GRESHAM COLLEGE

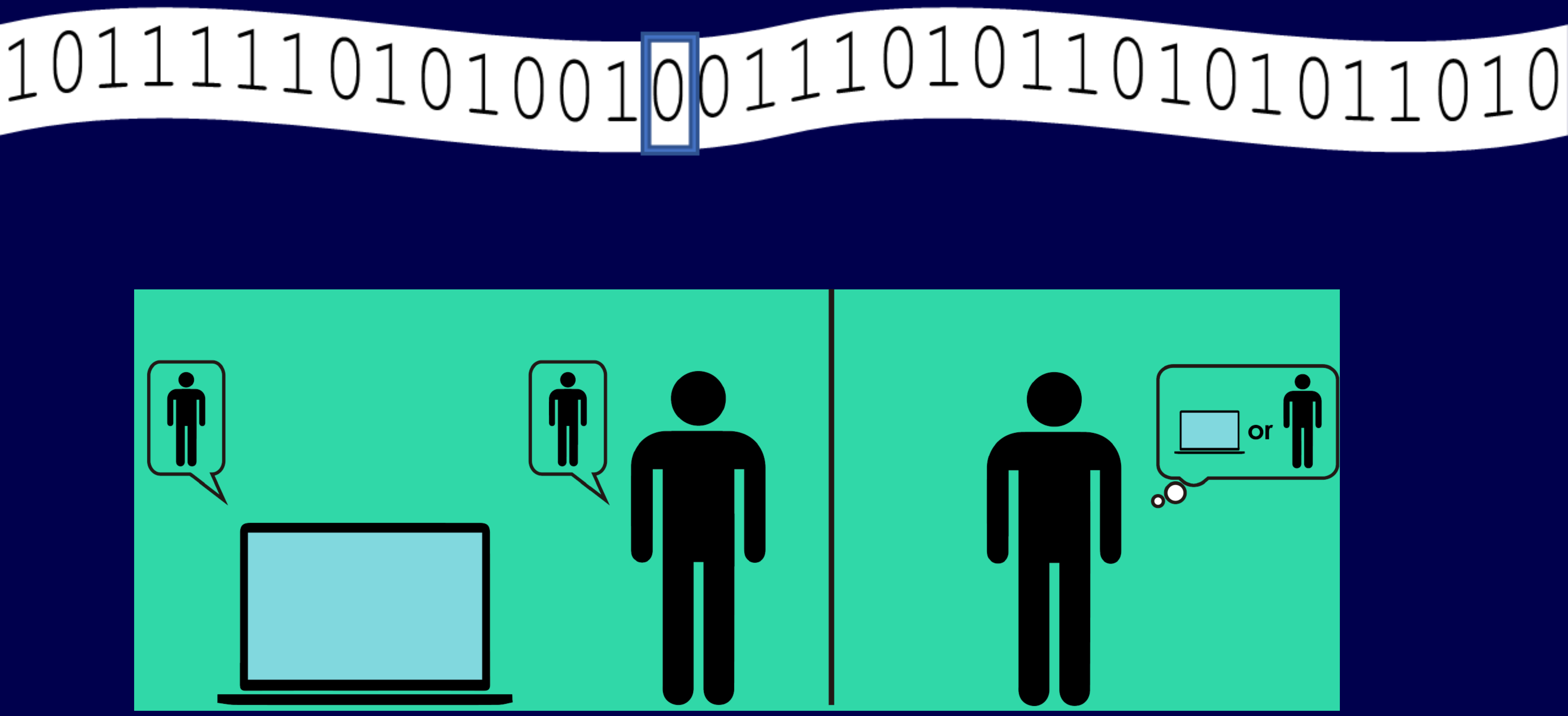
Alan Turing: Pioneer of Mathematical Biology

Professor Sarah Hart

Gresham Professor of Geometry

Birkbeck UNIVERSITY OF LONDON


Hockey, or, Watching the Daisies Grow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or

Enigma

- 158,962,555,218,000,000,000 settings
- 1 million/hour for 300 million years
- Turing reduced the problem to checking 1,054,560 settings.

