Watching the daisies grow: Turing and Fibonacci phyllotaxis

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Abstract

Turing's seminal 1951 paper on morphogenesis is widely known. Less well known is that he spent the last few years of his life further developing his morphogenetic theory and using the new computer to generate solutions to reaction-diffusion systems. Among other things, he claimed at one point to be able to explain the phenomenon of 'Fibonacci phyllotaxis': the appearance of Fibonacci numbers in the structures of plants. He never published this work, but did leave a nearly complete manuscript on morphogenesis and lattice phyllotaxis, together with more fragmentary notes on Fibonacci phyllotaxis. I discuss evidence that he did develop a number of key ideas close to modern thinking, and tantalising hints that he came very close to a mathematical explanation of how the 'daisy grows' into these patterns.

1 Introduction: Turing's last, lost work

Alan Turing is now well known as a pioneer in the logical and technical development of the computer. He is also widely recognised in mathematical biology for his discovery of the Turing instability, which generates pattern in reaction-diffusion systems. Less well known is that he spent the last few years of his life further developing his morphogenetic theory and using the new computer to generate solutions to reaction-diffusion systems. Some of this biological work was published in his lifetime; some, thanks to the editors of his Collected Works, was eventually published posthumously, and some has been preserved unpublished, mainly in the archives of King's College Cambridge[1]. The paper published in his lifetime has turned out to be seminal and widely cited in the mathematical theory of biological pattern formation, but the rest of his researches have remained obscure and ill-understood. It is the purpose of this paper to interpret some of this last work of Turing's. In particular, one of a number of problems he was trying to solve was the appearance of Fibonacci numbers in the structures of plants, and I will describe this problem and speculate about how far he succeeded with it.

I begin by describing briefly the problem of Fibonacci phyllotaxis, and then Turing's basic theory of reaction-diffusion systems. Then I describe Turing's geometrical lattice theory, and finally, and more speculatively, his application of reaction-diffusion theory to the Fibonacci problem, and the crucial introduction of growth to the analysis. The last decade has seen rather successful mathematical explanations of the problem Turing was trying to solve, and I will describe these briefly to explore how much Turing might have anticipated them.

2 Fibonacci phyllotaxis

Phyllotaxis means the arrangement of structures, such as leaves or florets on plants. To explain the problem of Fibonacci phyllotaxis, consider the arrangement of side branches on the main stems of many plants. A model example is shown in Figure 1, which draws 'obvious' spiral or *parastichies* through adjacent branching points. The *parastichy number* for a spiral counts how many of such spirals fit onto the cylinder, or equivalently how many points around the cylinder but not on the spiral have to be skipped in the vertical direction between two points of the spiral. Thus one prominent parastichy on the left hand slice of the specimen is a 5 parastichy because there are four other branching points spread around the cylinder between any two consecutive points on the spiral. The parastichy in the other direction is a 3 parastichy and the pair is called a (3,5) parastichy pair. A remarkable fact about the specimen is that, although it exhibits a number of different parastichy pairs, each of these pairs consists of two adjacent Fibonacci numbers from the sequence 1,1,2,3,5,8,13,21,34,55, ... in which each number is the sum of the preceding two. Yet more remarkable is that this property can be found in very many examples in many different species of plants. Explaining this ubiquity is the problem of Fibonacci phyllotaxis[2]. Perhaps the most striking examples of Fibonacci phyllotaxis of all occur in the sunflower *Helianthus annus* and the daisy *Bellis perennis* where the florets of the flowerhead are arranged in spirals, with the number of spirals clockwise and anticlockwise being successive and rather large Fibonacci numbers (Figure 2).

