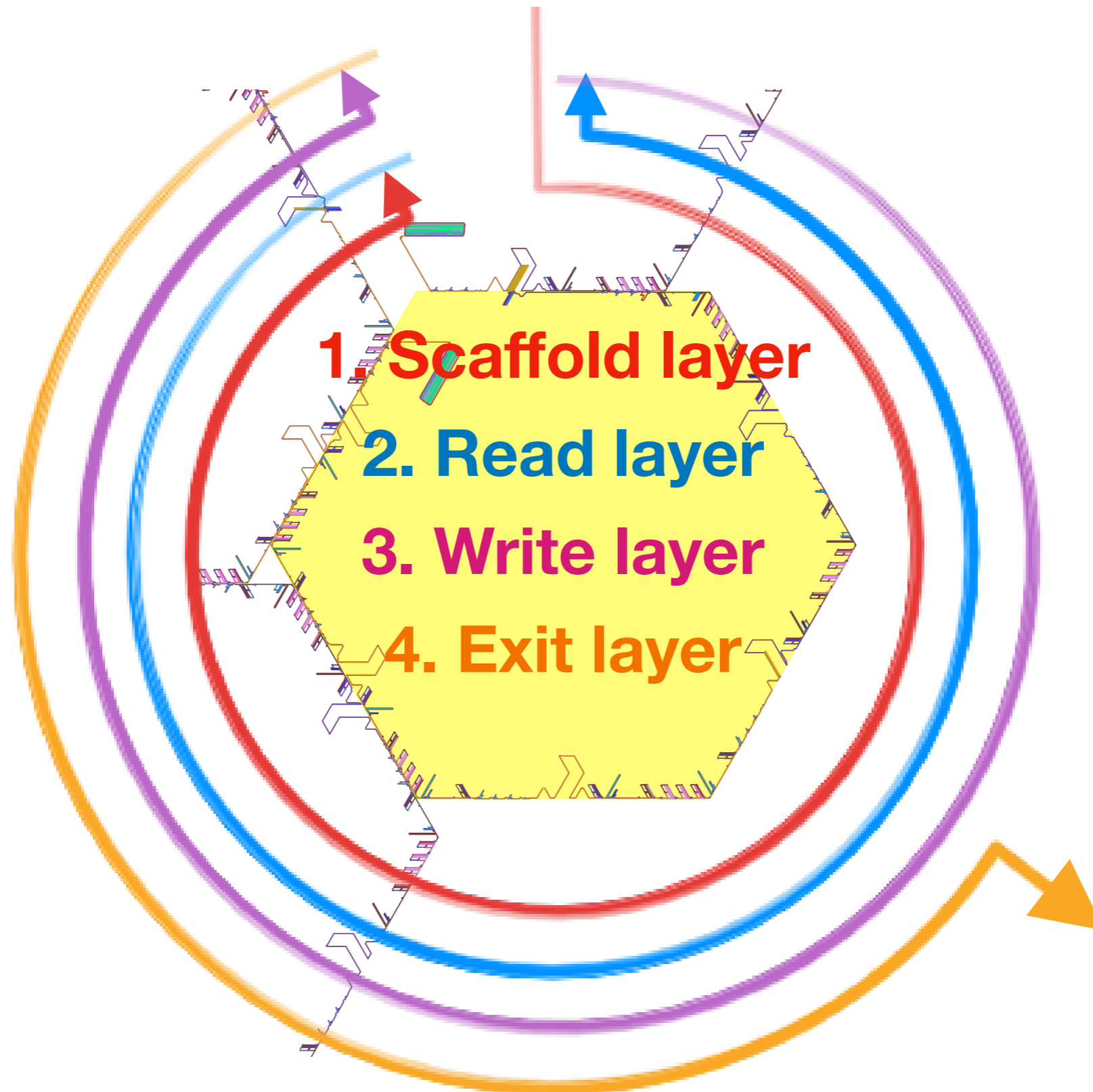
## Speedbumps [PSSU2020]