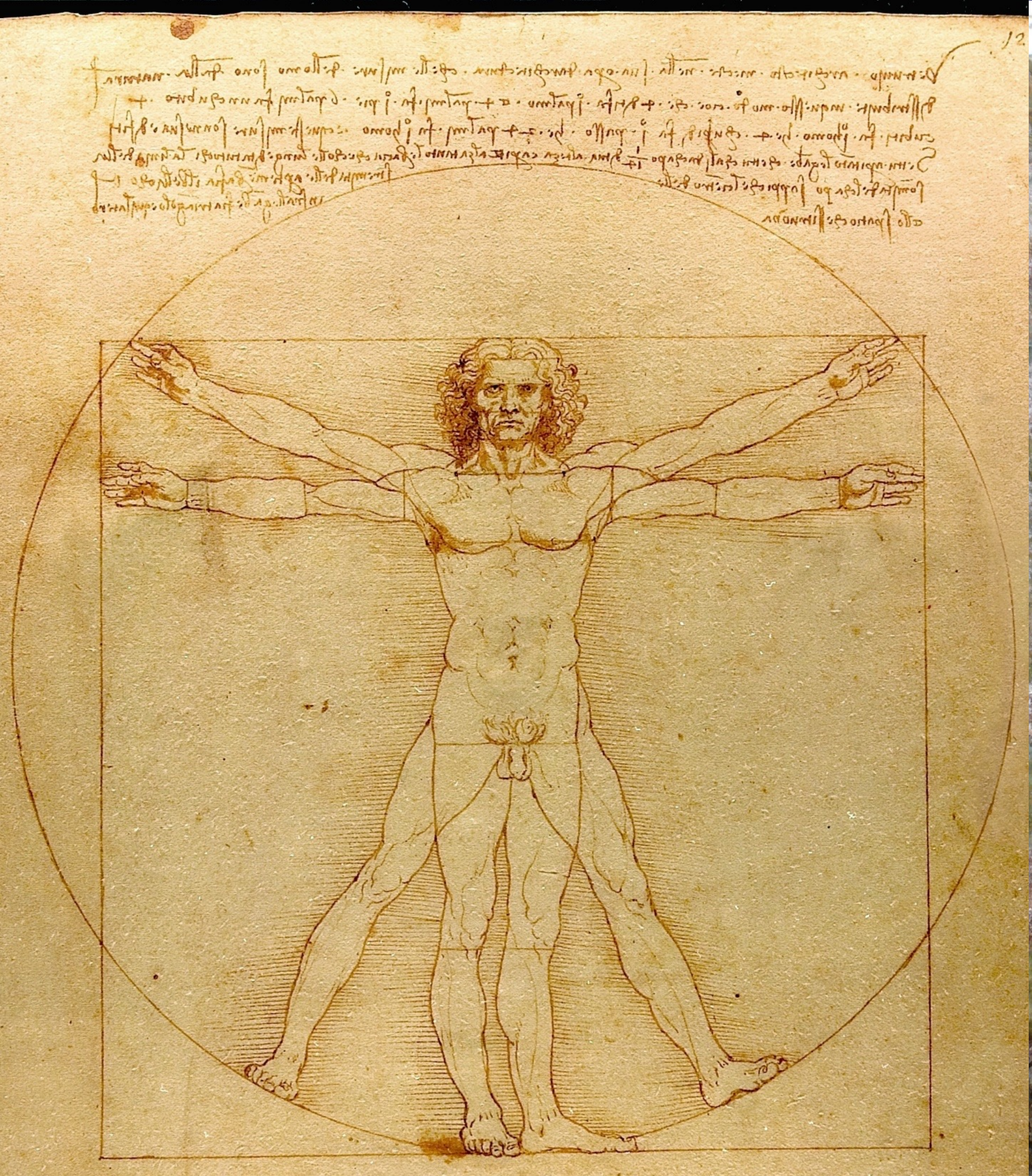
THE CHEMICAL BASIS OF MORPHOGENESIS

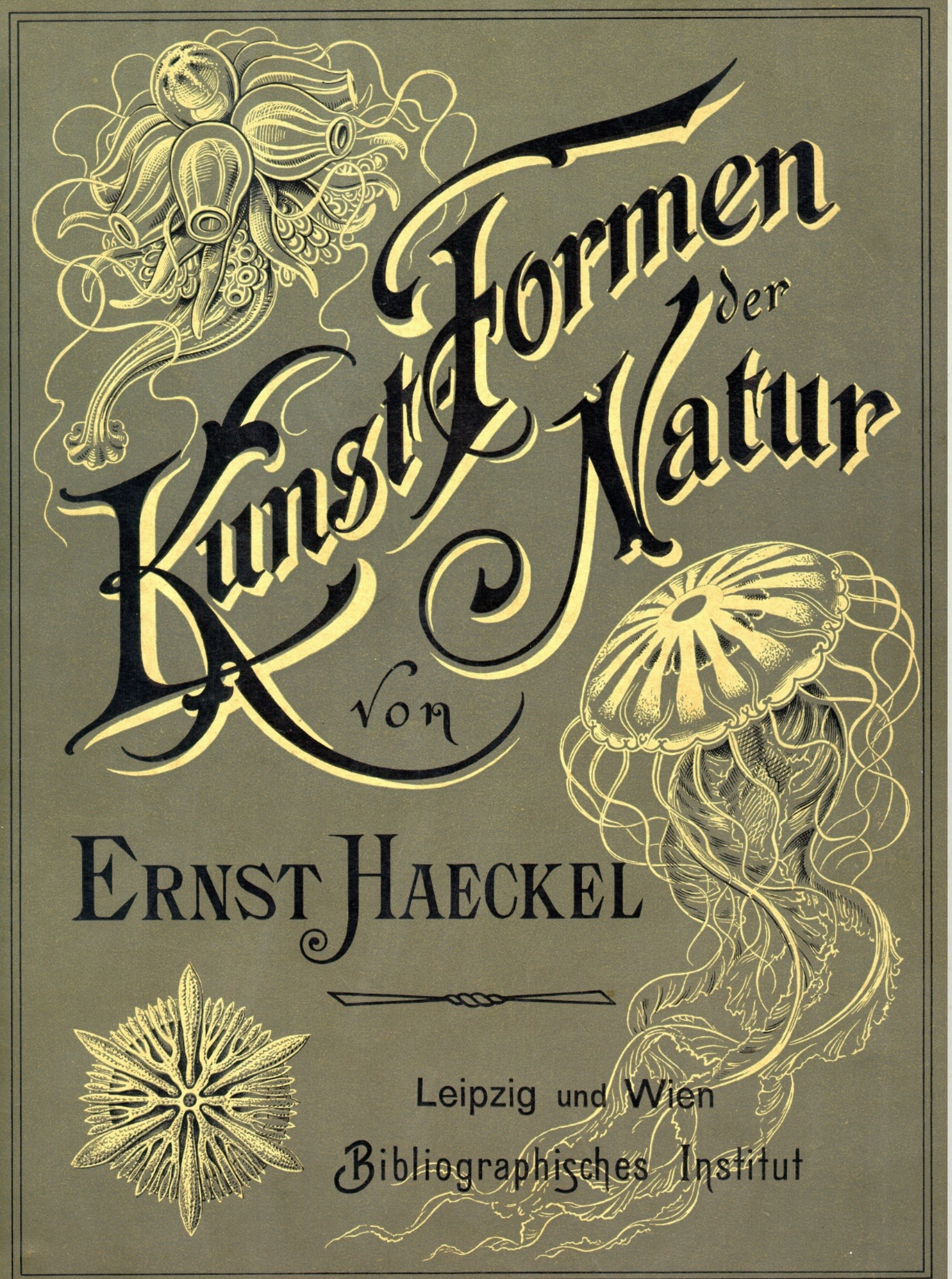
By A. M. TURING, F.R.S. *University of Manchester*

(*Received* 9 *November* 1951—*Revised* 15 *March* 1952)

It is suggested that a system of chemical substances, called morphogens, reacting together and diffusing through a tissue, is adequate to account for the main phenomena of morphogenesis. Such a system, although it may originally be quite homogeneous, may later develop a pattern or structure due to an instability of the homogeneous equilibrium, which is triggered off by random disturbances. Such reaction-diffusion systems are considered in some detail in the case of an isolated ring of cells, a mathematically convenient, though biologically unusual system. The investigation is chiefly concerned with the onset of instability. It is found that there are six essentially different forms which this may take. In the most interesting form stationary waves appear on the ring. It is suggested that this might account, for instance, for the tentacle patterns on *Hydra* and for whorled leaves. A system of reactions and diffusion on a sphere is also considered. Such a system appears to account for gastrulation. Another reaction system in two dimensions gives rise to patterns reminiscent of dappling. It is also suggested that stationary waves in two dimensions could account for the phenomena of phyllotaxis.

The purpose of this paper is to discuss a possible mechanism by which the genes of a zygote