The appearance of these numbers, or variants on them, is intimately related to the divergence angle, the difference in angle between successive points on the stem. If that angle in a cylindrical lattice is close to a simple function of the Golden Ratio, then Fibonacci numbers naturally appear. Moreover the Golden arrangement typically has the property of optimal packing. All of these relationships have been closely studied in the mathematical phyllotaxis and number theoretic literature (reviewed in Adler et al 1997; Jean and Barabé (1998)), and each of them has been adduced at one time or another as the explanation for Fibonacci phyllotaxis, often with varying degrees of mysticism or arguments from evolutionary optimality attached. Turing thought of the problem in terms of explaining the Fibonacci numbers of the parastichies, and it is this approach I concentrate on here. According to Adler et al (1997) the first to explicitly recognise that Fibonacci numbers were involved were Schimper (1830) and Braun (1831).

When and where did Turing's interest in this problem come from? The title of this paper comes from a sketch drawn by his mother (reproduced opposite the title page in Saunders (1992)) showing a schoolboy paying attention to the daisies rather than a hockey game. We know that at school he was well acquainted with D'Arcy Thomson's classic On Growth and Form that discusses it; decades later, Turing is recorded as discussing daisies and fir-cones during off-duty periods at Bletchley Park[3]. We have little concrete idea of his thinking on the subject until 1951. When Turing returned to Cambridge for a year in 1947-1948 he attended the undergraduate physiology lectures of Lord Adrian, and Hodges has plausibly speculated that his prime interest by now was the possibility of a logical description of the nervous system[4]. Indeed it was in a correspondence with the zoologist JZ Young, after a discussion on the needs of a physiological theory of the brain that he continued:

> *'...my mathematical theory of embryology...is yielding to treatment, and it will so far as I can see, give satisfactory explanations of*
> *(i) gastrulation*
> *(ii) polygonally symmetrical structures, e.g. starfish, flowers*
> *(iii) leaf arrangements, in particular the way the Fibonacci series (0,1,1,2,3,5,8,13,...) comes to be involved*
> *(iv) colour patterns on some animals, e.g. stripes, spots and dappling*
> *(v) pattern on nearly spherical structures such as some Radiolara...'*[5]

Whatever the original trigger, these were strong claims and it is the purpose of this paper to examine why Turing felt able to make them and claim (iii) in particular. In the same month he also wrote in a letter that

> *'Our new machine is to start arriving on Monday. I am hoping to do something about 'chemical embryology'. In particular I think I can account for the appearance of Fibonacci numbers in connection with fir-cones'*[6]

He certainly could do something about chemical embryology. By November of that year he had submitted a paper to Philosophical Transactions. This paper, *The Chemical Basis of Morphogenesis*, has become celebrated in its own right for introducing what is now known as the Turing instability, and provides a framework for understanding Turing's later, unfinished work.

In 1952 he wrote that he had ‘Had quite a jolly time lecturing on fir cones’[7] in Cambridge, and in 1953 wrote to HSM Coxeter:

> *…During the growth of a plant the various parastichy numbers come into prominence at different stages... Church is hopelessly confused about it all, and I don’t know any really satisfactory account, though I hope to get myself one in about a year’s time.*[8]

Between 1952 and 1954 he drafted parts of a paper on the Morphogen Theory of Phyllotaxis. This work was left incomplete, and indeed Gandy wrote, after Turing's death, that

> *‘When I was staying with Alan the weekend before Whitsun he also told me more or less where the computations had got to; but since his methods were so individual, he was unmethodical, I imagine it will be almost impossible for anyone to go on with the programme where he left off.’*[9]

In fact Nick Hoskin did manage to make some progress with preparing the work for publication, and Bernard Richards provided a third section based on the MSc thesis he started under Turing. But the resulting typescript was not published until 1992 (Saunders (1992)) and was recently discussed by Allaerts (2003). More details of the archive papers and their relationship to the published volume can be found at my website (Swinton 2003). We will return to their contents after discussing the Turing instability.

3 Where do spots come from? The Turing instability

This section provides a brief non-technical discussion of the Turing instability introduced in Turing (1952). Nanjundiah (2003) gives a good discussion of the impact and reception of this paper. Turing provided a hypothesis to explain the generation of pattern when smooth sheet of cells develop pattern during development in a wide variety of settings including the formation of leaf buds, florets, skin markings, and limbs. According to this hypothesis, chemicals called morphogens generate organs when present in sufficient density, and the pattern is created through mechanisms of reaction and diffusion. The corresponding reaction-diffusion models are by now well known to mathematical biologists, and for the mathematically inclined the books by Meinhardt (1982) and Murray (1993) can give much more detail.