**Can absorb  
any offset  $\leq W$   
(in Zig-Zags! 🙄)**



# the Macrocell



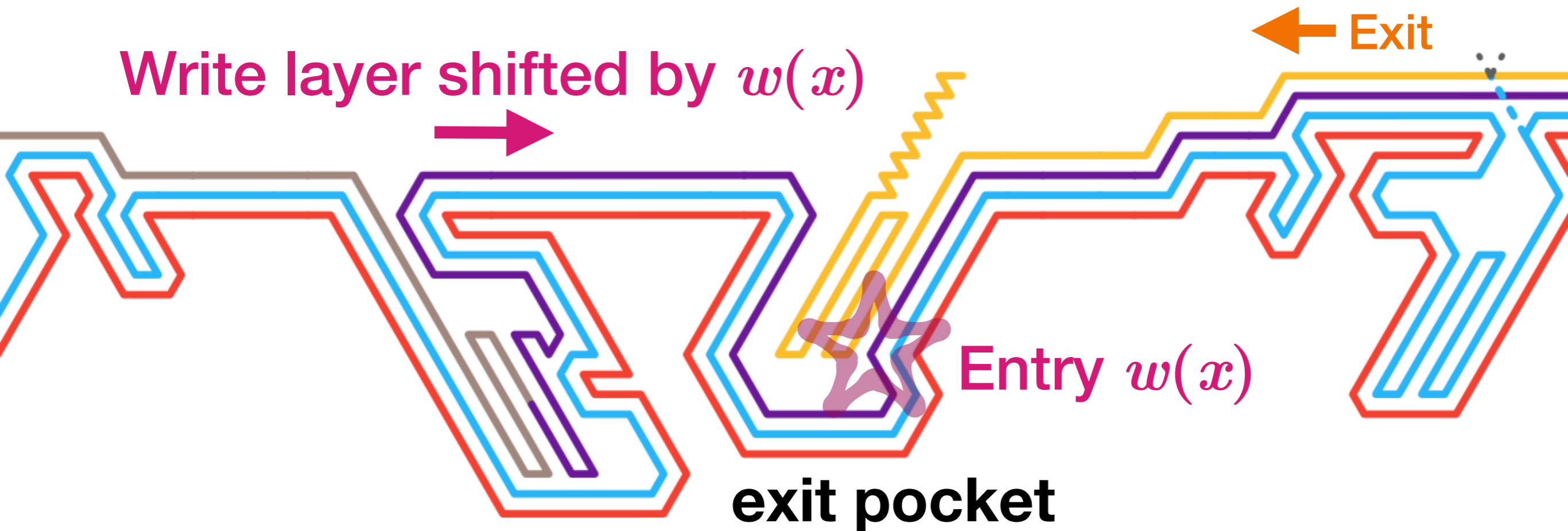
# Exiting... or not



By default, **exit layer** follows the border of the exit box

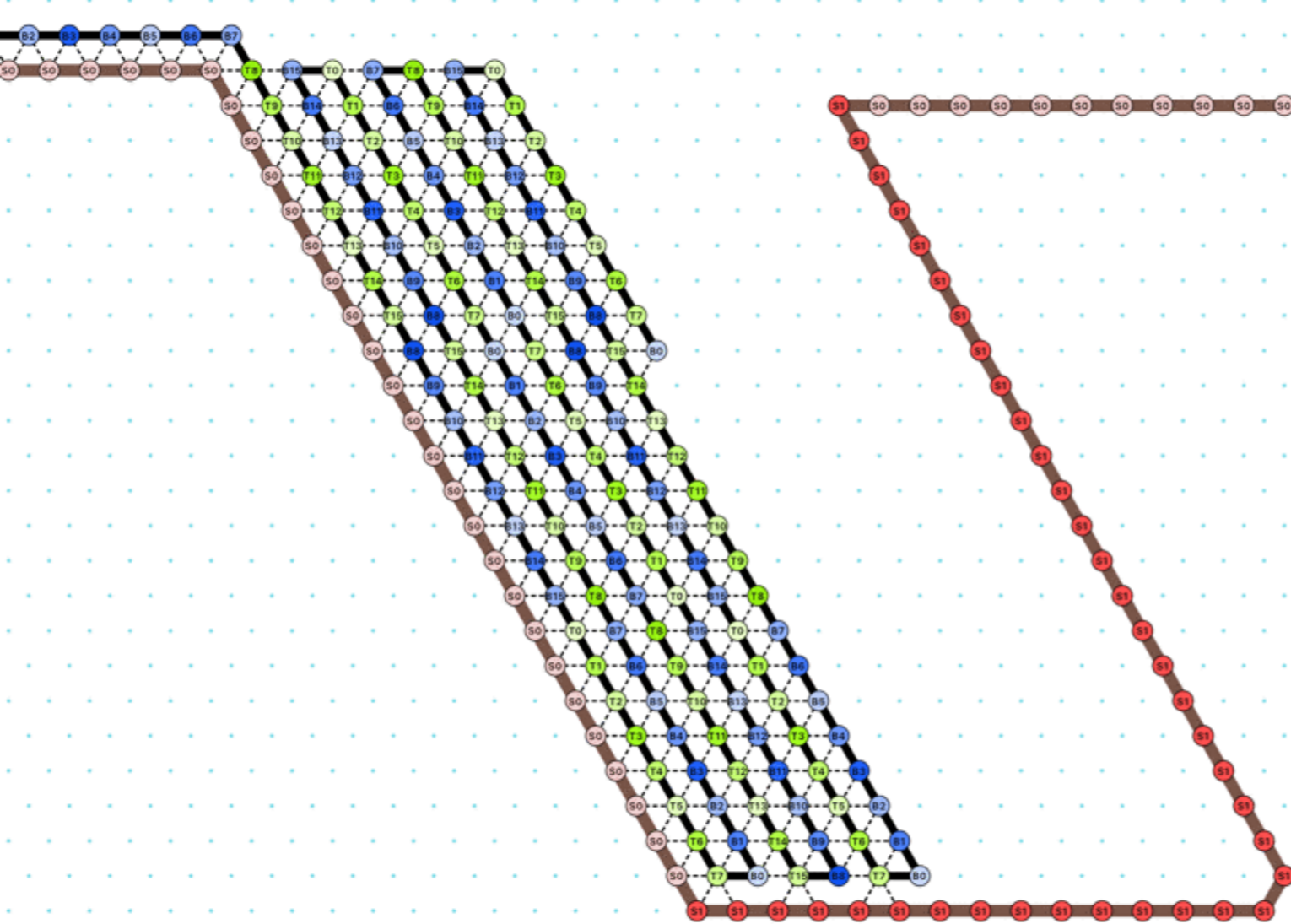


# Exiting... or not



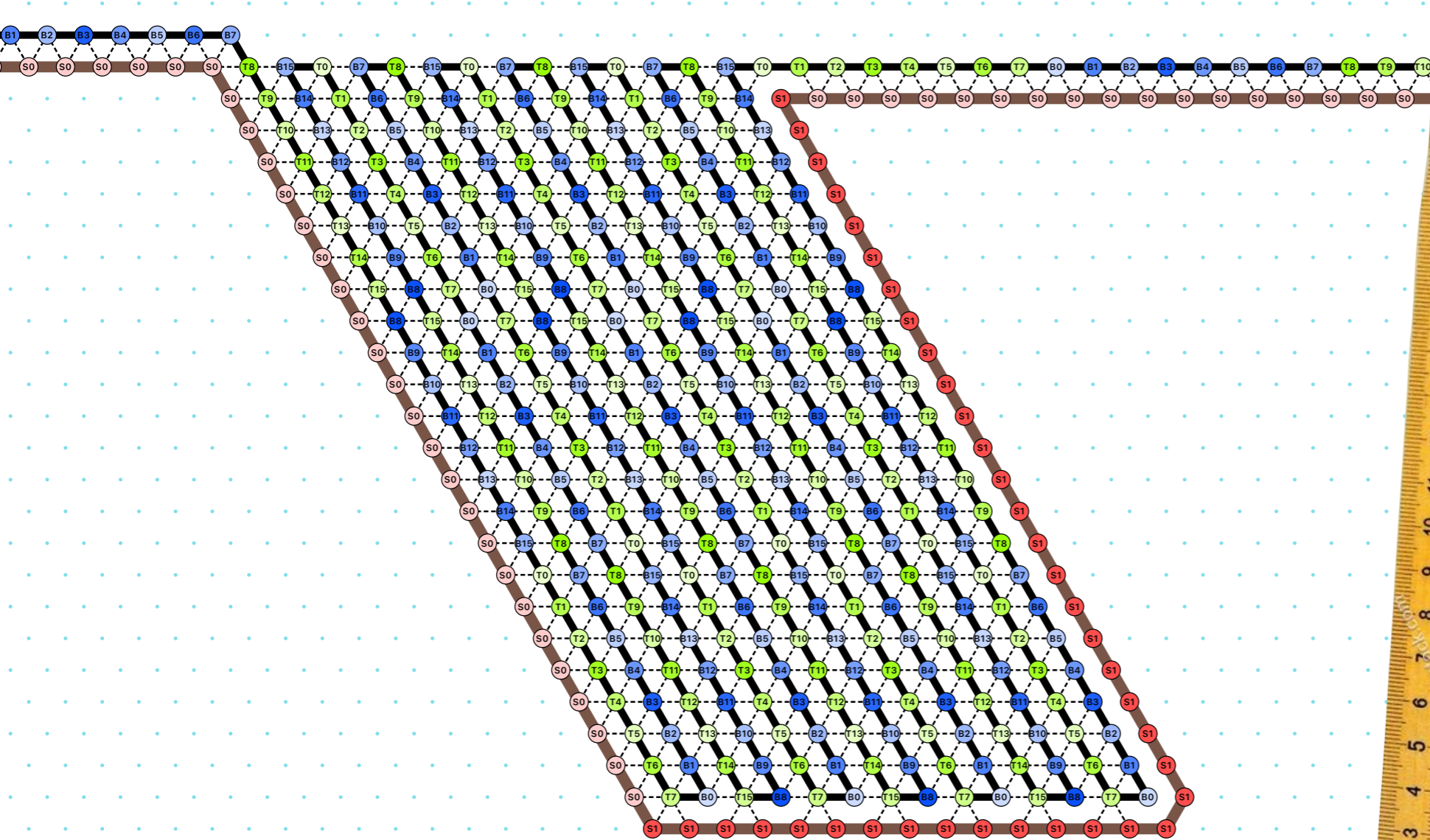
With the proper signal (offset!), **exit layer** folds upon itself and... **exit!**

# Key new tool: Folding meter



it folds upon itself into pockets

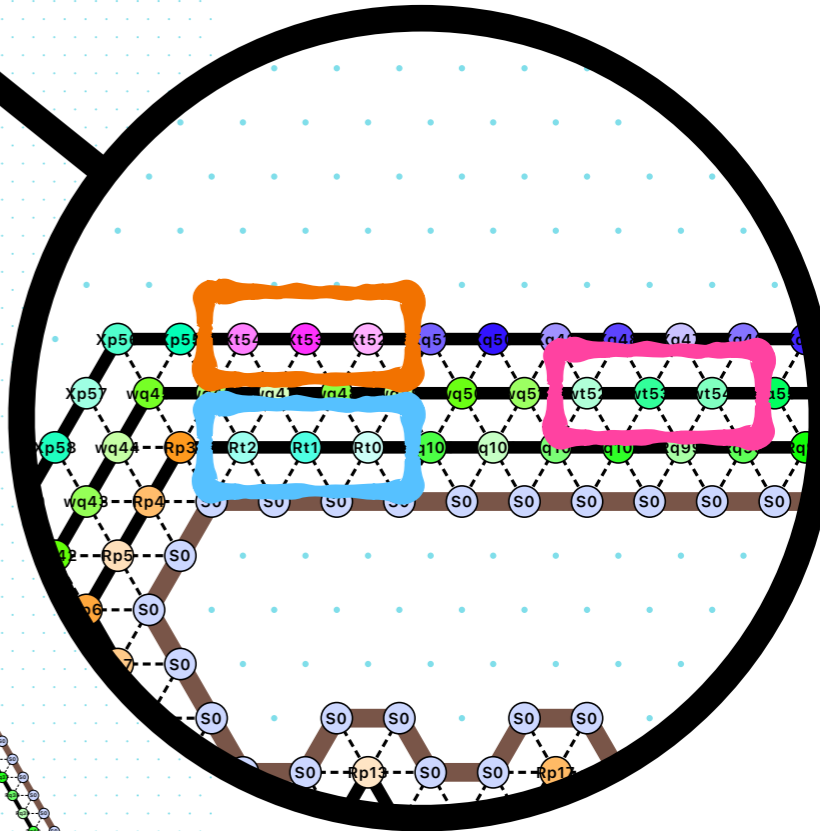
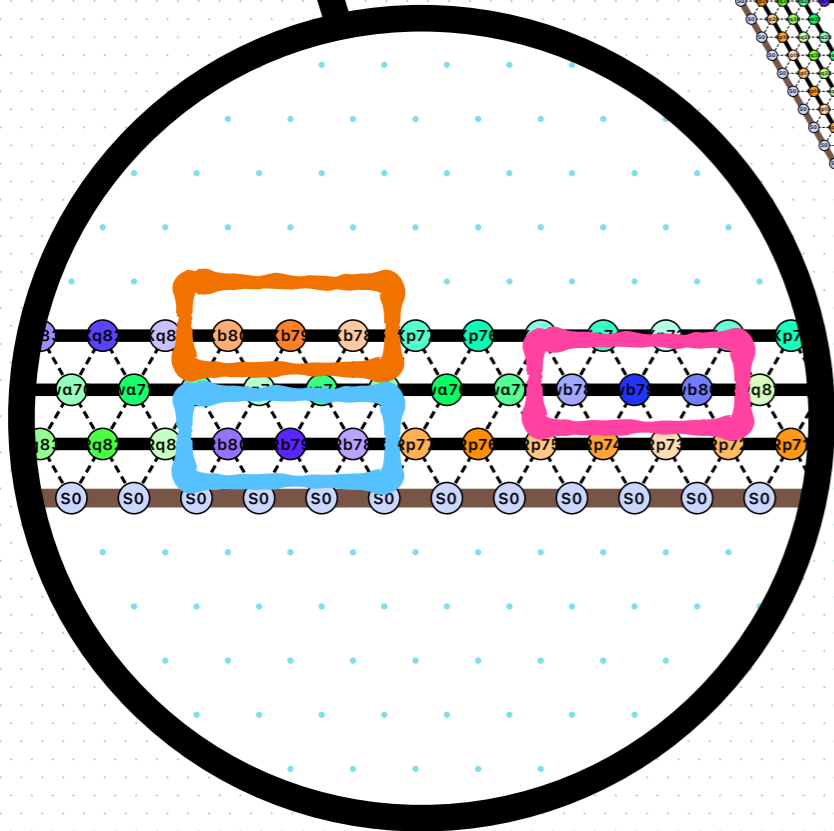
# Key new tool: Folding meter