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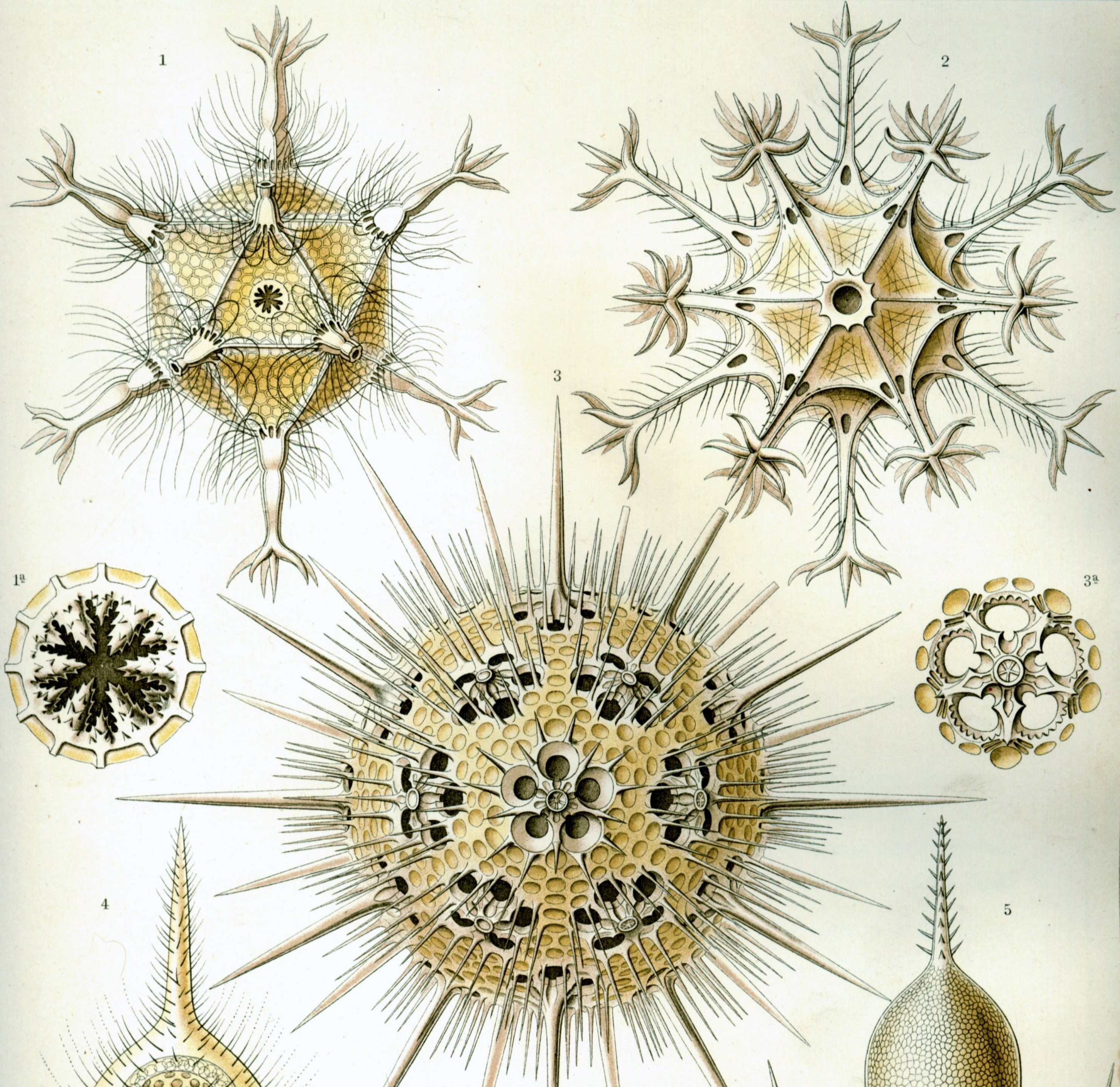
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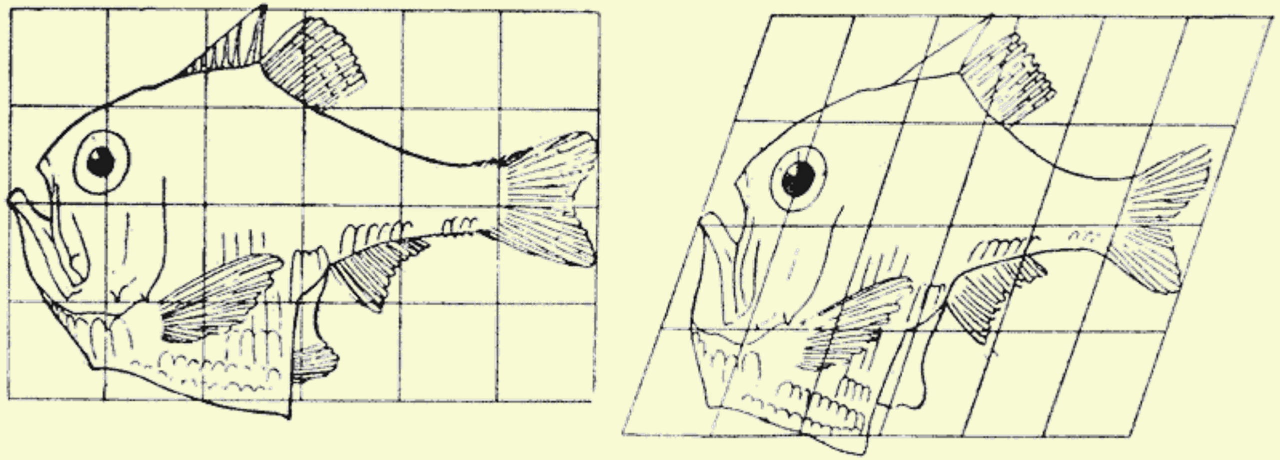
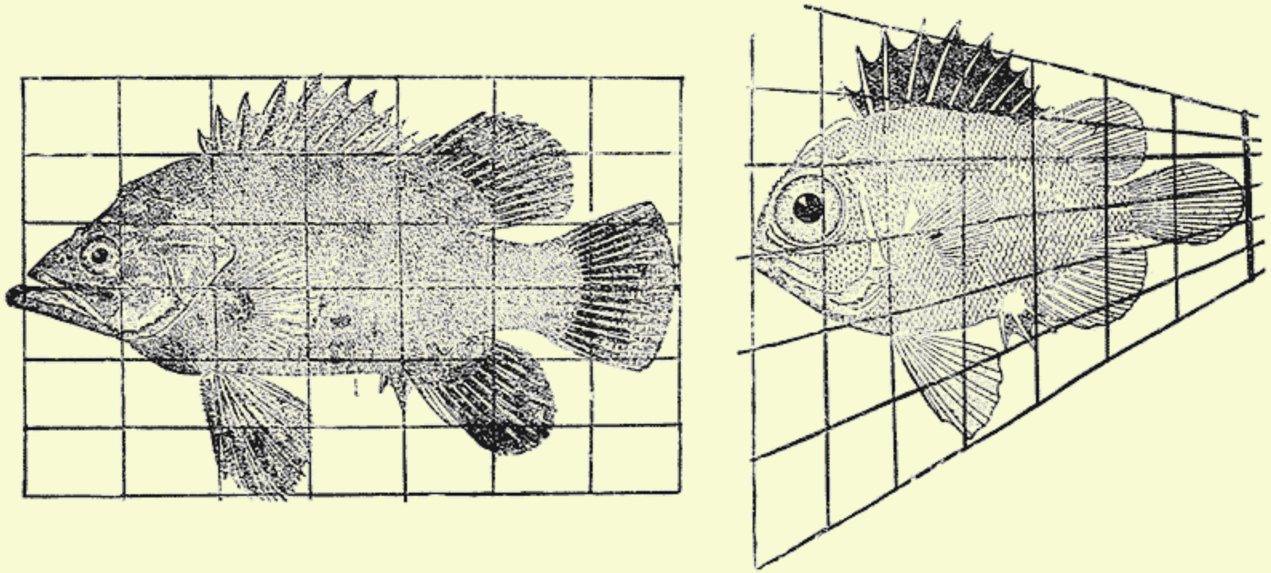
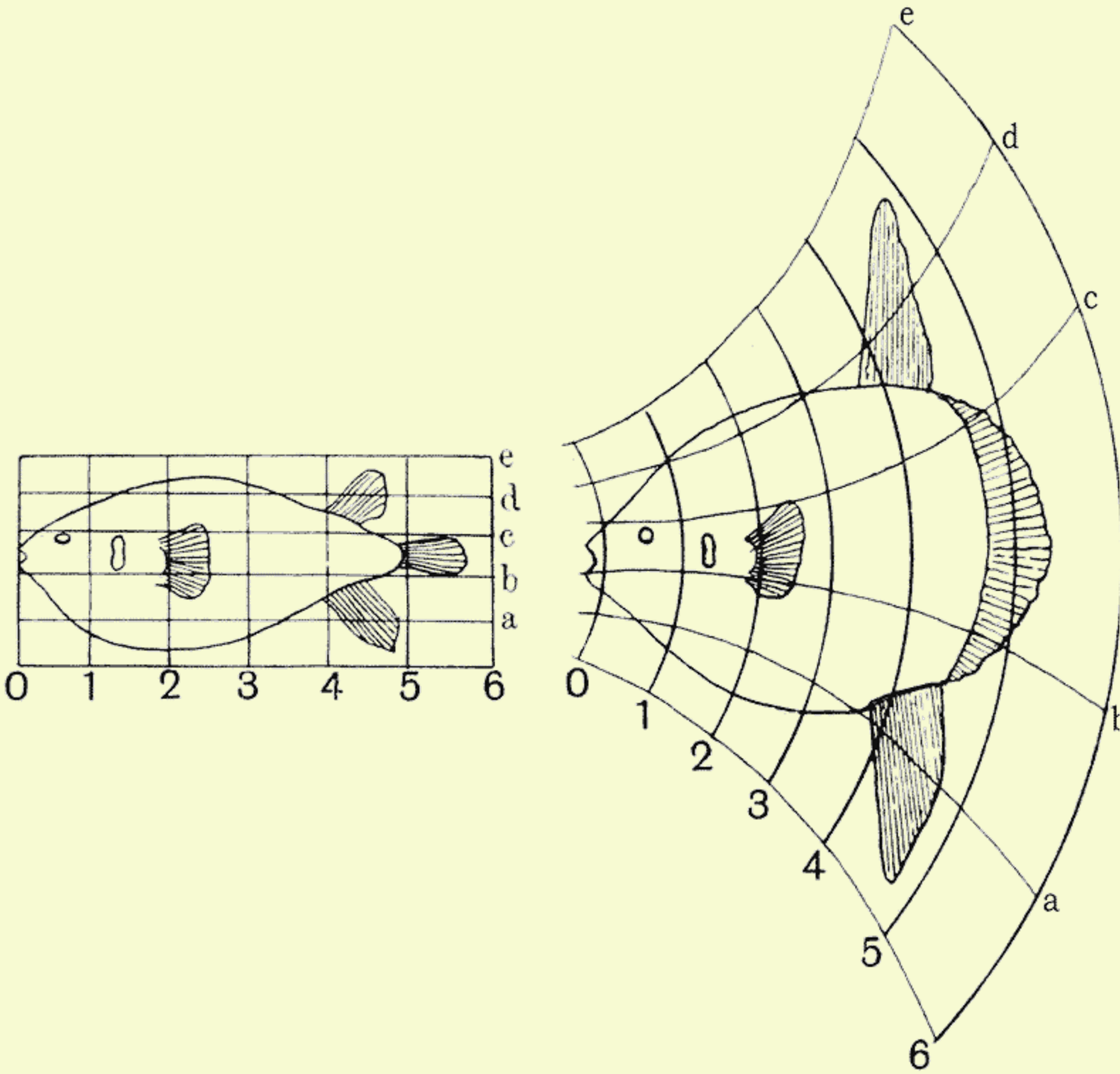
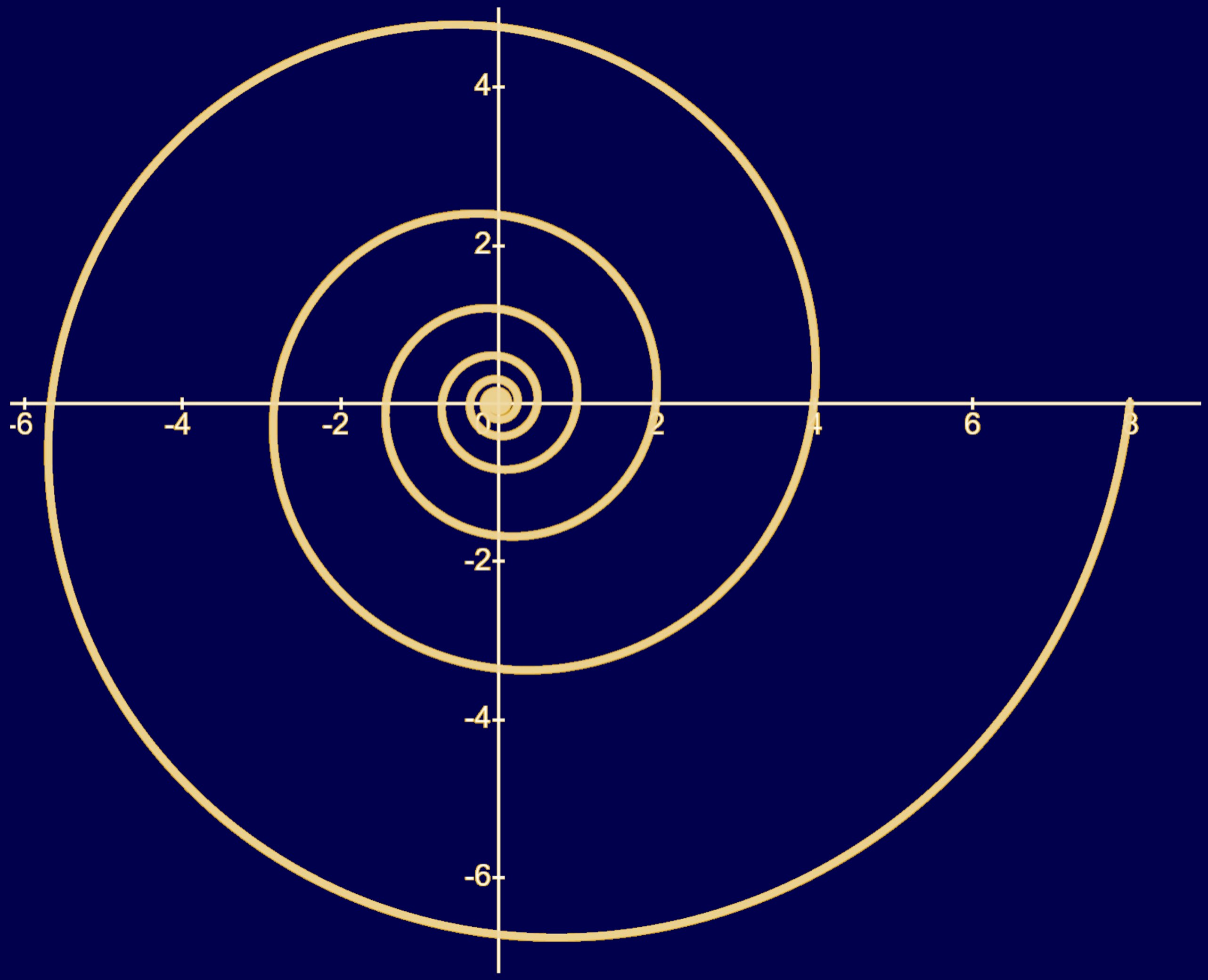
D’Arcy Thompson – On Growth and Form (1917)