3.1 Reaction...

One way of understanding the reaction-diffusion process is an analogy which Turing himself used at least once, in a slightly different model: cannibals and missionaries (Figure 3). An island is supposed to be populated by a population of cannibals and missionaries. The missionaries are all celibate and thus depend on recruitment from the external world to maintain the population as its members gradually die. Cannibals also die, but can also reproduce, so that the population naturally increases. However when two missionaries meet a cannibal, the cannibal is converted to missionary status. (If this seems a politically incorrect island it might be worth pointing out that under a commoner interpretation the cannibals are the growth promoters and the missionaries are the poison). This tension between production and transformation means that a balance is reached when both populations are mixed together.[10] If this balance is disturbed by a small amount of noise, the tension will act to restore the balance: the system is stable.

3.2 ...and diffusion

Now we imagine that the two populations, instead of mixing completely together, are spread out in a thin ring around the rather narrow beach of the island. Now individuals react (that is, reproduce or convert) only with their immediate neighbours, but they also move around at random in a diffusive way. Moreover the members of the two populations move at different speeds: the missionaries have bicycles and move faster. This is enough to destabilize the system. For if there is at any point a small excess of cannibals, say, then this will be followed by excess ‘production’ of more cannibals, and then of more missionaries (since they have more targets for conversion). Without the spatial dimension the extra production of missionaries would in turn reduce the cannibal excess and the system would return to balance. But because the missionary excess is transported away more quickly, a pattern develops in which there is a near excess of cannibals and a far excess of missionaries. Moreover the distance between these zones of relative excess is determined by the interaction between the reaction and the diffusion: a length scale, which is what is required for the emergence of pattern from non-pattern, has emerged from the dynamics.

3.3 Where did the bicycles come from?

The key to making this idea work is the missionaries’ bicycles: more technically that the inhibitor morphogen has a higher coefficient of diffusivity. Once the reaction-diffusion system is set up, a simple linear analysis makes this an obvious requirement for heterogeneity, but that was an analysis that no one, to Turing’s knowledge, had done at that time. We have no record of Turing’s thought process in developing the model idea and whether the diffusivity constraint came before or after the reaction-diffusion model itself. His analysis in Turing (1952) and Turing (1992) in terms of Fourier modes would have been second nature to him (for example his pre-war project to compute the zeroes of the Riemann zeta function using an analogue computer used a similar basic analysis). The formal theory in *The Morphogen Theory of Phyllotaxis* shares some structure with the then new quantum mechanics he had learned as a student in Cambridge, but presumably many of the techniques were in the armoury of any applied mathematician at the time. As Allaerts (2003) points out, Jeans’ 1927 book on Electricity and Magnetism, which Turing cited, is a source for many of the techniques, particularly spherical harmonics. But the source of the key scientific innovation is harder to pin down. It’s not even obvious that Turing himself appreciated it that it *was* key: it is hardly emphasised in either Turing (1952) or Turing (1992).

Turing was not alone in arriving at these ideas. Jeans states that similar ones were also introduced by Kolmogorov, Petrovski and Piskunov (1937), and Rashevsky (1940), although they remained largely unknown in the West for many decades; Nanjundiah (2003) discusses the (lack of) influences in more detail.

The 1952 paper actually dealt with a number of important and more complex issues usually glossed over in the standard undergraduate accounts. Turing also discussed tricky issues of mode selection and the effect of noise, and extended the model to two dimensions to produce an example of dappling.

By the time of the drafting of *The Morphogen Theory of Phyllotaxis*, the theory had been developed yet further, particularly by a representation in terms of spherical harmonics, and by an application to the particular case of a sphere, done as an MSc project by Richards (Richards 1998). This more general theory, which has been recently reviewed by Allaerts (2003), is, though relatively technical, conceptually a fairly straightforward development of the original idea.