it folds upon itself into pockets

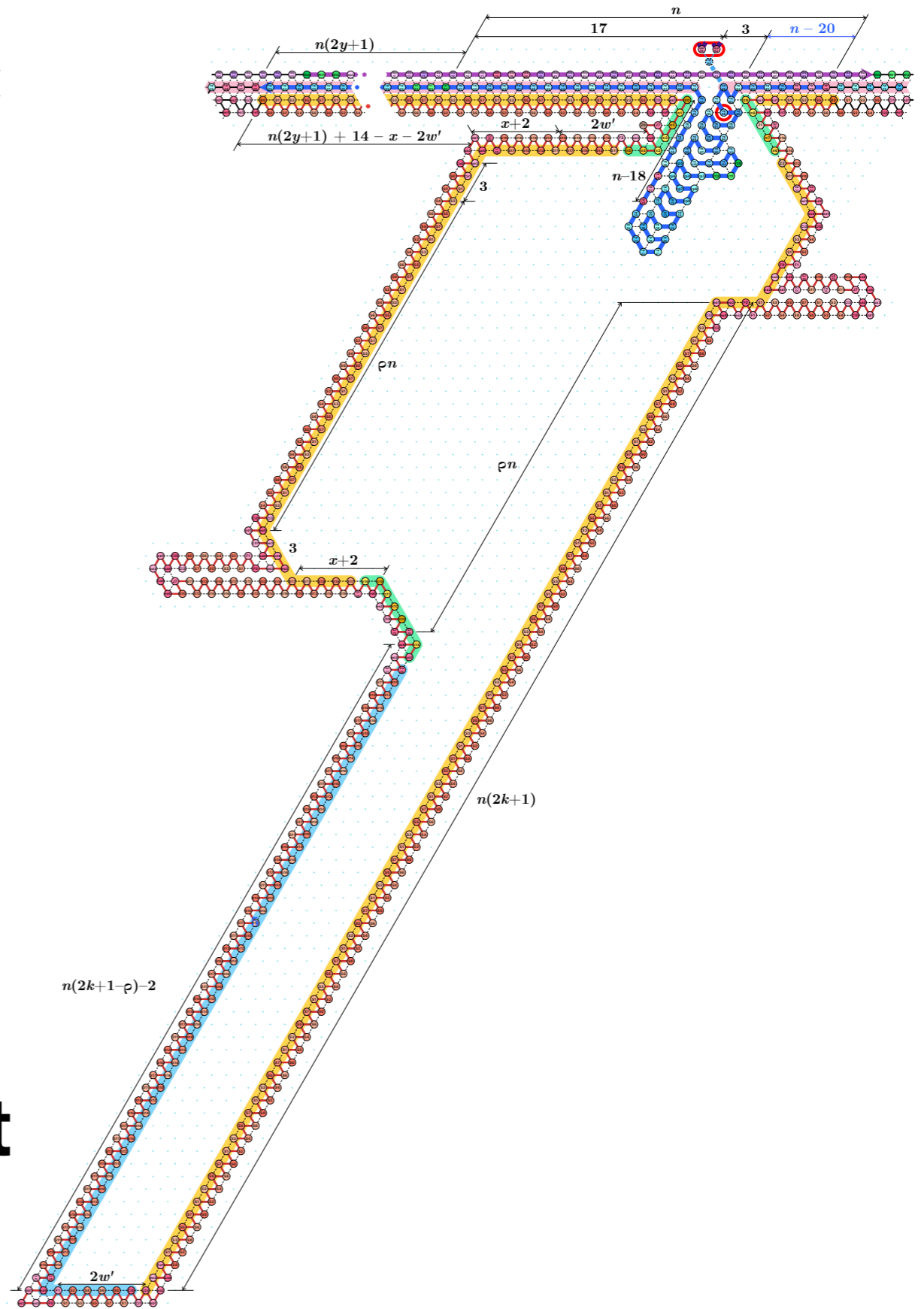
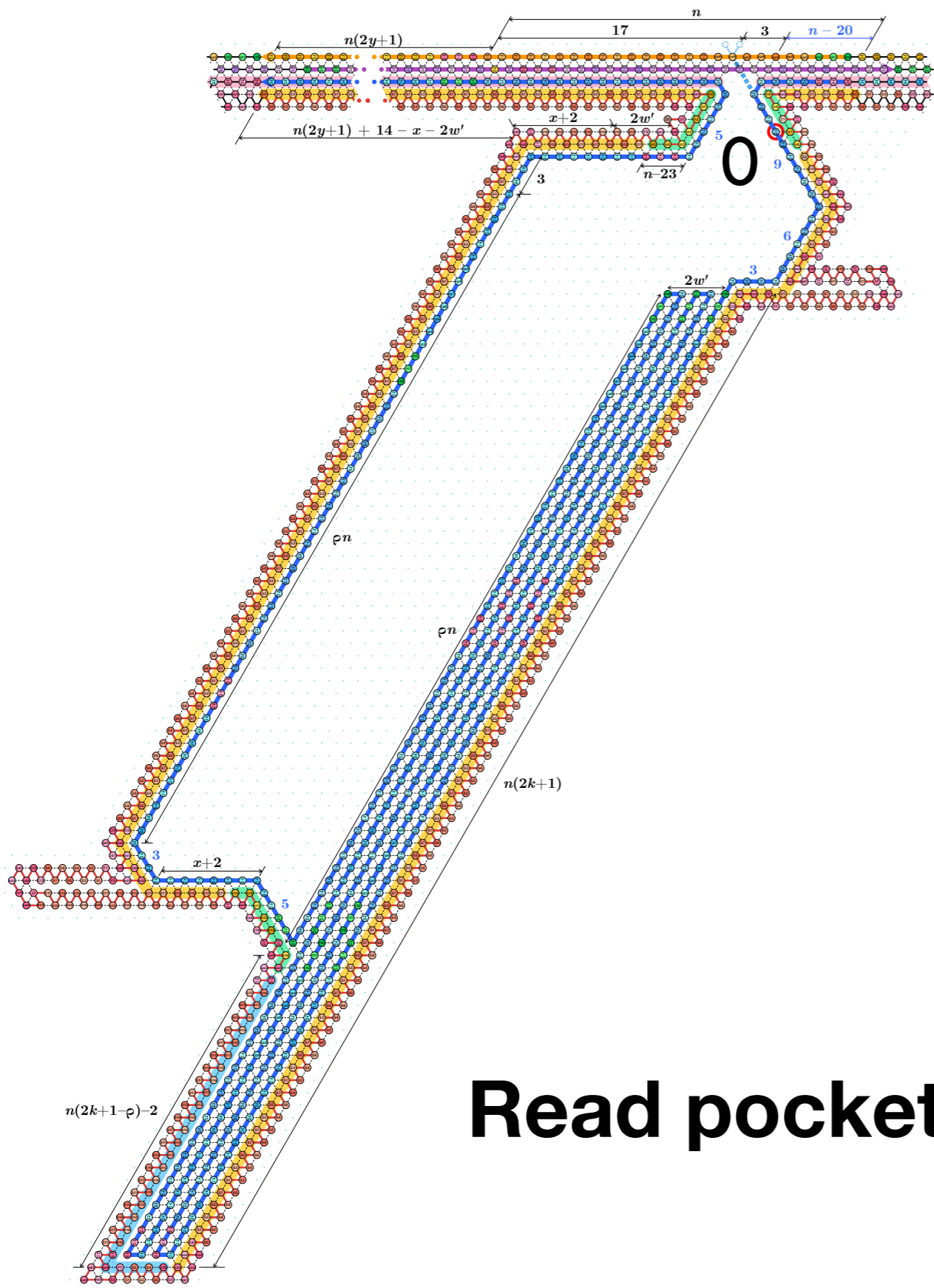
# Suspiciously simple fact