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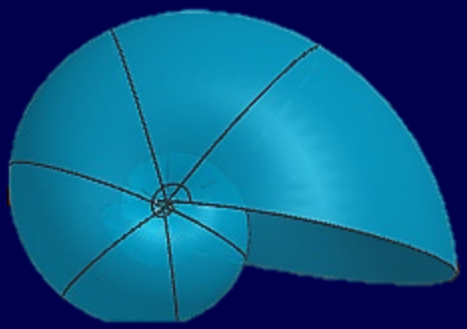

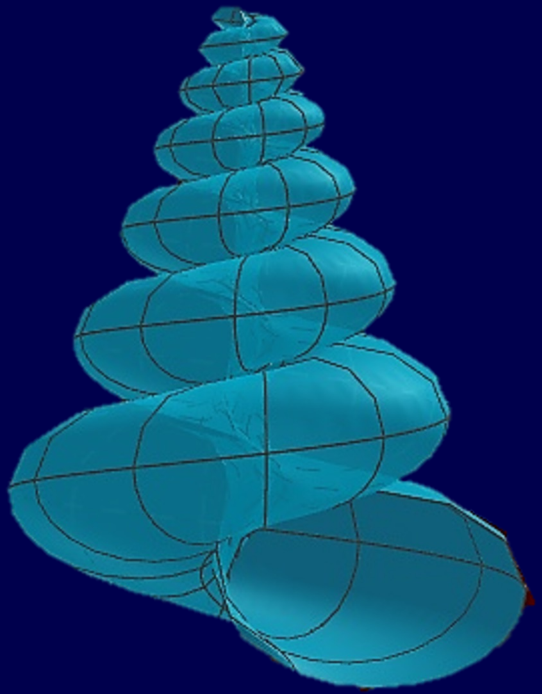

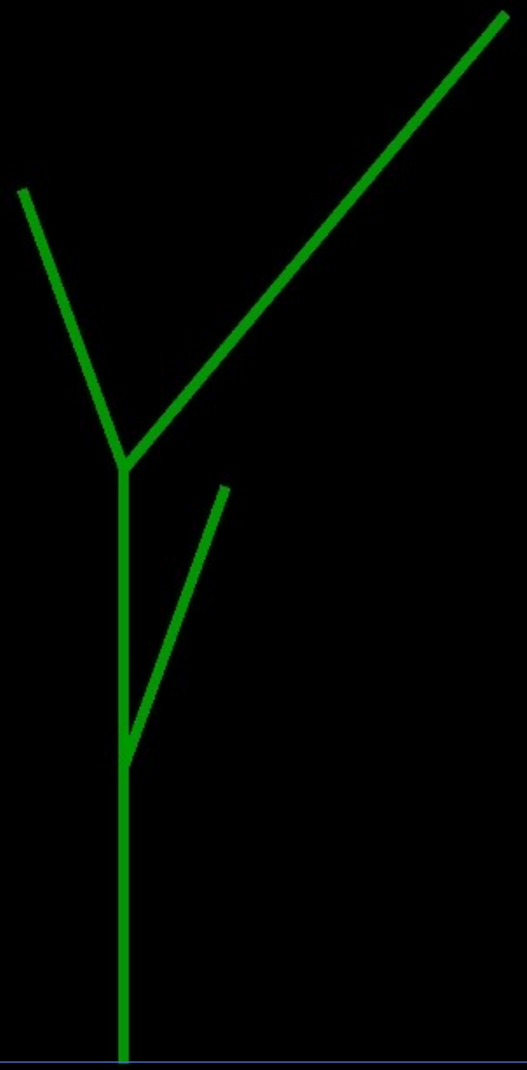


THE CHEMICAL BASIS OF MORPHOGENESIS

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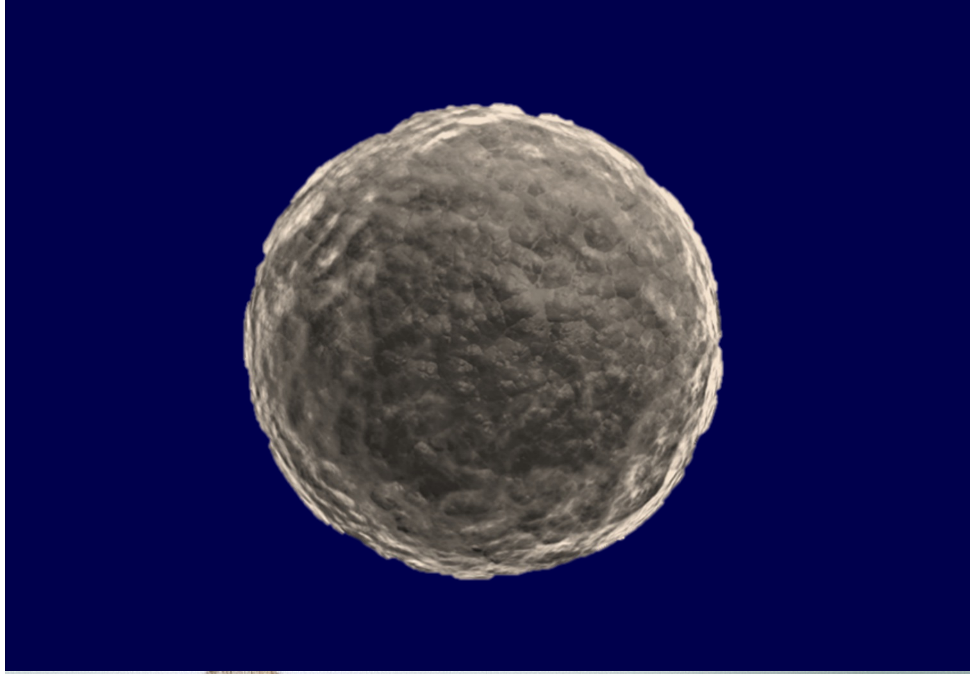
It is suggested that a system of chemical substances, called morphogens, reacting together and diffusing through a tissue, is adequate to account for the main phenomena of morphogenesis. Such a system, although it may originally be quite homogeneous, may later develop a pattern or structure due to an instability of the homogeneous equilibrium, which is triggered off by random disturbances. Such reaction-diffusion systems are considered in some detail in the case of an isolated ring of cells, a mathematically convenient, though biologically unusual system. The investigation is chiefly concerned with the onset of instability. It is found that there are six essentially different forms which this may take. In the most interesting form stationary waves appear on the ring. It is suggested that this might account, for instance, for the tentacle patterns on *Hydra* and for whorled leaves. A system of reactions and diffusion on a sphere is also considered. Such a system appears to account for gastrulation. Another reaction system in two dimensions gives rise to patterns reminiscent of dappling. It is also suggested that stationary waves in two dimensions could account for the phenomena of phyllotaxis.

The purpose of this paper is to discuss a possible mechanism by which the genes of a zygote may determine the anatomical structure of the resulting organism. The theory does not make any new hypotheses; it merely suggests that certain well-known physical laws are sufficient to account for many of the facts. The full understanding of the paper requires a good knowledge of mathematics, some biology, and some elementary chemistry. Since readers cannot be expected to be experts in all of these subjects, a number of elementary facts are explained, which can be found in text-books, but whose omission would make the paper difficult reading.