3.4 The Turing instability: summary

In one dimension, then, the Turing instability introduced in the 1952 Transactions paper provides a natural mechanism for generating spots. Such patterns emerge from the interaction between the length-scale implicit in the reaction-diffusion dynamics and the geometry of the arena. This has provided a central paradigm for modern morphogenesis, at least from a mathematical perpective. While patterns have been seen in real chemical systems, it remains a challenge to explain 'stripes, spots and dappling'.

4 Lattice generation

So far, the discussion has been in terms of a one-dimensional pattern wrapped around a ring. What happens if we have the same reaction and diffusion mechanism but now allow it to act in a two-dimensional arena? In terms of the cannibals and missionaries, we might imagine that the beach of the island is now rather wide (relative to the length scale defined above). In this case, the Turing instability generically generates not a ring of points but a *lattice* of points[11]. Might this by itself be enough to explain the occurrence of Fibonacci phyllotaxis? With no constraints, (i.e. a cylinder of large enough radius, and ignoring the complexities of the inception and quenching of pattern formation), the instability typically generates hexagonal lattices (Murray (1993): see an example in Figure 4) and this class of lattices certainly include some Fibonacci ones. But it also includes many that are not Fibonacci.

Thus by itself it could not explain Fibonacci phyllotaxis, as Turing well understood. For when discussing phyllotactic systems defined as solutions to the reaction-diffusion model defined without growth constraints, he wrote

> ...'*the phyllotactic systems of botany do not arise in this way*'.[12]

Might it be that there are other constraints acting to select Fibonacci ones? First there are the geometrical constraints arising from the particular arena. Patterns on a cylinder may be different from those on an infinite plane where the periodicity constaint does not apply, and different again from those on a cone, but this does not promote any special Fibonacci structure. Then there are the dynamical constraints: the pattern does not suddenly appear, but emerges as a result of nonlinear interactions between morphogens over time. Finally there are growth constraints: during the emergence process, the arena itself may be growing with the plant. More discussion of these constraints is put aside until after a discussion of describing the patterns themselves.

5 Geometrical phyllotaxis

In this section we put aside the radically new contribution of Turing (a mechanism for dynamic production of lattices) to discuss his (slightly) more conventional treatment of the static properties of lattices, more commonly called geometrical phyllotaxis. Turing consolidated a general theory of lattices on cylinders

> *'expounded...by some previous writers but often in a rather unsatisfactory form, and with the emphasis misplaced'*[13]

which was (mostly) published for the first time in the 1992 Collected Works Turing (1992)). This kind of analysis has a long history, at least as far back as the brothers Bravais (Figure 5), but Turing's geometrical theory added several new insights: flow matrices, the 'hypothesis of geometrical phyllotaxis' discussed below, and the 'inverse lattice', a Fourier representation of the patterns essential to understanding many of the archive pictures though not discussed further here.

5.1 Turing's lattice theory

Part I of the Morphogen Theory of Phyllotaxis (from p49 of Turing (1992) is a fairly coherent and fully worked out manuscript. Two theorems are of particular relevance here.

For any lattice, such as the one in Figure 5, there are not just two rather obvious parastichies (here 2 and 3 are drawn with dashed lines) but a whole series of less obvious ones, which can all be defined relative to lines from the origin (i.e. the point labelled 0) through the other numbered points. The 1-parastichy is the solid line, and the eye can pick out the 4 parastichy by visualising a line through the points numbered 0 and 4 and 8 and so on. What Turing called the 'principal parastichies' were the ones in which the nearest points in the parastichy were closest to the origin – in other words Figure 5 has principal parastichy (2,3) because the points numbered 2 and 3 are the ones closest to the point numbered 0. (The geometrical details are related to but different from, say Jean (1994): primarily because Jean also needs to ensure that the parastichies wind in opposite directions round the cylinder) .