All layers stay synchronized



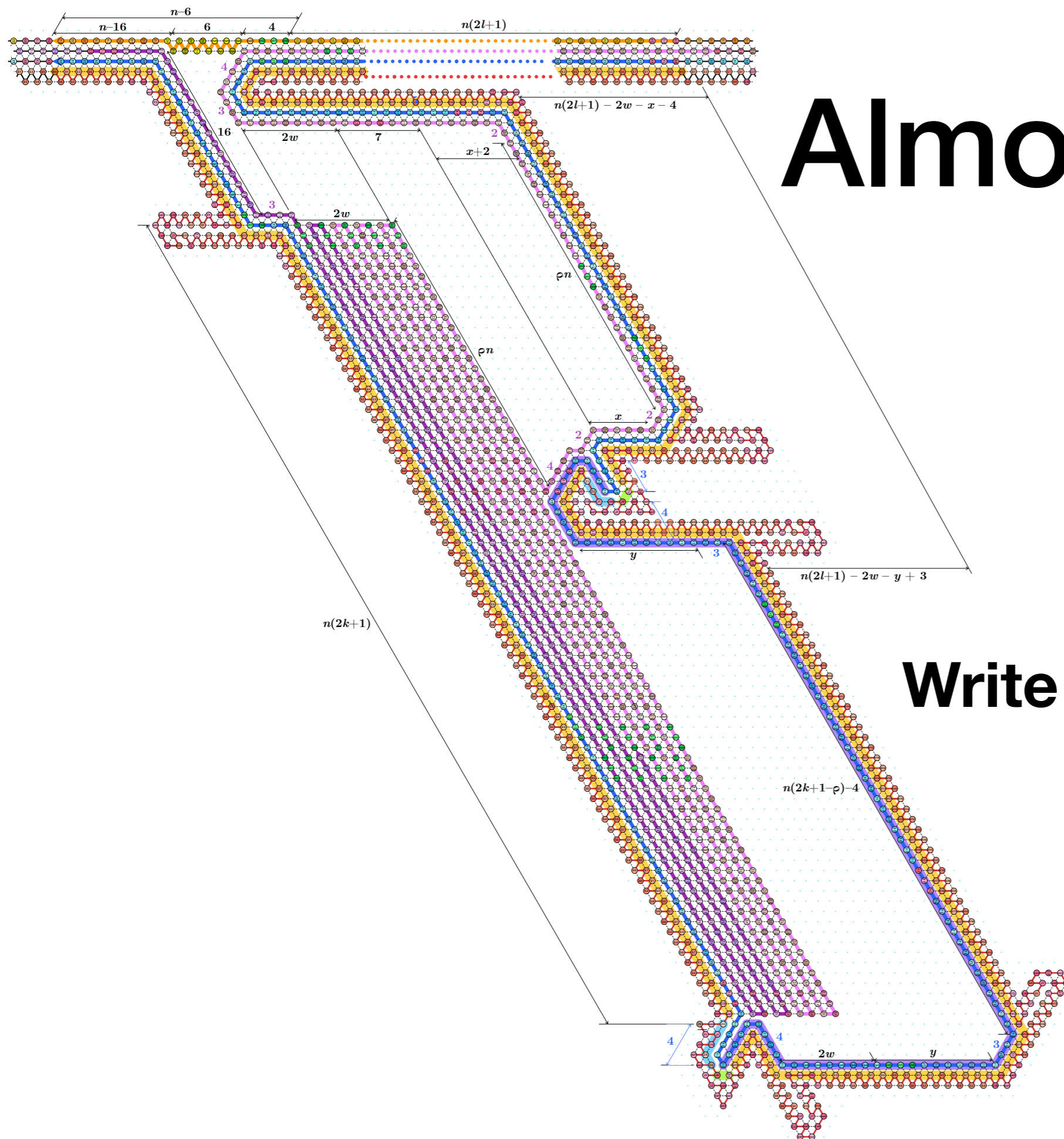
# Almost there

1



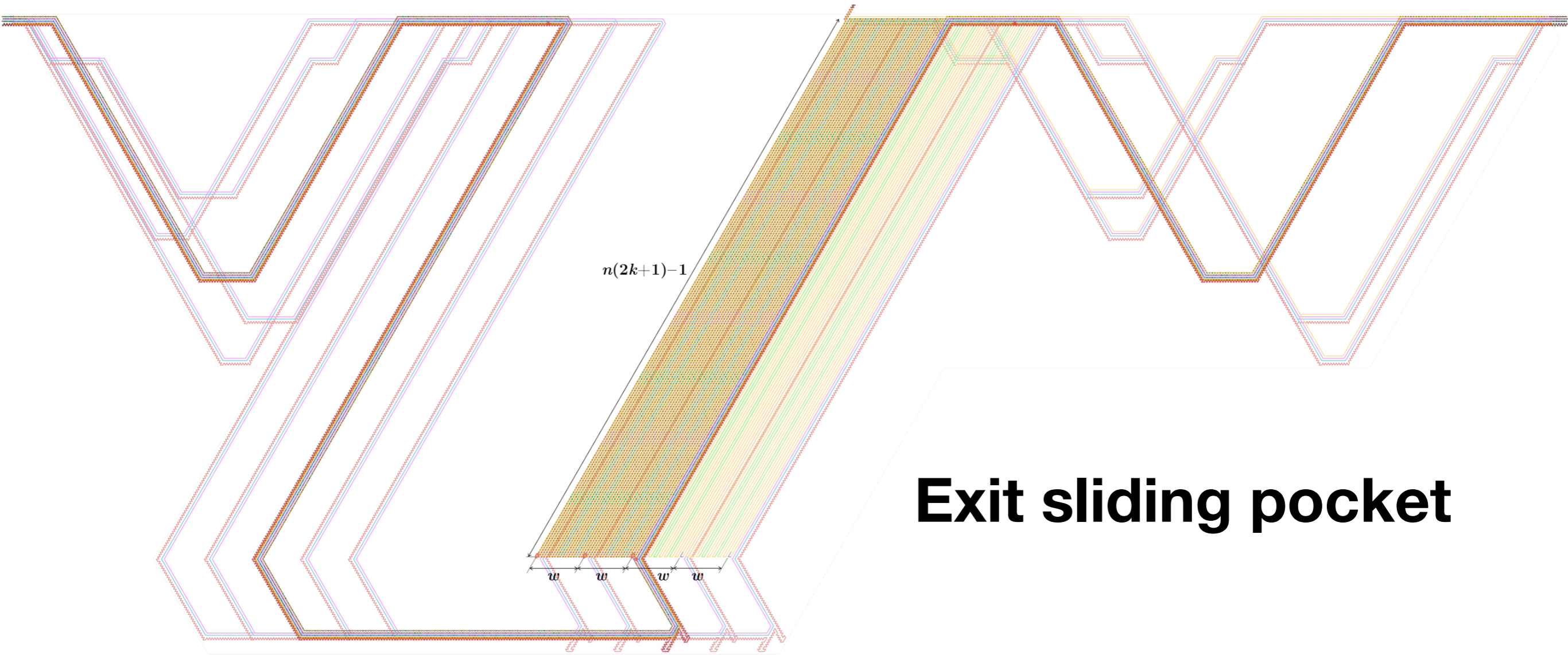
Read pocket

# Almost there



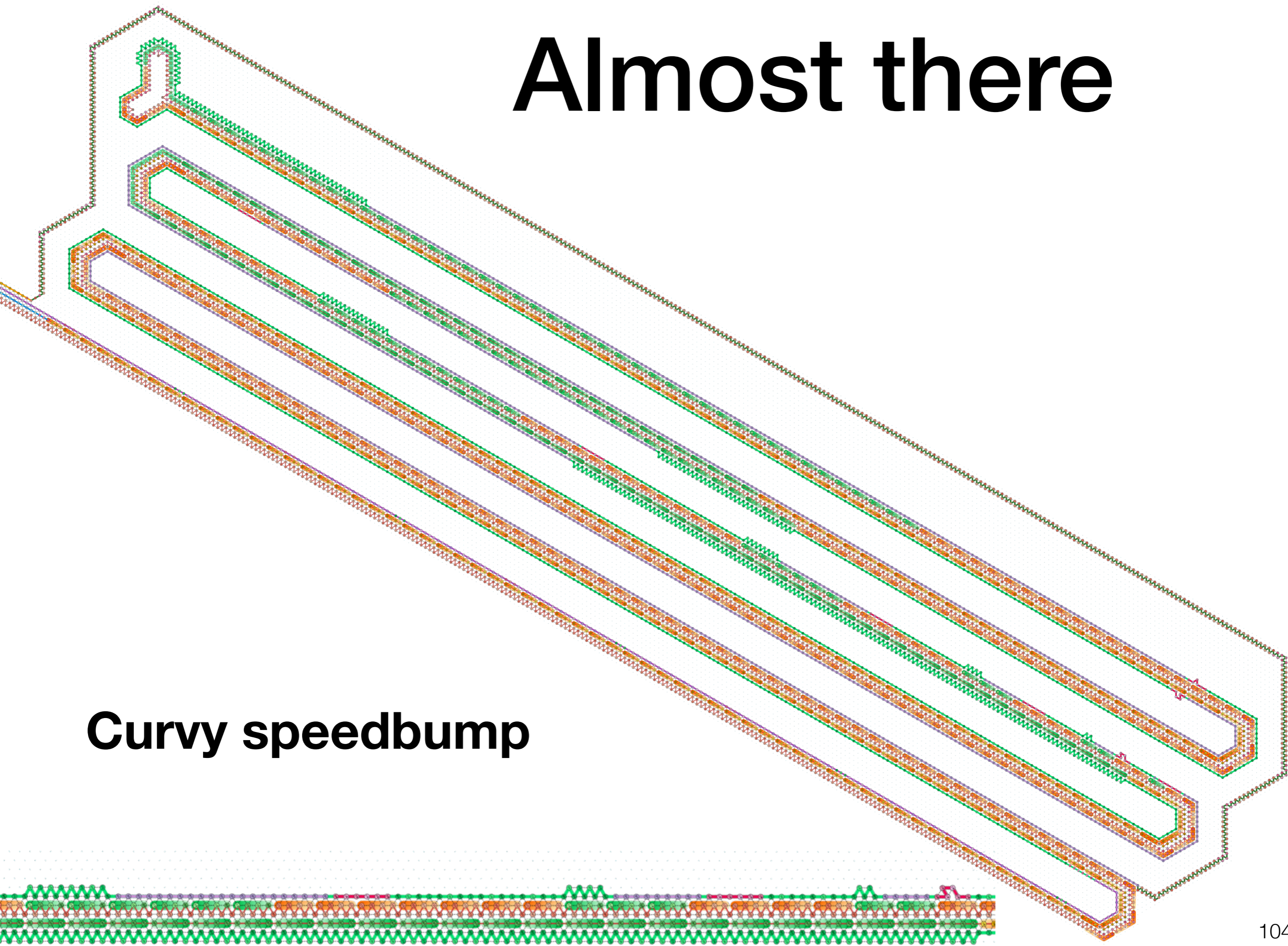