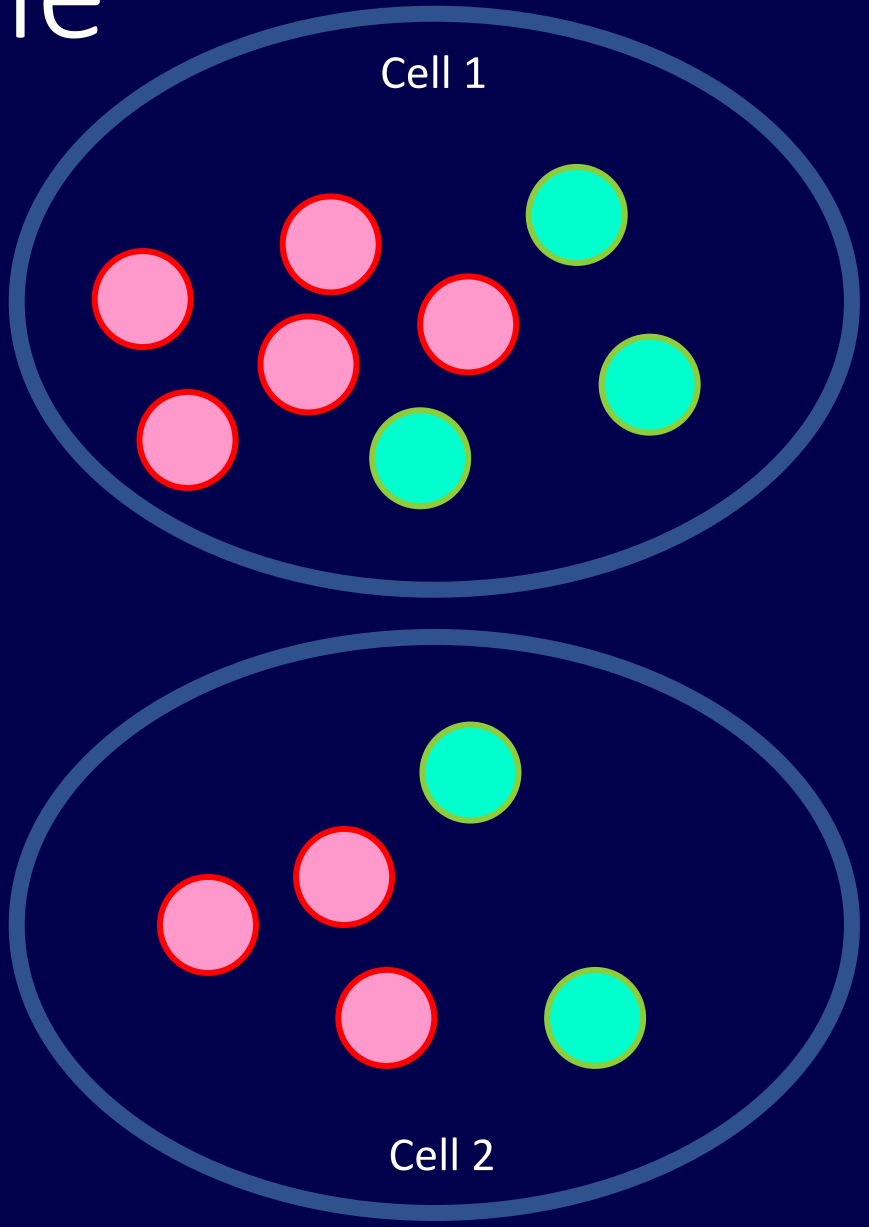
1. A model of the embryo. Morphogens

In this section a mathematical model of the growing embryo will be described. This model will be a simplification and an idealization, and consequently a falsification. It is to be hoped that the features retained for discussion are those of greatest importance in the present state of knowledge.



A diffusion-reaction example

Morphogen x Morphogen y



Diffusion – between cells

- Concentration of x: X_1 in Cell 1; X_2 in Cell 2
- x diffuses to Cell 2 at rate $0.5(X_1 - X_2)$
- So rate of change of X_1 is $0.5(X_1 - X_2)$
- Eg here initial diffusion rate = 1

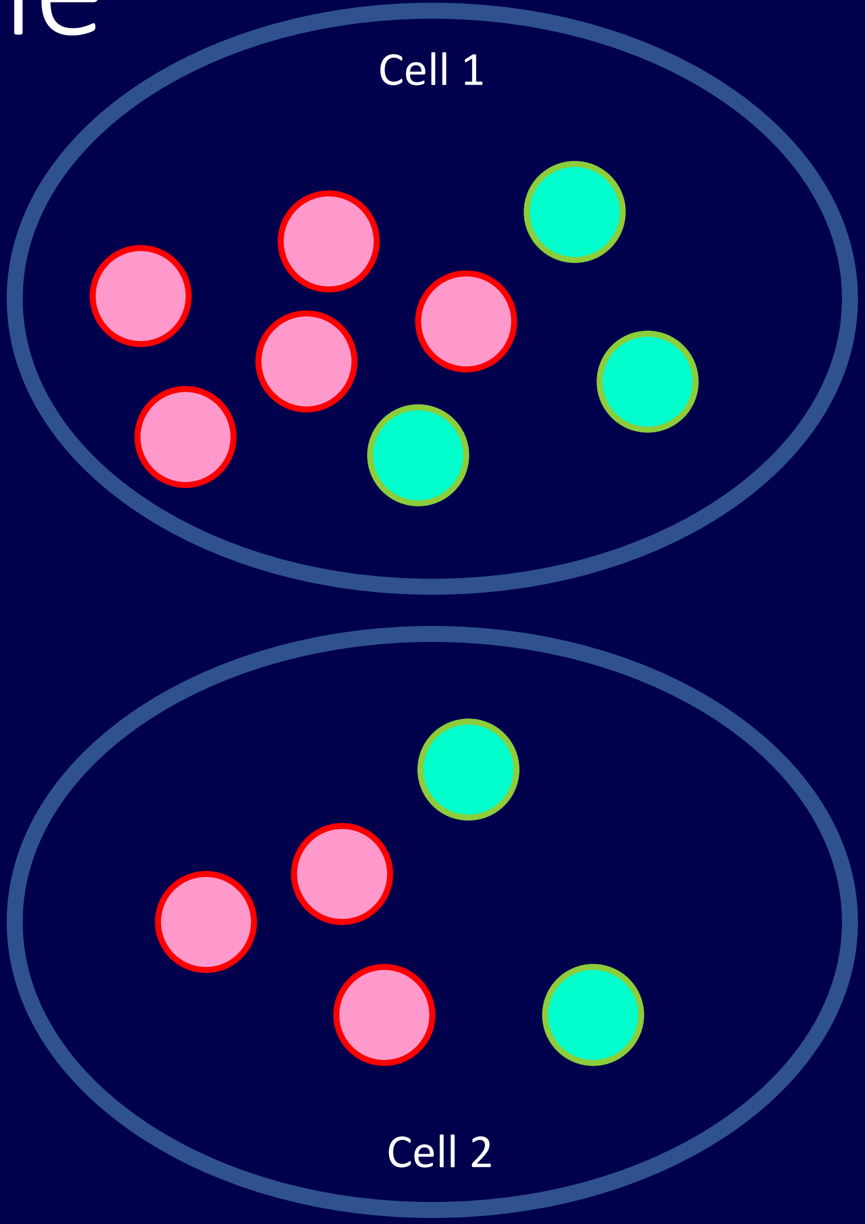
Reaction – inside cells

- Rate of production of x in Cell 1 is $5X_1 - 6Y_1 + 1$
- Eg here rate of change of X_1 is +8

"rate of change" of eg X_1 denoted $\dot{X}_1$.

A diffusion-reaction example

Morphogen x Morphogen y

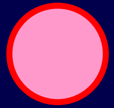
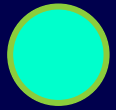