A second key theorem is that the third parastichy (in this case 1 since 1 is the next closest point) must be the sum or difference of the first two parastichy numbers, a theorem Turing proves neatly on p57 of Turing (1992).

5.2 'Hypothesis of geometrical phyllotaxis'

After this theory of lattices on cylinders, Turing went on to consider lattices of more variable geometry. This raises the question of what kinds of transformations of parastichy numbers are possible when a phyllotactic lattice is deformed. As it is deformed, the principal parastichies will in general remain unchanged. They will only change when a new lattice point from a different parastichy moves so as to become closer to the origin, but generically the point that does so must have previously been the third parastichy. Thus one of the two principal parastichy numbers, together with the third parastichy number, will become the new principal parastichy number.

Turing showed[14] that if that third parastichy number (in the example above, 1), never lies between first and second parastichy number (here (2,3) then a Fibonacci property, once begun, would persist. This constraint he named the Hypothesis of Geometrical Phyllotaxis.

It was this insight which was surely the cause of Hoskins' view, reported in Max Newman's 1955 Royal Society memoir[15] that Turing had shown that a Fibonacci system, once established, would always remain Fibonacci. But the truth, as Turing recognised[16], is that this relies on the HGP being true and the theory so far provides no reason why it should be. However this idea is still worthwhile: the key insight it embodies is that of continuous change. Phyllotactic lattices are not laid down all at once on an infinite cylinder: they are produced locally, node by node, and the resulting pattern is also deformed by growth.

6 Dynamic phyllotaxis

The Turing instability by itself, then, can't provide an explanation for the generation of Fibonacci phyllotaxis, as Turing well understood. For when discussing phyllotactic systems defined as solutions to the reaction-diffusion model defined without growth constraints, he wrote

> ...*'the phyllotactic systems of botany do not arise in this way'.*[17]

However there are strong indications in Turing's later manuscripts, particularly the fragmentary *Outline of the development of the daisy*[18], that he had conceived an additional mechanism to provide that explanation. As hinted above, that mechanism is that there is a small arena in which the Turing instability is at work, laying down spots in lattices and then leaving them behind as the arena follows the growth of the plant. Moreover that arena itself changes, growing in diameter, providing a continuously changing lattice to which the the theories of geometrical phyllotaxis could be applied.

The first evidence of this is in *Morphogen Theory of Phyllotaxis* Part I; in section 13 Turing establishes a formalism of flow matrices for the change in lattice parameters with a parameter called time, adding that

> *'a convenient way of picturing flow matrices is to imagine the change in the lattice as being due to the leaves being carried over the surface of the lattice by a fluid whose velocity is a linear function of position'*[19]

This was a way of modelling phyllotactic patterns, building on the continuous change models of Richards (1948). But this remains an essentially static picture of spots being passively transported over a changing geometry. What Turing was able to go on and create, with the aid of his new spot-generation model, was a concrete model for dynamic phyllotaxis.

In the later work, Turing typically expressed his reaction diffusion model in operator notation, with forms similar to

$$\begin{aligned} \frac{\partial U}{\partial t} &= \varphi(\nabla^2)U + GU^2 - HUV \\ V &= \psi(\nabla^2)U^2 \end{aligned} \qquad (*)$$

with

$\varphi(\nabla^2) = I_2(1+\nabla^2/k_0^2)^2$ and $\psi(\nabla^2) = 1/(1-\nabla^2/R^2)$ (cf equation III.1.2 of MTP, p107 of Turing (1992)). Here $U(x,t)$ is the morphogen and $V(x,t)$ is the 'poison'; the ψ function represents the implicit solution of its partial differential equation in terms of the slower diffusing morphogen. The H terms represents the effect of the poison on the morphogen, the G term the morphogen's autocatalytic nature, and the φ term its diffusive nature, parameterised by the natural wavenumber k_0.