# Write pocket

# Almost there



**Exit sliding pocket**

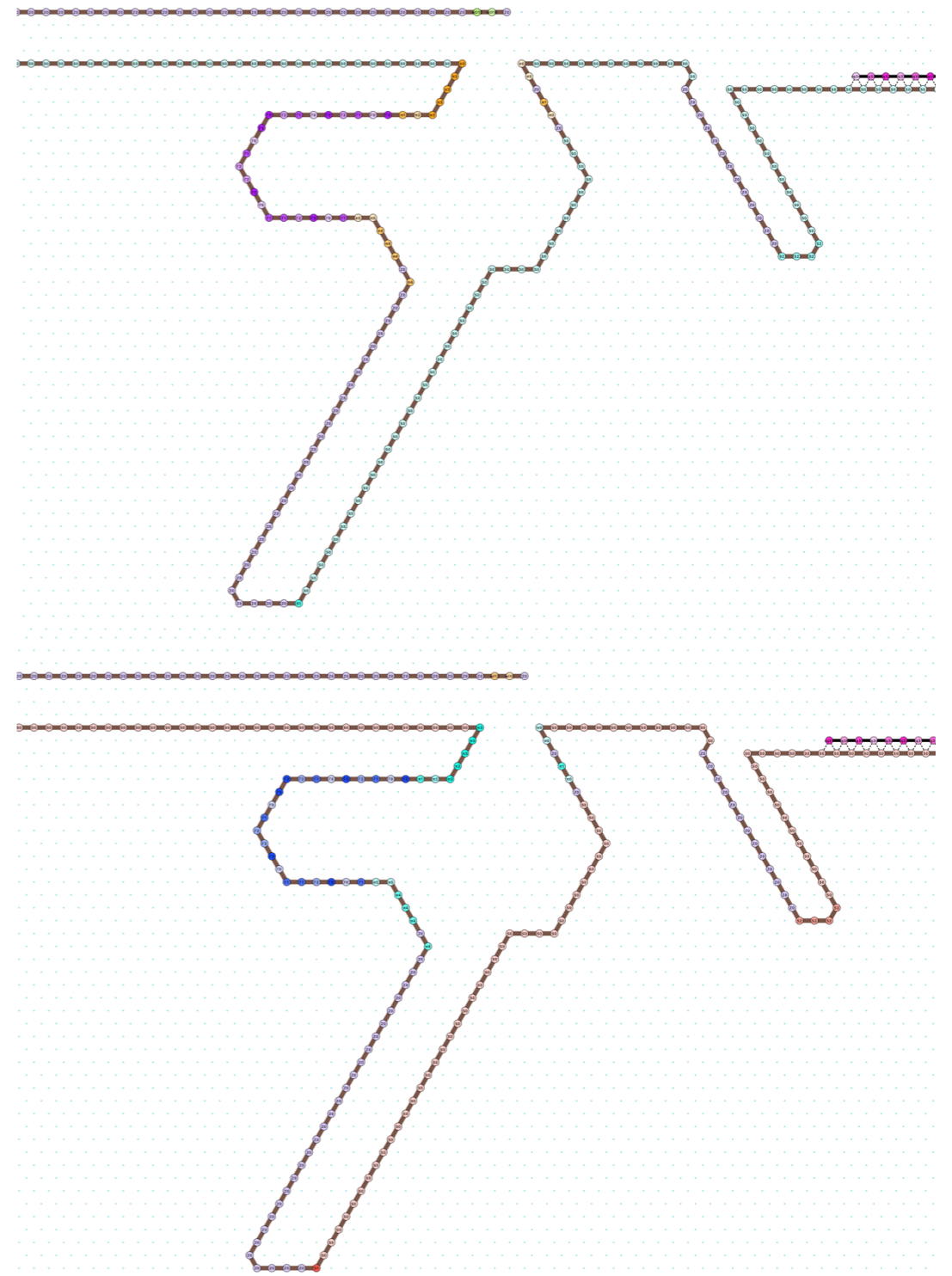
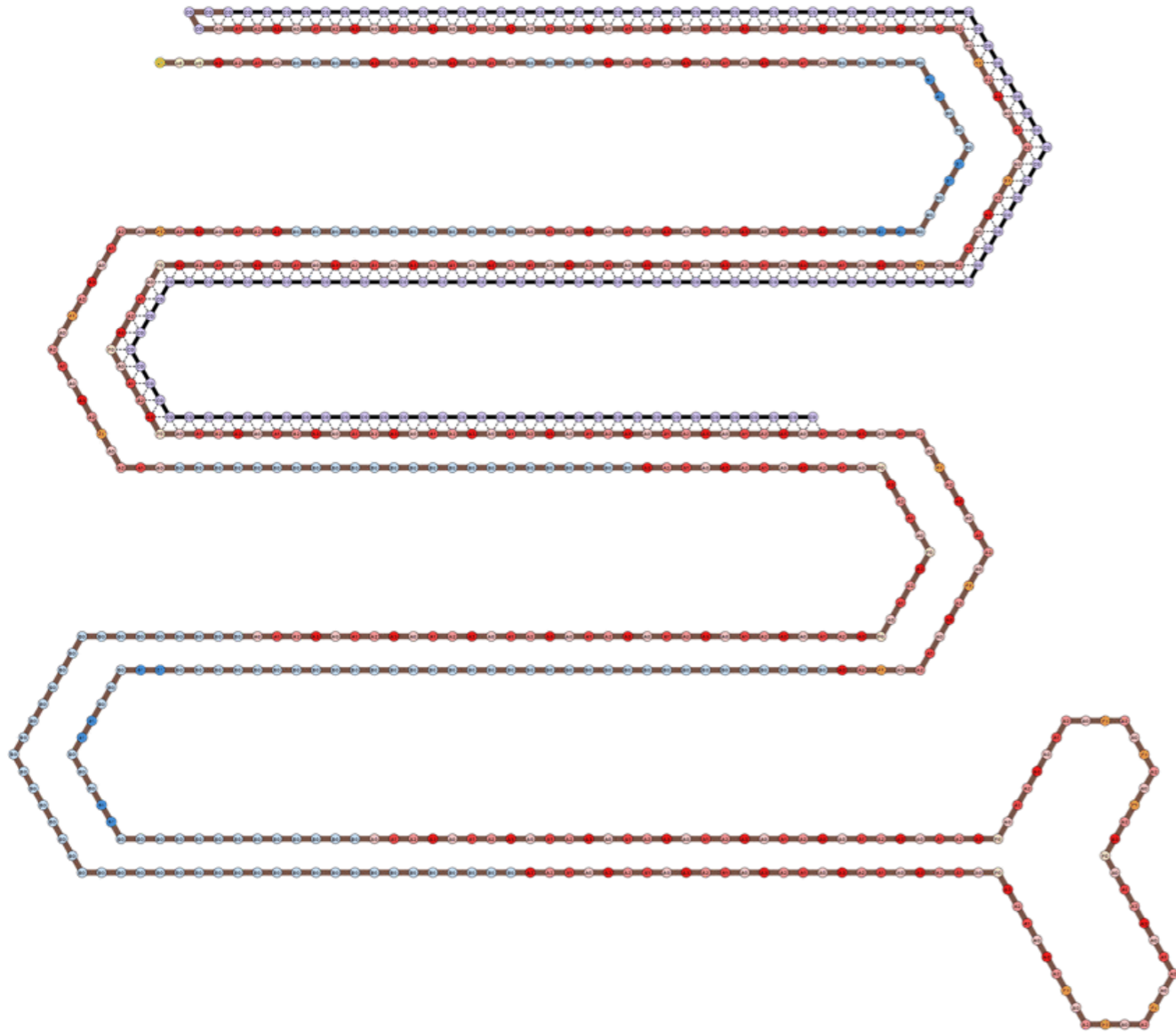
# Almost there