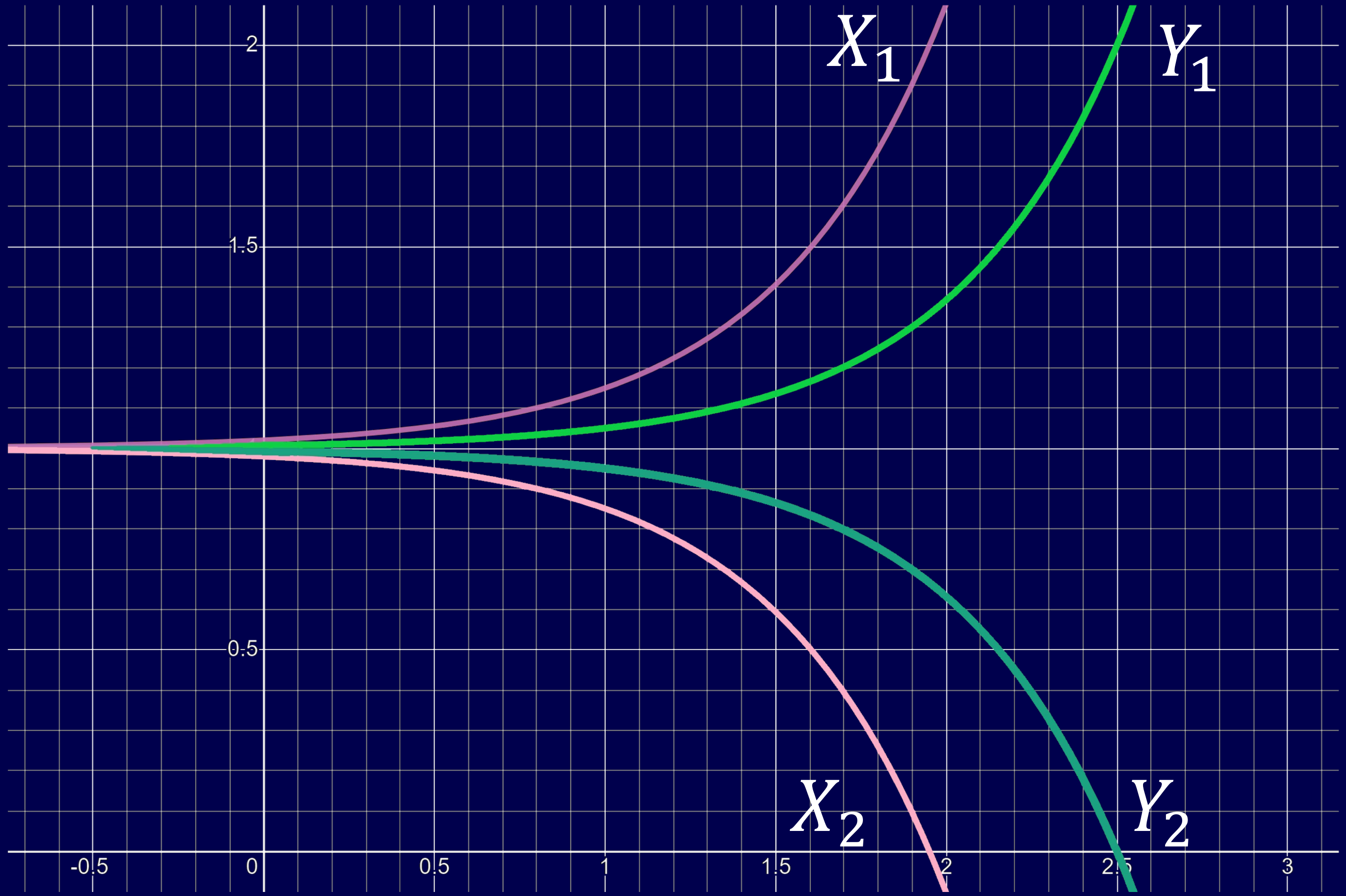
The four equations

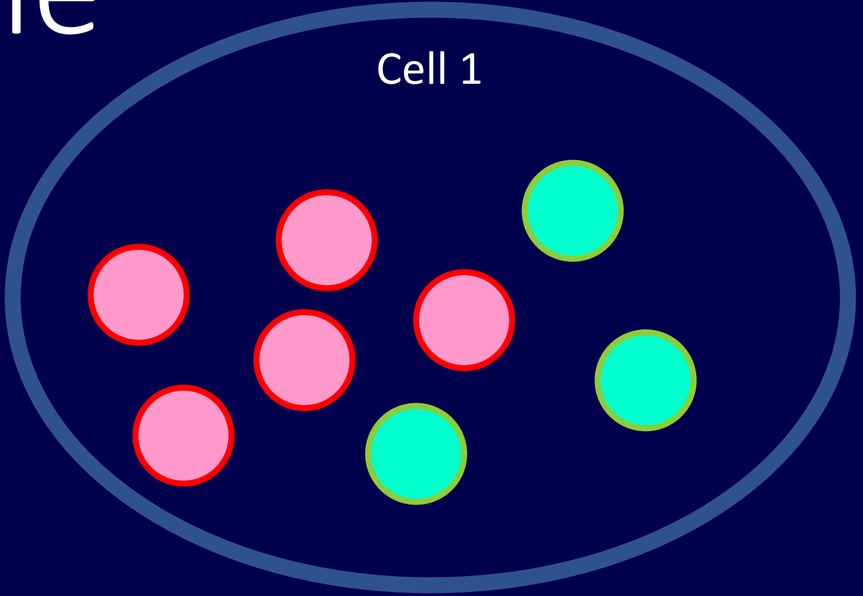
$$\dot{X}_1 = 0.5(X_1 - X_2) + 5X_1 - 6Y_1 + 1$$
$$\dot{X}_2 = 0.5(X_2 - X_1) + 5X_2 - 6Y_2 + 1$$
$$\dot{Y}_1 = 4.5(Y_1 - Y_2) + 6X_1 - 7Y_1 + 1$$
$$\dot{Y}_2 = 4.5(Y_2 - Y_1) + 6X_2 - 7Y_2 + 1$$

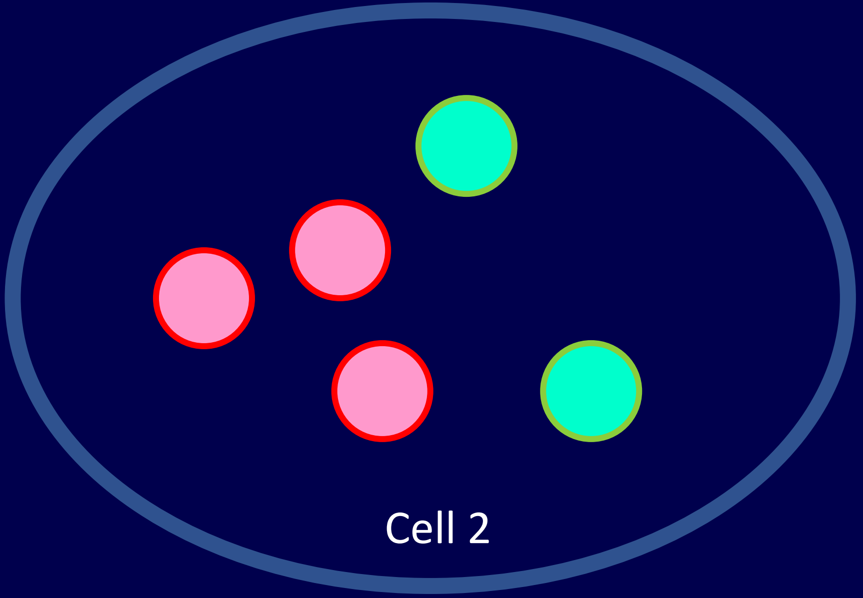
- If $X_1 = X_2 = Y_1 = Y_2 = 1$, equilibrium.
- Suppose $X_1 = 1.06$, $Y_1 = 1.02$, $X_2 = 0.94$, $Y_2 = 0.98$.
- Then $\dot{X}_1 = 0.18$, $\dot{X}_2 = -0.18$, $\dot{Y}_1 = 0.22$, $\dot{Y}_2 = -0.22$