However in *Outline of the Development of the Daisy,* there is a crucial extra spatiotemporal term $I(x,t)U$:

$$\begin{aligned} \frac{\partial U}{\partial t} &= \varphi(\nabla^2)U + I(x,t)U + GU^2 - HUV \\ V &= \psi(\nabla^2)U^2 \end{aligned} \qquad (**)$$

(note that the Saunders edition has a typo for the H and the ψ). An even more revealing version of this equation is in AMT/C/27/28 (Figure 6). This additional I term is designed to capture the effect of the variation in the geometry of the arena for morphogenesis with time due to growth of the underlying tissue: see the picture of a growing apical meristem region in Figure 6.

Turing not only conceived this idea; he clearly made substantial progress with a numerical implementation of it. At one point of the *Daisy* draft (AMT/C/24/12; omitted from the Saunders version), he comments on the number of parameters needed, '*when actual computations are being carried out the number of quantities to be specified is again increased..'* in a manner suggesting that this had been done in practice. Moreover one of the subroutines that has survived is labelled KJELL[20], and AMT/C/27/C25, entitled *Kjell theory*, works out the algebra in Fourier space of the coefficients of an equation such as the daisy one, including the crucial growth term. (Figure 7).

Also in the archives are a number of solution plots (eg Figure **8**). Based on their form they are probably solutions of the reaction-diffusion equations of forms similar to (*) or (**). Whether they are directly relevant to the Fibonacci problem or as more general illustrations of morphogenesis is hard to say. My speculation is that they are the former, since there is little evidence of any other computationally active project.

7 Routes to phyllotaxis

In addition to direct numerical simulation, there is evidence that Turing explored a more analytical approach to the problem. The best evidence comes from two sheets (Figure 9 and Figure 10) in the National Archive for the History of Computing[21]. Figure 9 is a diagram displaying possible parastichy transitions, from the homogenous (Hom) state up to 4+7 parastichies. A similar sheet includes the comment

> *Probable paths: Hom* $\rightarrow (0)_R \rightarrow (0+1) \rightarrow (1+1) \rightarrow (1+2) \rightarrow (2+3) \rightarrow (3+5)\ldots$ [22]

The question is what Turing meant by 'probable'. It might be a simple harking back to the hypothesis of geometrical phyllotaxis, but on another sheet (Figure 10: MAN/M/8) he classifies a number of possible transitions by more empirically geometric observations.

These kinds of parastichy transitions were not entirely new: van Iterson (1904) studied static sphere packings and generated a parameter map of all possible such packings (Figure 11). Turing at one point dismisses the 'touching circles hypothesis' – that each new point is introduced as though it was at the centre of a hard disk of a certain radius

– although that he is referring here to the process on a static cylinder: as discussed below touching circles is an adequate model provided the cylinder is allowed to grow in diamter.

There is clearly a concern here with the dynamic stability of given phyllotactic patterns and their dependence on the rate of growth of the morphogenetic arena. In identifying the Fibonacci transitions as the probable ones, he is trying to identify reasons why the Hypothesis of Geometrical Phyllotaxis might be true. It may be relevant that quite a large number of the archive sheets (unpublished in Saunders (1992)) are concerned with the dynamics and the stability of lattices: see Swinton (2003) for more details.

7.1 Turing's progress

As the Turing's theory progresses from reaction-diffusion to lattices and then to parastichy transitions, the surviving documents become sparser and less coherent, so assessments of his progress between 1951 and his death on June 7th 1954 become correspondingly more speculative. There is no concrete archival support for that claim in 1951 to explain fir cone patterns. A possible explanation is that Turing saw clearly that he had a spot generation mechanism and assumed, incorrectly, that this would be sufficient to generate Fibonacci lattices. There is a quote from a Ferranti engineer, from before the summer of 1953, that

> *...with a random starting disturbance the final configuration was displayed on the MkI's monitors. It was always of interest to those of us watching to see what Fibonacci configuration would result.*[23]

Turing was certainly producing spotty patterns by 1953. It seems plausible that what the engineer saw was actually more similar to those than to explicitly Fibonacci patterns.[24]. Support from this comes from a letter of Turing's of May 1953:

> *According to the theory I am working on now there is a continuous advance from one pair of parastichy numbers to another, during the growth of a single plant ... You will be inclined to ask how one can move continuously from one integer to another. The reason is this - on any specimen there are different ways in which the parastichy numbers can be reckoned; some are more natural than others. During the growth of a plant the various parastichy numbers come into prominence at different stages. One can also observe the phenomenon in space (instead of in time) on a sunflower. It is natural to count the outermost florets as say 21+34, but the inner ones might be counted as 8+13. Church is hopelessly confused about it all, and I don't know any really satisfactory account, though I hope to get myself one in about a year's time.*[25]

None of the fragmentary material can be reliably dated; some of the probably relevant computer printouts are dated[26] May 24th, but give no year. In addition several years of computing would have generated rather a lot of output, so the fact that all we have is a few sheets, and those not obviously archival records, hints that what we do have is the end of a series of ephemeral documents. So a speculation would date the latest analysis to within weeks of Turing's death. It is then likely that this was what Gandy was referring to when he wrote of hearing of Turing's individual and unmethodical computations.

In considering Turing's state of mind at his suicide, Hodges wrote that

> *Possibly the morphogenetic work had turned out plodding and laborious. It was three years since he had claimed he could account for the fir cone pattern and he had still not achieved it when he died*[27].

The morphogenetic work was not plodding: the bifurcation tree of parastichy numbers was new and, as discussed below, on the right lines. The computer simulations, even for the author of *Computable Numbers* (or more relevantly of the first programming manual), must though have been laborious and frustratingly slow to get right. Although they were apparently producing at least some meaningful output, Turing might have become the first to appreciate the sheer craft needed in computational biology. Probably Turing had not, indeed, accounted for Fibonacci phyllotaxis when he died, but he had got much further, and in the right direction, than he was in 1951.

8 Turing and modern approaches to Fibonacci phyllotaxis

At Turing's death, all of his post 1951 developments remained unpublished. Hoskin, Newman and Gandy tried to prepare what could be prepared for publication, but none of them had any particular expertise in the problem. Bernard Richards might have developed his MSc with Turing (on reaction diffusion systems on a sphere) into this broader question, but moved on to other areas (Richards 1998). Unsurprisingly the work remained almost unknown. The only citation I've found before 1992 came at one of Waddington's select meetings on theoretical biology held at Lake Como in the late 1960s, where Scriven described his

> '*treatment, developed from Turing's paper on morphogenesis, based on transport processes to move things from place to another. (Robin Grands [sic] has a Turing manuscript for the nonlinear case treatment)*[28]

Turing had discussed the morphogenesis work with Wardlaw, who subsequently published several papers explaining and discussing the reaction-diffusion hypothesis (Wardlaw 1953, 1954). Wardlaw is reported to have maintained a long interest in Fibonacci phyllotaxis though it seems to have gone unpublished.[29]

Some of the subsequent studies of phyllotaxis[30] concentrated on, and gave more rigorous mathematical theories of, the 'static' phyllotactic problem of the classification of lattices, and, for example, the relationship between the divergence angle and the visible opposed parastichies (Adler et al (1997), Jean (1994)). A second strand used numerical approaches based on dynamic models in which the appearance of a new point was governed by a rule which was some variant of 'far away from previous points'. Some even used reaction-diffusion equation to do so (Veen and Lindenmayer (1977) were the first to do this).

The earliest, clearest and most undercited explanation for Fibonacci phyllotaxis was developed by Mitchison (1977). Writing in *Science*, Mitchison deftly used the simple touching circles hypothesis for new points appearing in the cylindrical region formed by the apical meristem, and identified the key parastichies as what Jean would later call the visible opposed parastichies, those winding in opposite directions. He then showed that as the diameter of that region slowly changed, the bifurcations of parastichy number would, as Turing saw, replace one of the pair (m,n) with $m<n$ by $m+n$, and that as Turing hypothesised but failed to demonstrate, that the new visible opposed pair would have to be $(n,m+n)$ effectively because the pair $(m,m+n)$ would both wind in the same direction. This general hypothesis about which of two possible choices will be made at each stage, combined with the necessary geometric clarity to see that there are only two choices, and a dynamical system which can generate movement through the bifurcation diagram, is what is needed to explain Fibonacci phyllotaxis.