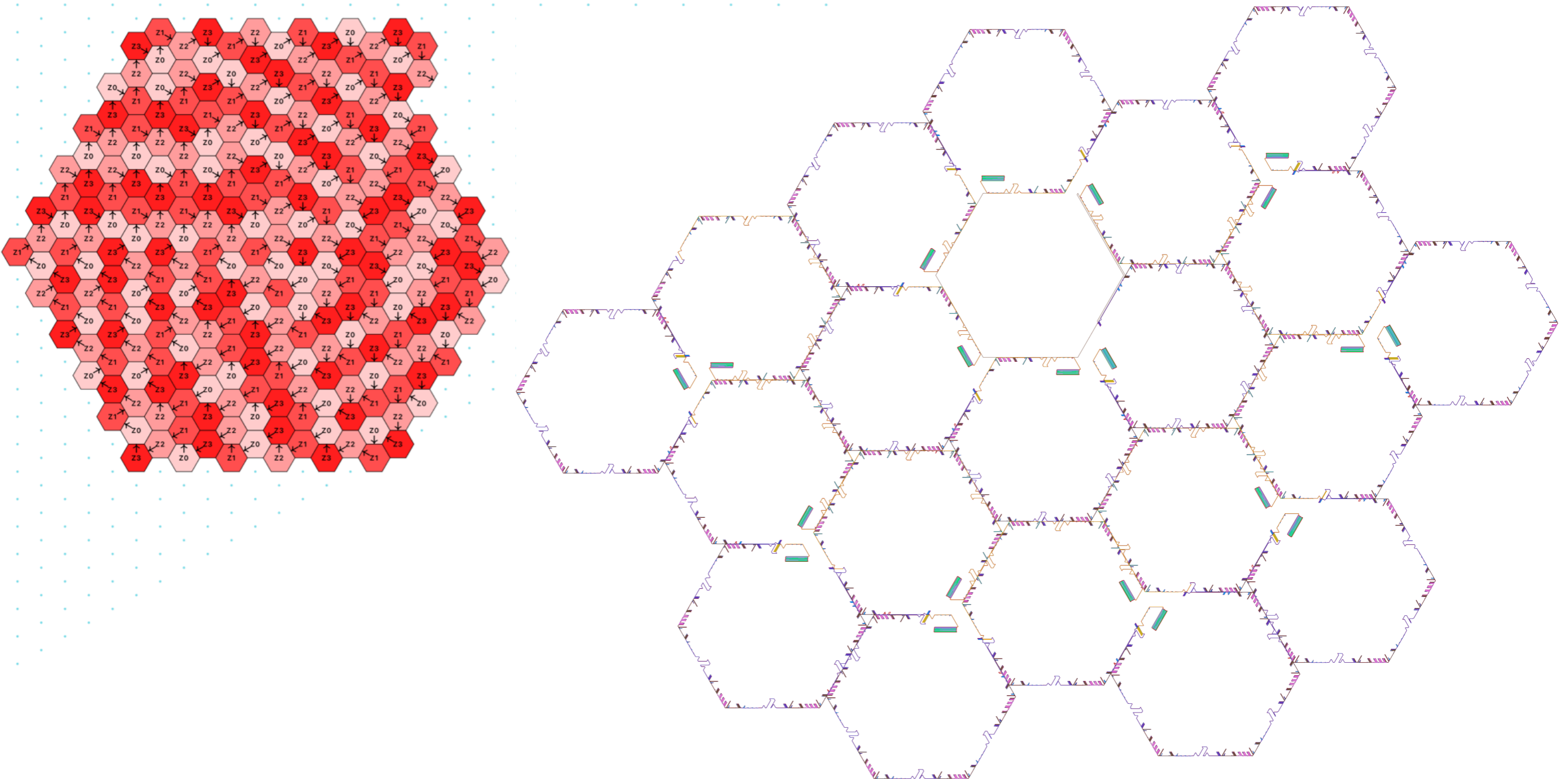
**Curvy speedbump**



# Almost there

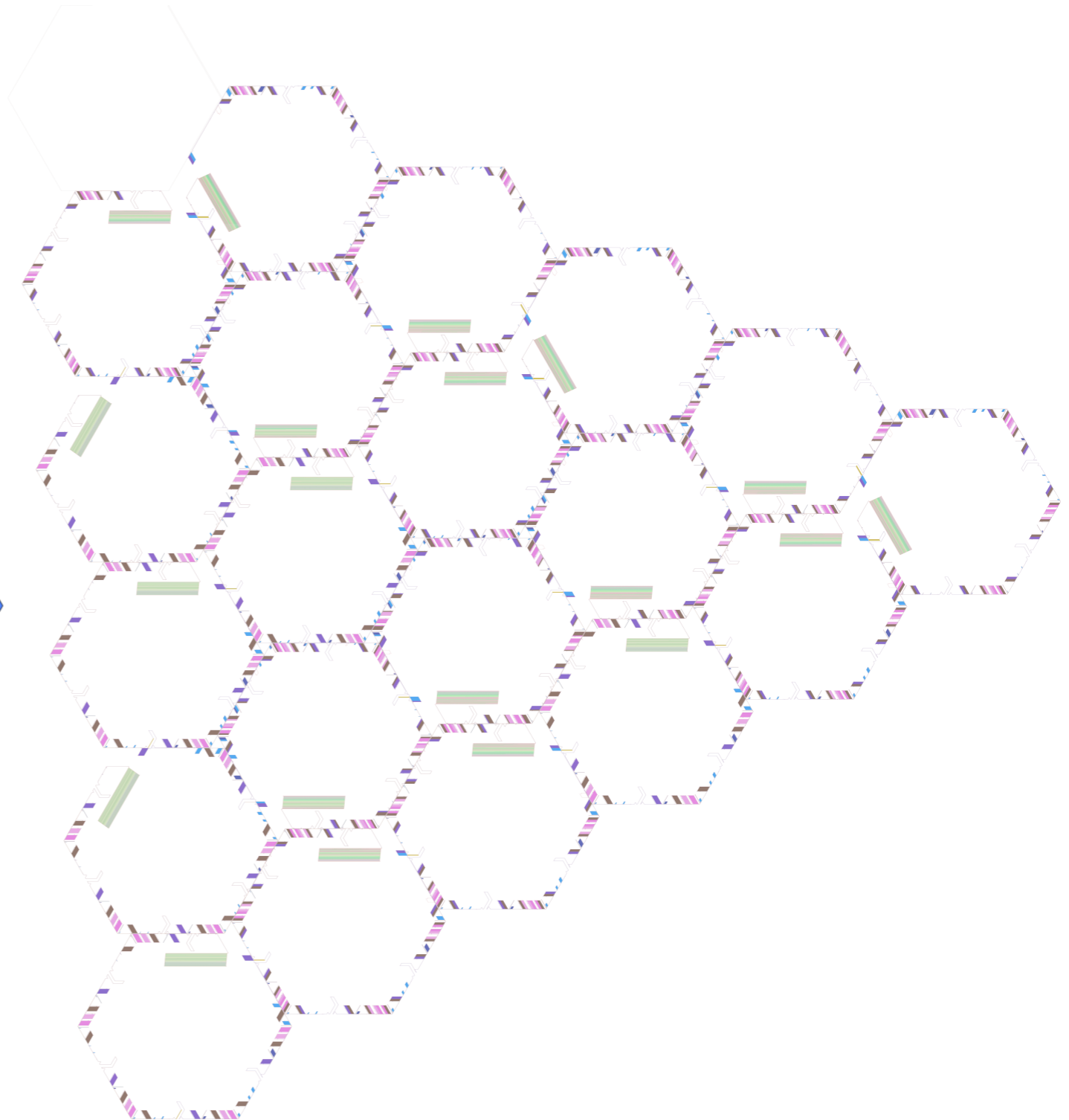
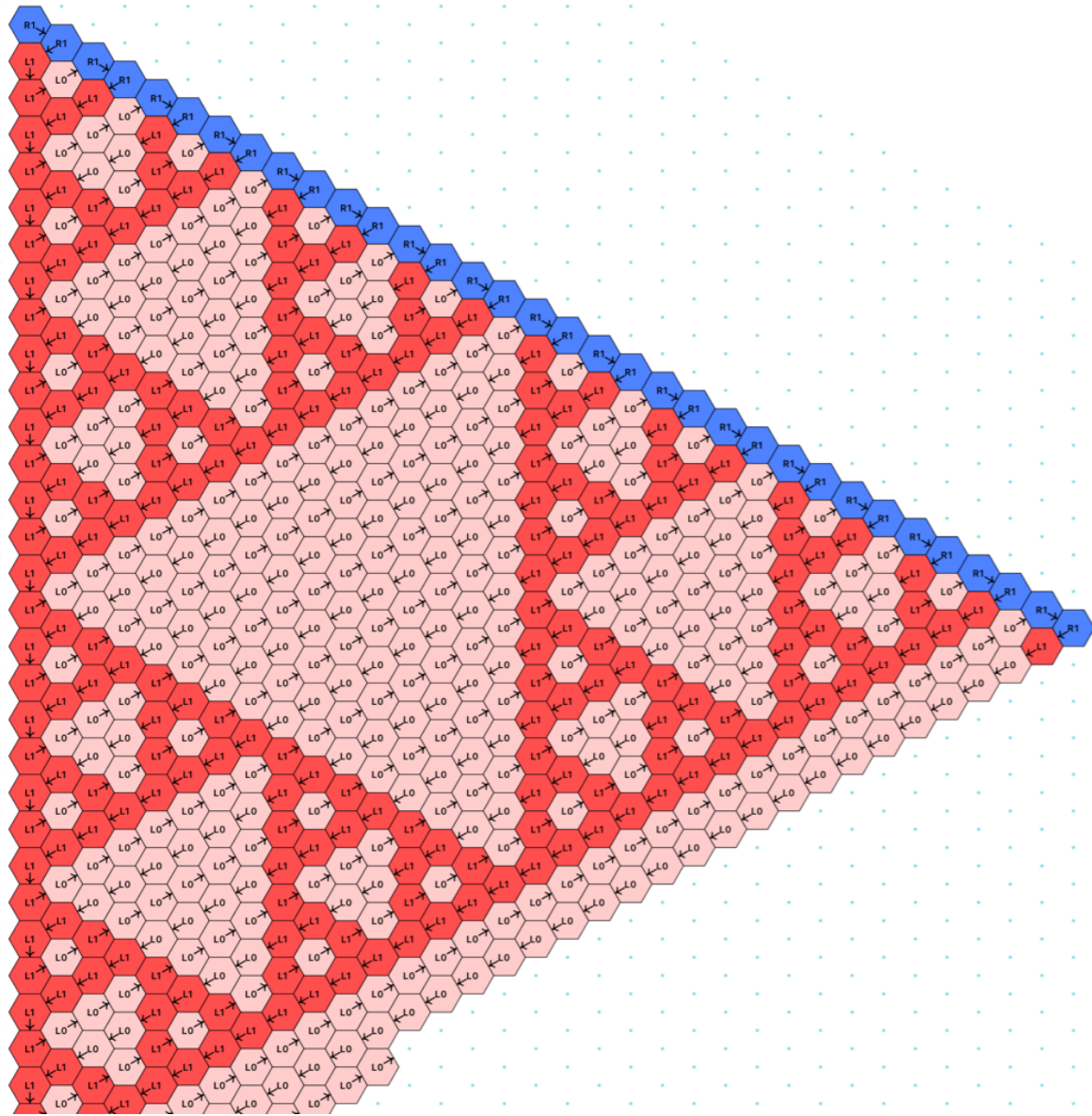


# Theorem 2. Delay-3 oritatami simulates intrinsically radius-1 turedos



**Example: A bouncy right hand turedo**

# Some examples



**A Sierpinsky turedo**

The background features a complex geometric pattern of red polygons of various shapes and sizes, separated by white paths. Overlaid on this pattern is a network of lines. A primary network of yellow lines connects several vertices, forming a series of interconnected paths. A secondary network of blue lines follows a similar but slightly offset path, creating a layered or double-line effect. The overall appearance is that of a mathematical or computational diagram, possibly representing a graph or a flow network.