A diffusion-reaction example

Morphogen x  Morphogen y 







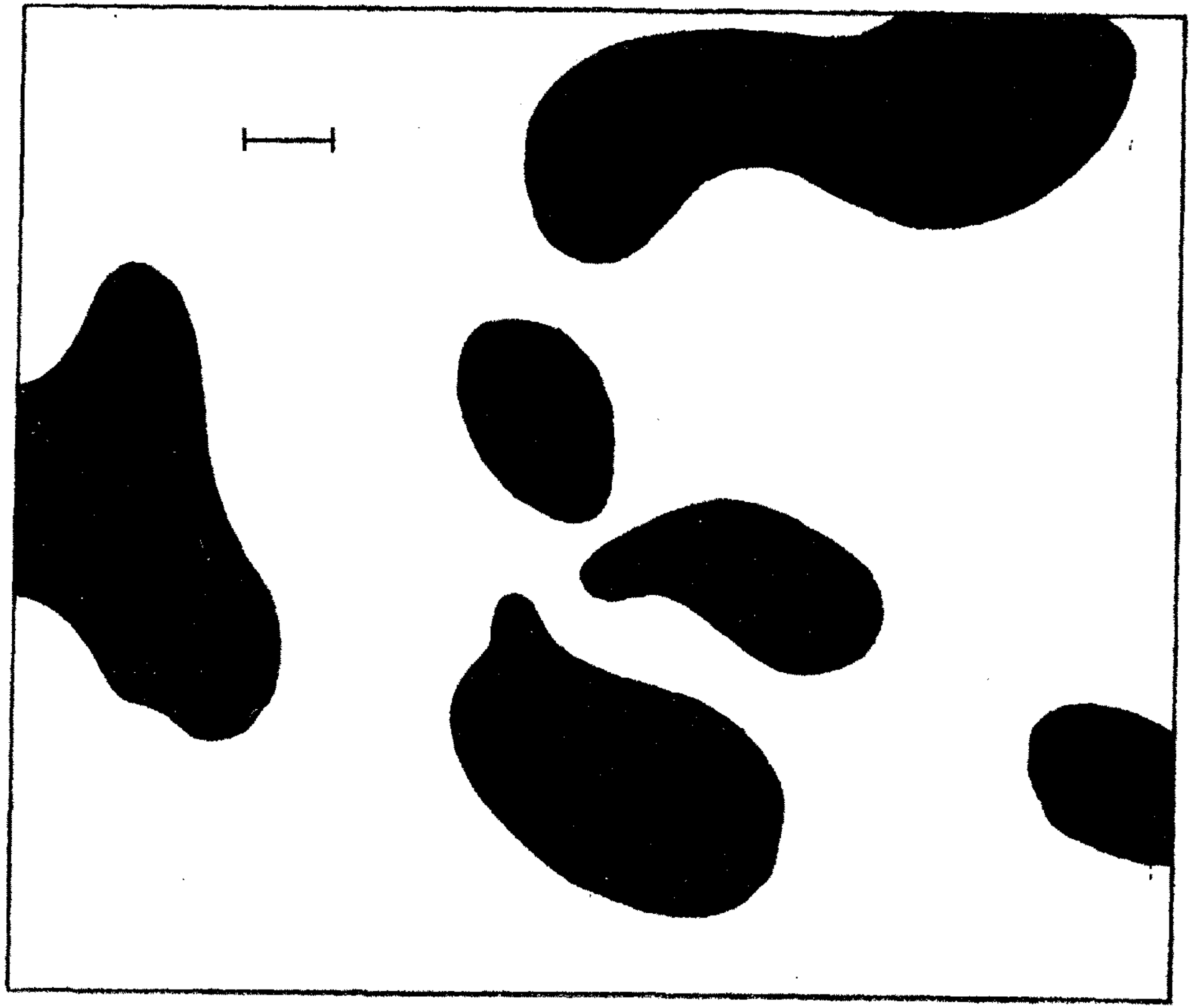
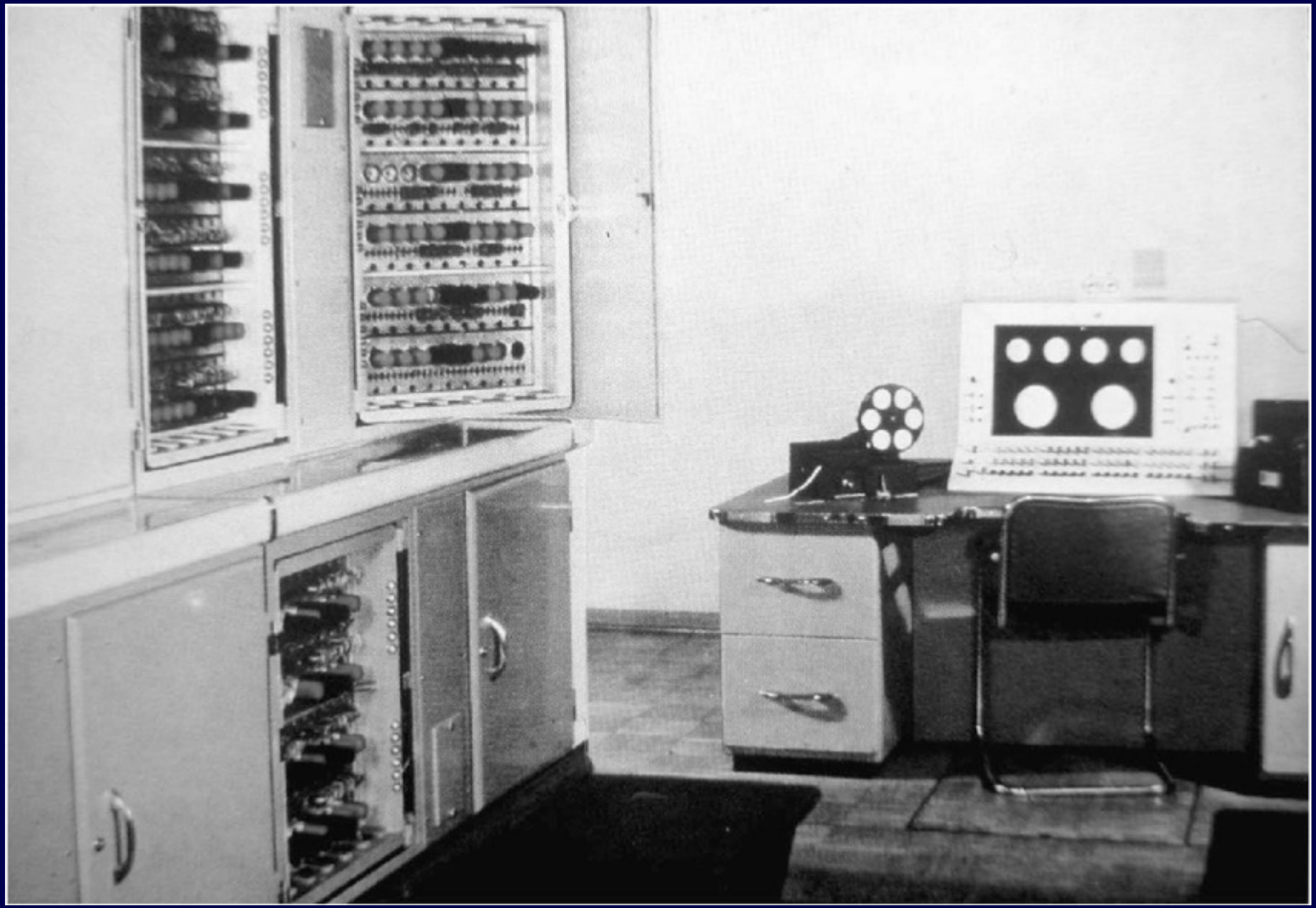
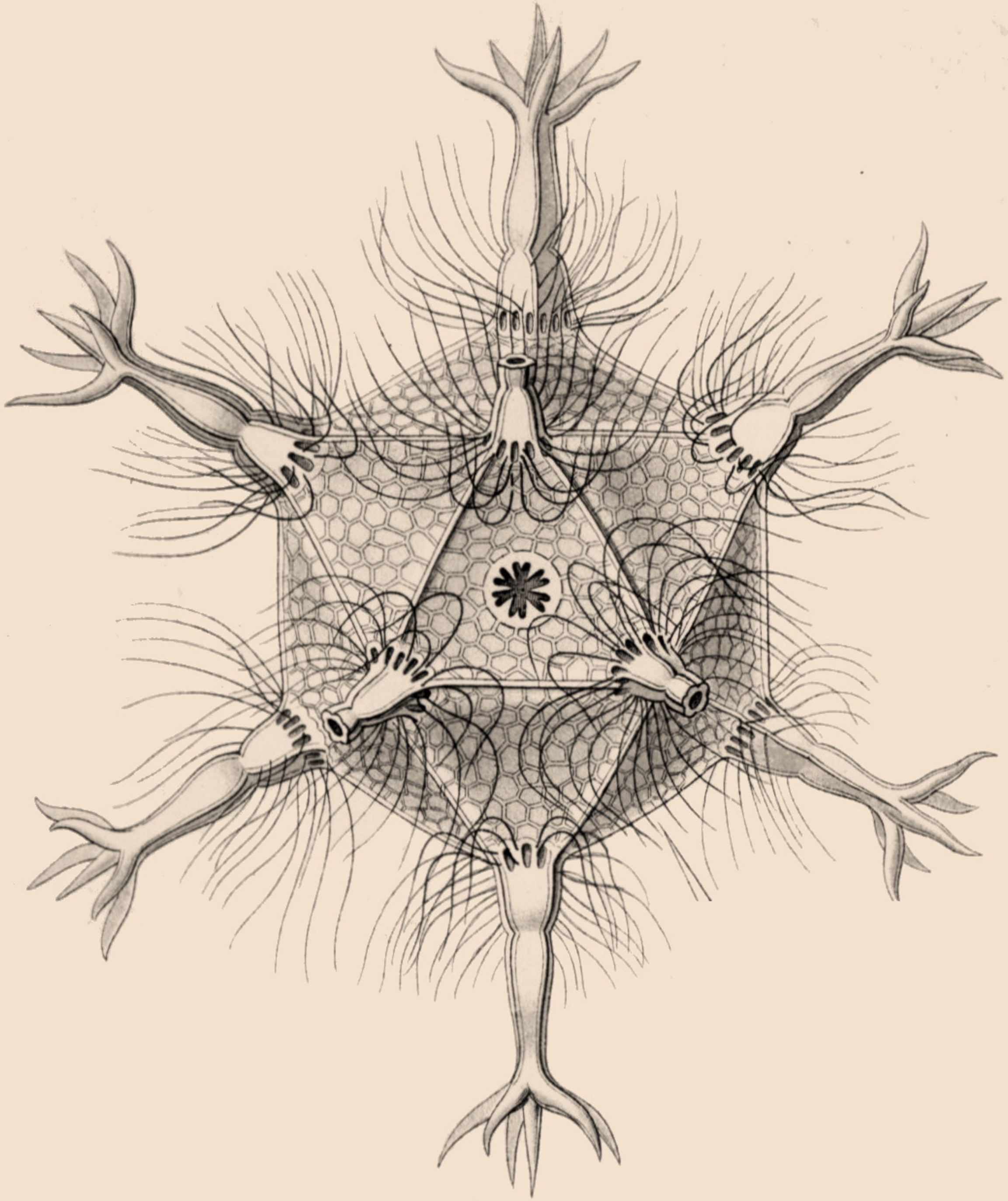


FIGURE 2. An example of a 'dappled' pattern as resulting from a type (*a*) morphogen system. A marker of unit length is shown. See text, §9, 11.

Radiolaria and the Ferranti Mark I



49	66	89	52	28	98	10	36	33	83	2	13	26	5	38
62	72	31	79	53	39	37	13	74	83	16	59	74	49	40
32	29	32	86	97	78	92	55	91	27	62	94	62	97	40
67	30	93	15	76	34	69	7	64	53	36	66	46	16	90
4	4	56	74	20	83	30	38	89	70	87	63	94	69	88
41	63	71	7	36	61	63	73	58	96	28	23	38	1	49
26	98	45	4	99	54	90	65	14	24	48	20	41	45	86
0	52	25	10	34	92	37	30	33	85	98	92	95	16	92
64	22	2	96	47	90	99	60	56	68	17	66	66	3	11
22	46	69	52	21	53	77	45	2	56	33	39	75	24	27
50	84	26	3	73	73	35	82	30	85	8	82	71	46	97
54	29	9	93	97	38	7	60	58	90	34	6	73	69	89
65	22	66	28	35	12	94	71	43	21	66	25	46	19	20
73	97	18	20	32	52	60	47	71	73	27	31	63	13	27
81	39	52	42	50	2	72	15	71	96	99	39	20	71	98
50	82	34	90	12	69	83	32	38	81	84	13	48	53	84
20	32	84	72	14	32	85	63	30	95	0	4	37	30	83
13	33	85	31	32	77	55	27	2	15	54	79	66	61	19
6	12	9	9	67	53	54	88	87	36	99	51	41	22	76
27	9	86	36	36	17	66	84	75	1	36	11	88	73	67