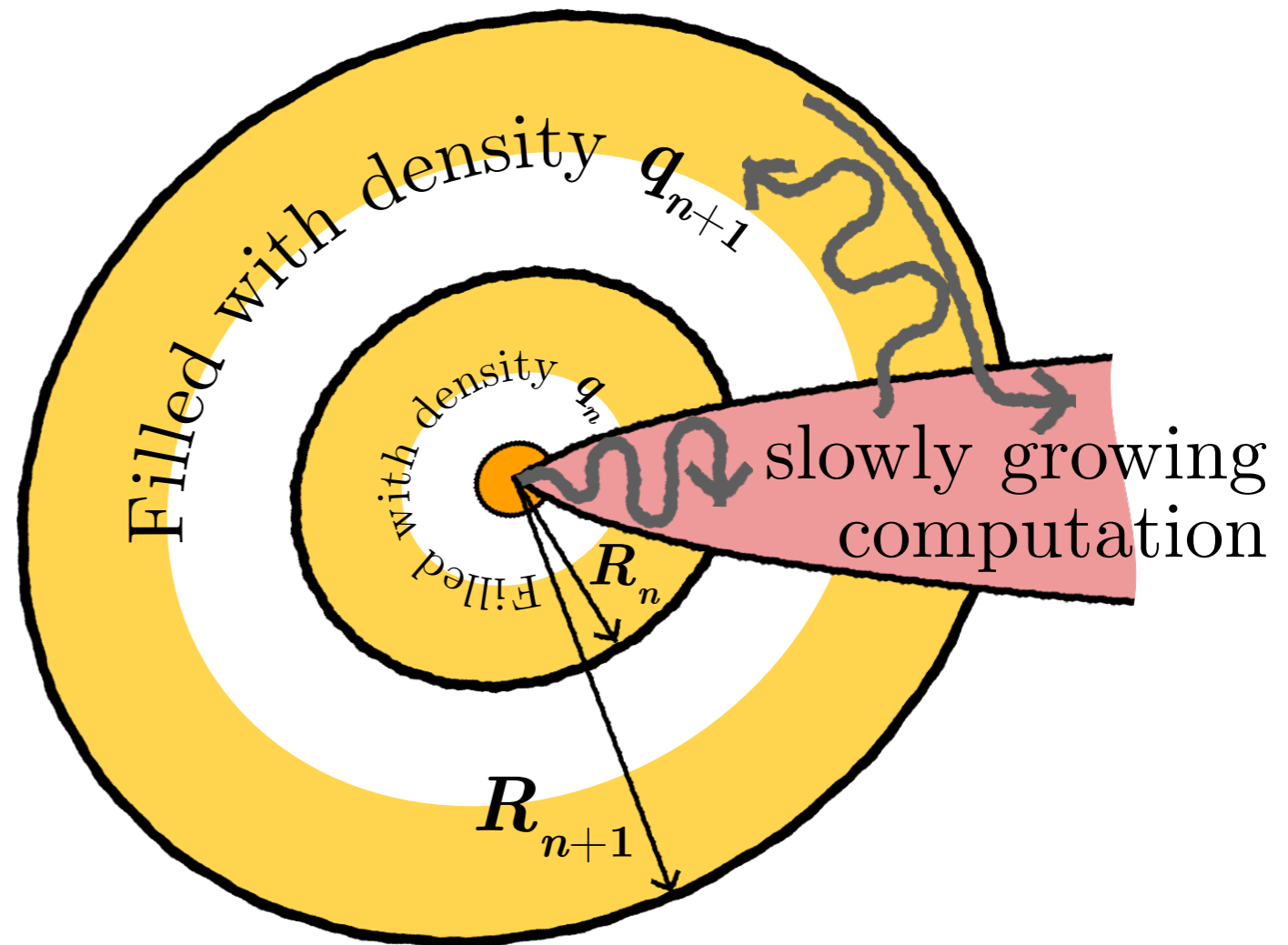
# The density of limit configurations

# Theorem 3. The densities of radius-1 Turedos limit configuration are all $\Pi_2$

$$\limsup_n q_n = q \in \Pi_2$$

Next annulus erases previous one by computing  $R_n$  such that:

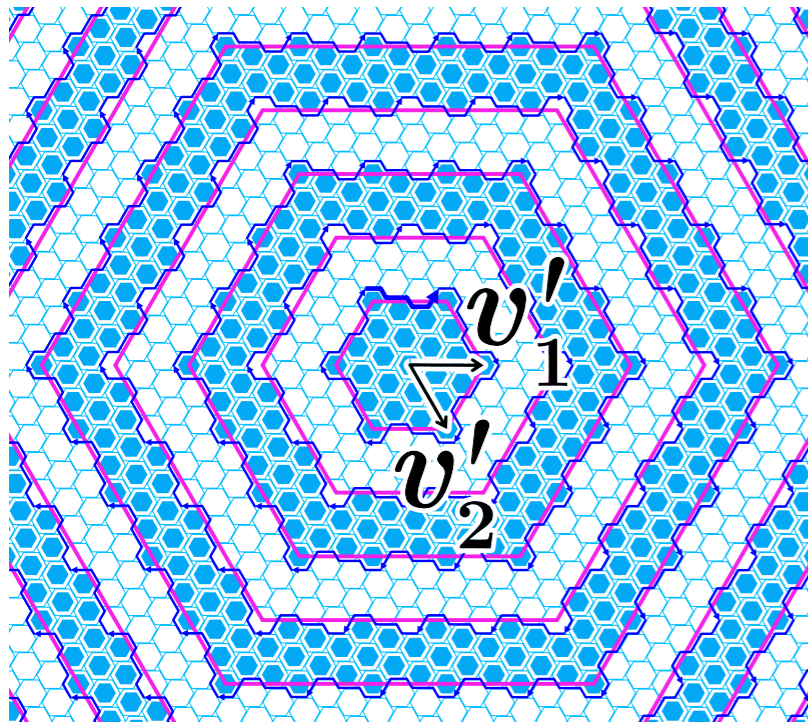
$$(R_{n+1})^2 q_{n+1} \gg (R_n)^2 q_n$$



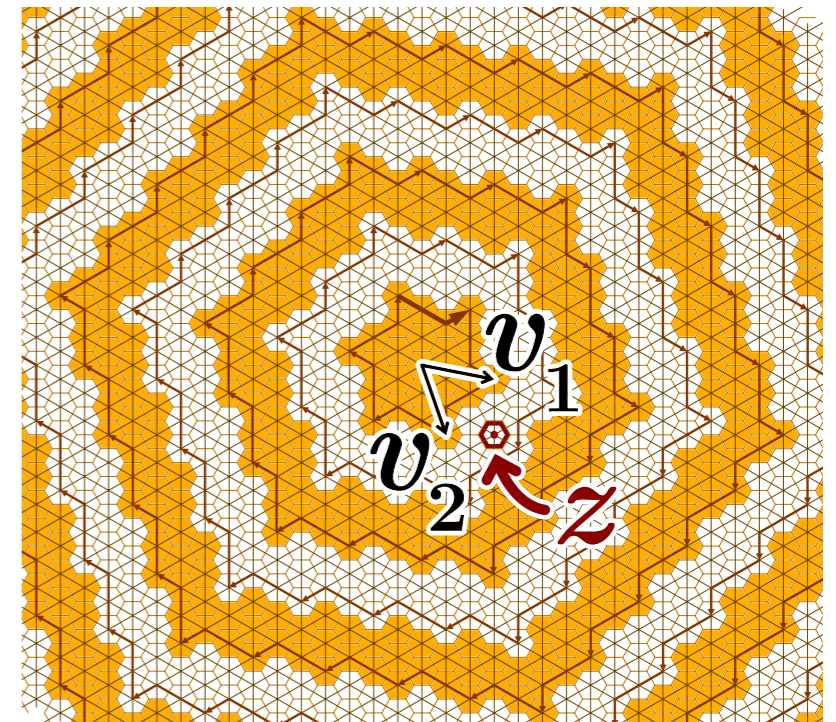
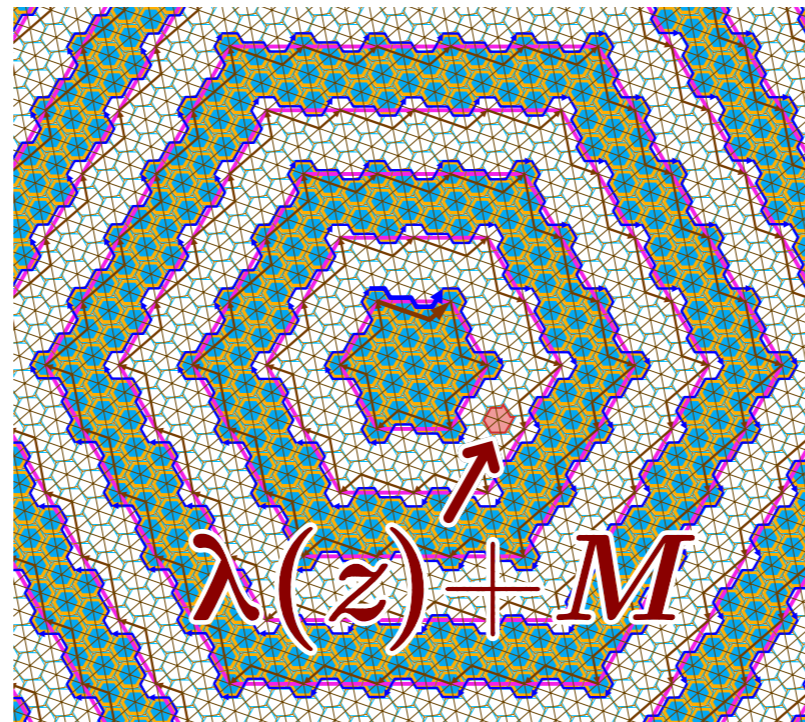
**Fact.** The densities of limit configurations for directed aTAM and freezing cellular automata belong to  $\Pi_2$  also.

# Corollary. The densities of oritatami limit configuration are all $\Pi_2$

Must beware of the **rotation induced** by the oritatami simulation



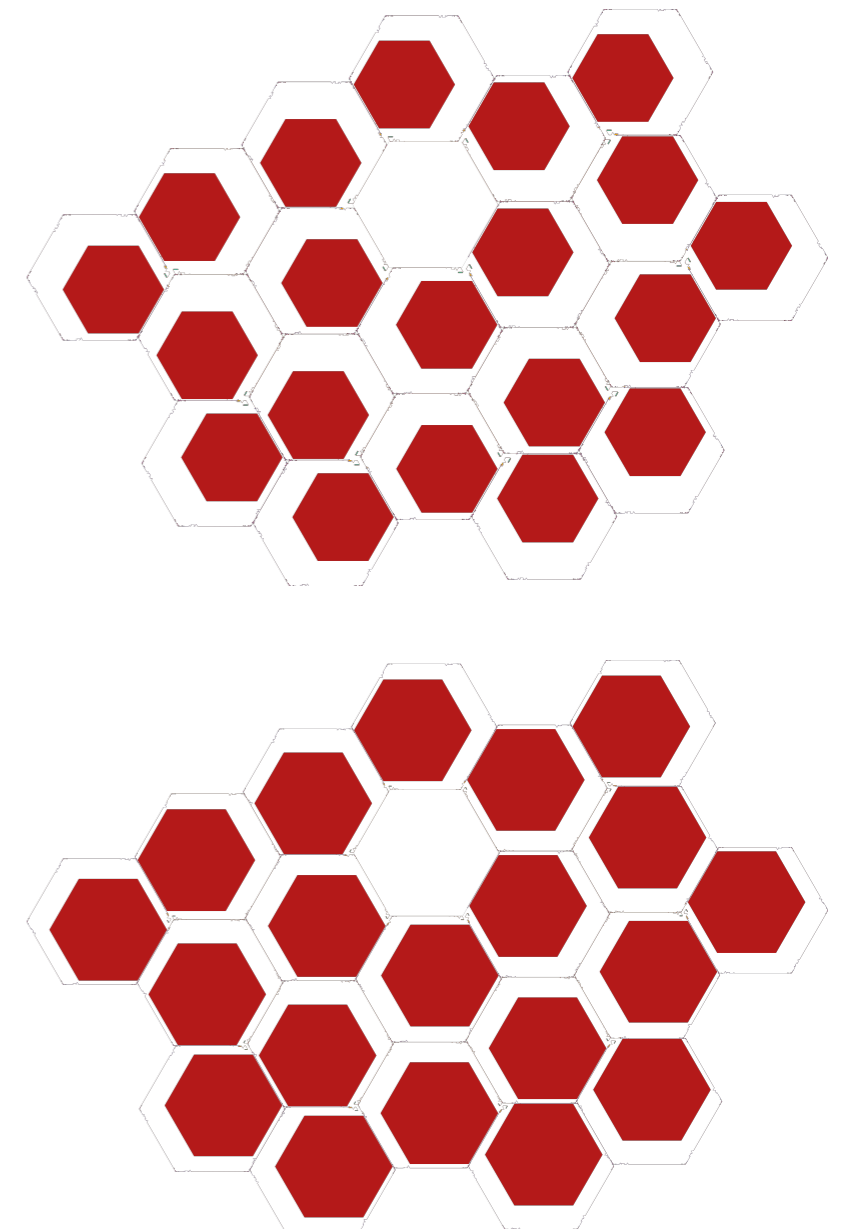
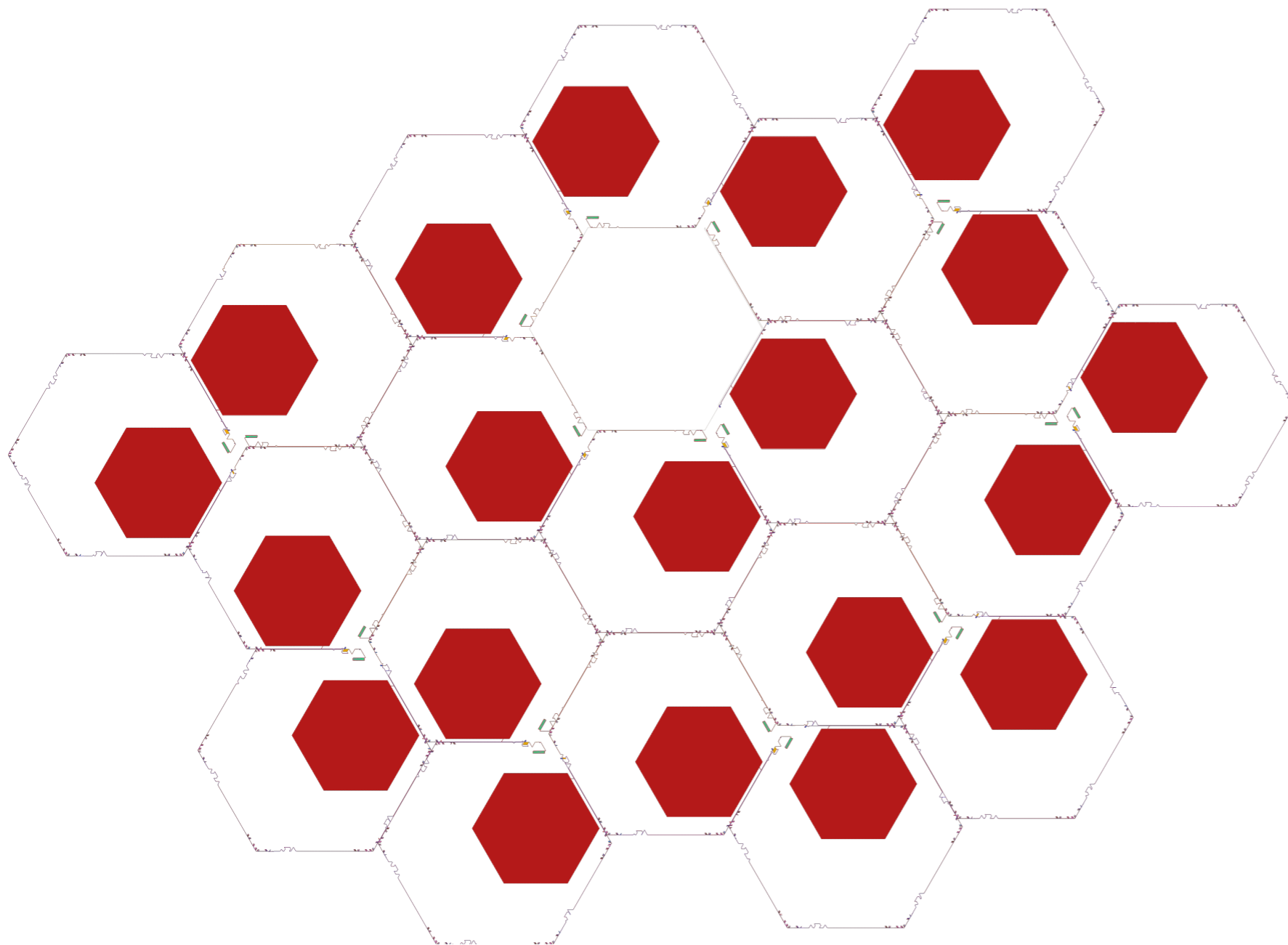
Oritatami world  
The target balls



Turedo world  
The simulated balls

# Corollary. The densities of oritatami limit configuration are all $\Pi_2$

Fill a hardcoded hexagon in the center of an extended macrocell



# Conclusion

- **No need for parallelism**
- **No need for 3D**
- Lines just don't cross!
- We have a running implementation:  
<https://hub.darcs.net/turedo2oritatami/turedo2oritatami/>
- New tools for Oritatami: **Folding meter, pockets, distant sensor & crazy-curvy speedbump, and... Turedo!**
- Some interesting turedos implemented in oritatami and... RNA ?  
e.g.: **simple plane filling oritatami**
- **What about turedos ?** → S. Nalin & G. Theyssier (*coming soon*)