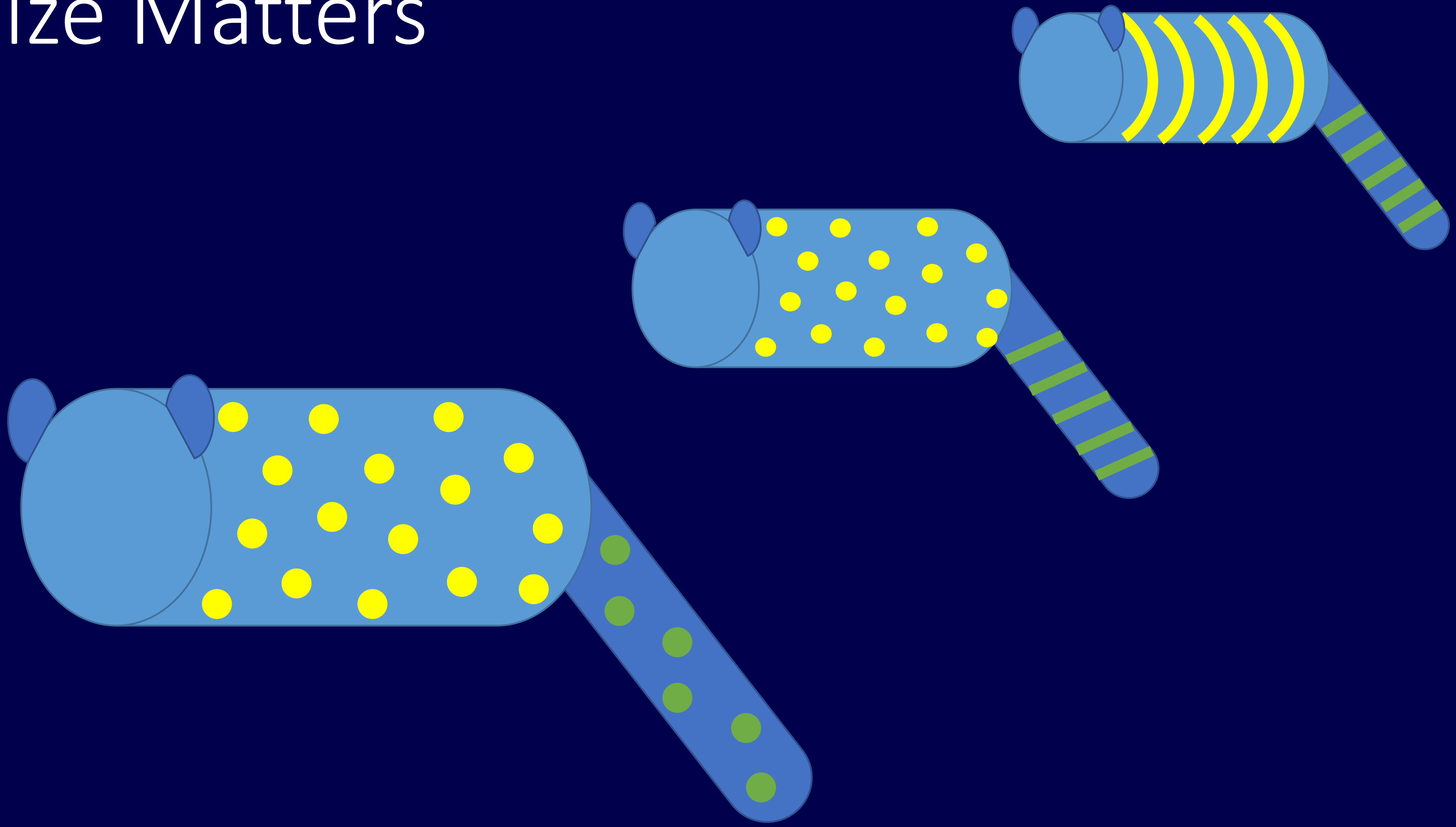



Reaction and Diffusion of the Theory

- Activator-inhibitor model
  - Activator self-catalysing, slowed down by inhibitor
  - Inhibitor diffuses faster than activator

- More than two morphogens (eg fingerprints)

Size Matters



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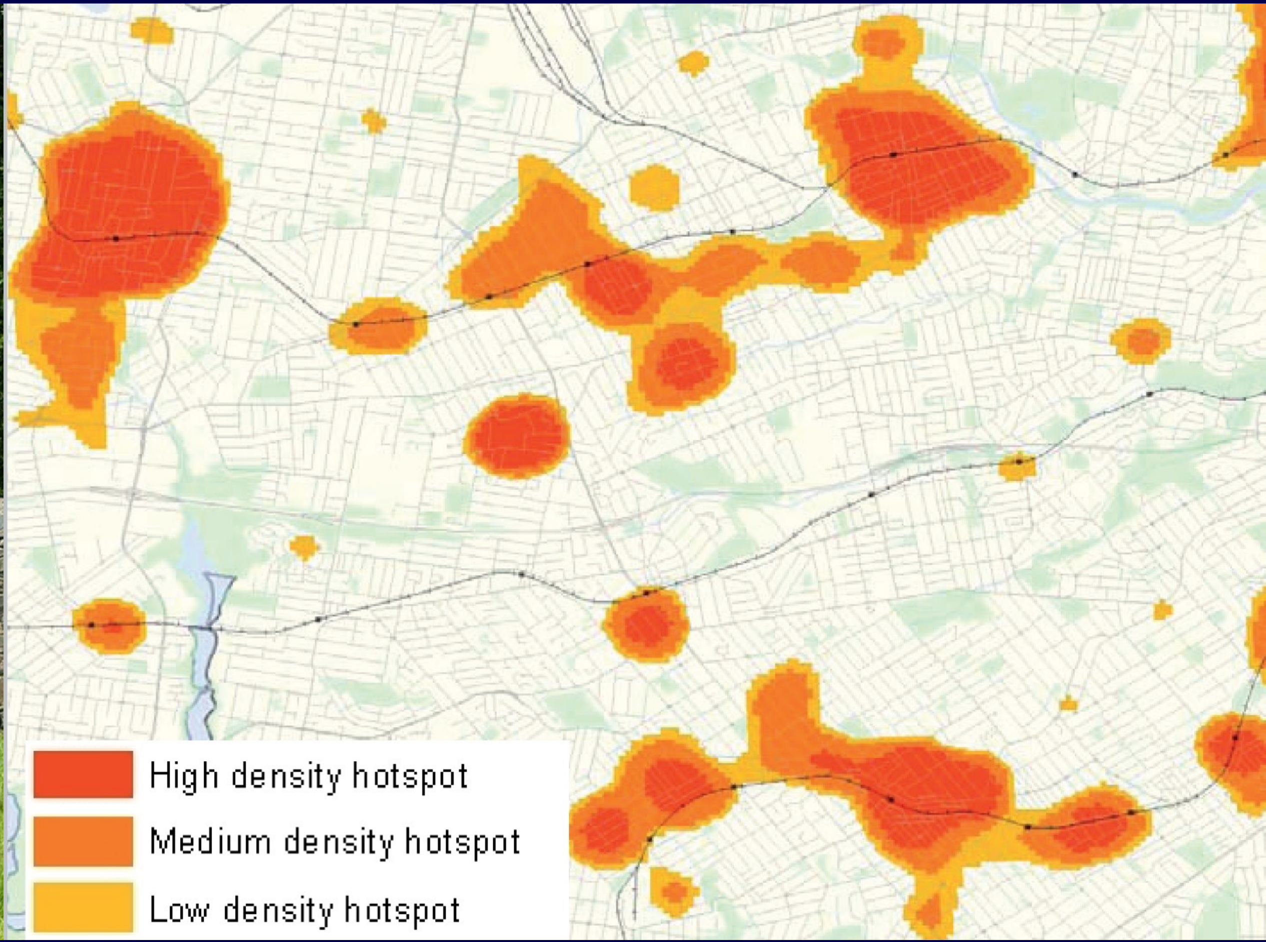
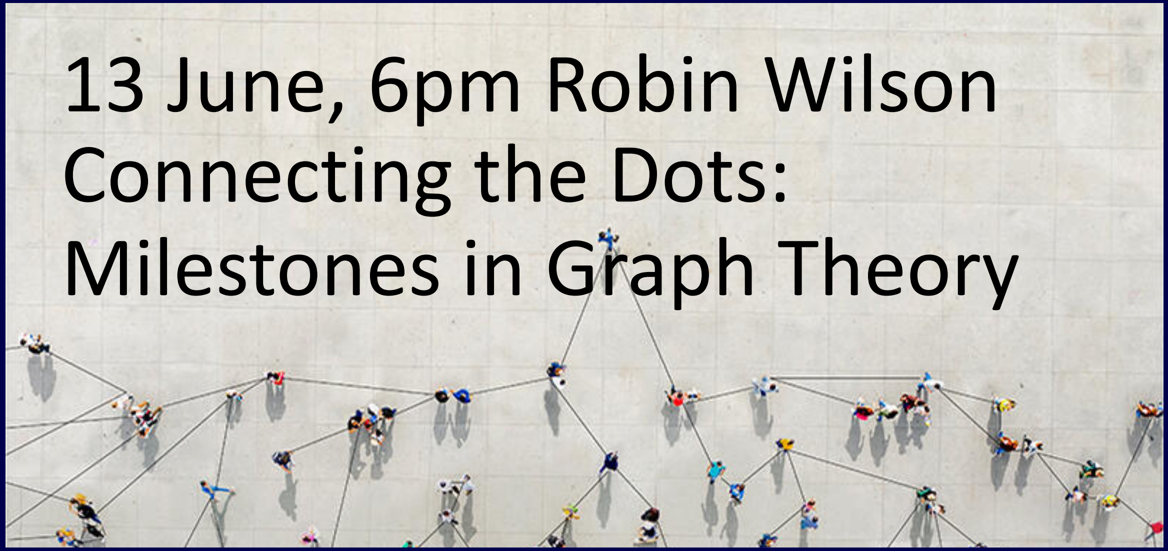
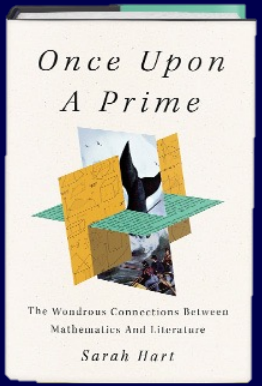

High density hotspot
Medium density hotspot
Low density hotspot

Coming up at Gresham



13 June, 6pm Robin Wilson
Connecting the Dots:
Milestones in Graph Theory

10 October, 1pm, Sarah Hart
The Maths of Board Games



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