Through the 1990s other workers exhibited lattice Fibonacci structures experimentally (eg Douady and Couder 1996I) computationally (eg Douady and Couder 1996II) or analytically (eg Kunz and Rothen 1992; Levitov 1991; Atela et al 2002). This new generation used a variety of models, but the common feature is that each exhibited a bifurcation tree corresponding to all possible parastichy pairs, and showed, by local analysis at each bifurcation point, that the single branch traversable by continuous variation of a bifurcation parameter was the Fibonacci branch (Figure 12). This local constraint is what Turing would have called the Hypothesis of Geometrical Phyllotaxis.

9 Conclusion

This paper has concentrated on Turing's approach to the specific problem of Fibonacci phyllotaxis, and left largely undiscussed his wider legacy in mathematical biology. Any discussion of that legacy would have to cover the failure of reaction-diffusion models to sustain much favour with developmental biologists, combined with a persistent ability to remain in mathematical accounts. Keller (2002) has recently given a most insightful and informed account of this complex story. Yet reaction diffusion models only provide one possible mechanism for the spot creation process. It should not be thought that a failure to exhibit a morphogen, is a failure for the generic process of pattern generation that he was beginning to grasp.

Despite his confident words in 1951, Turing probably did not have an explanation for Fibonacci phyllotaxis either then or later. But he came close. As we have seen, such patterns can arise naturally as the product of iterated creation processes with simple rules. In his reaction diffusion systems he had the first and one of the most compelling models mathematical biology has devised for the creation process. In his formulation of the Hypothesis of Geometrical Phyllotaxis, work done by 1954 but not published until 1992, he expressed simple rules adequate for the appearance of Fibonacci pattern. In his last, quite unfinished work he was searching for plausible reasons why those rules might hold, and it seems only in this that he did not succeed. It would take half a lifetime before others, unaware of his full progress, would retrace his steps and finally pass them in pursuit of a rather beautiful theory.

10 Acknowledgements

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12 Figures

Figure 1 Parasitchy systems ranging from (3,5) through (5,8) and (8,13) to (13,26) on a single Euphorbia wulfenii stem. From Figure 8 of Church (1904).

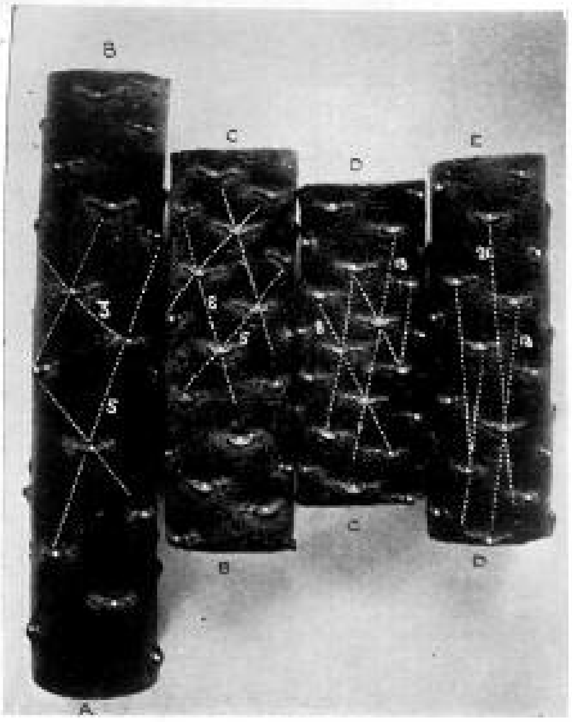


Figure 2 A sunflower head, with some of the florets removed to show the (34,55) parastichies. From Figure 15 of Church (1904).

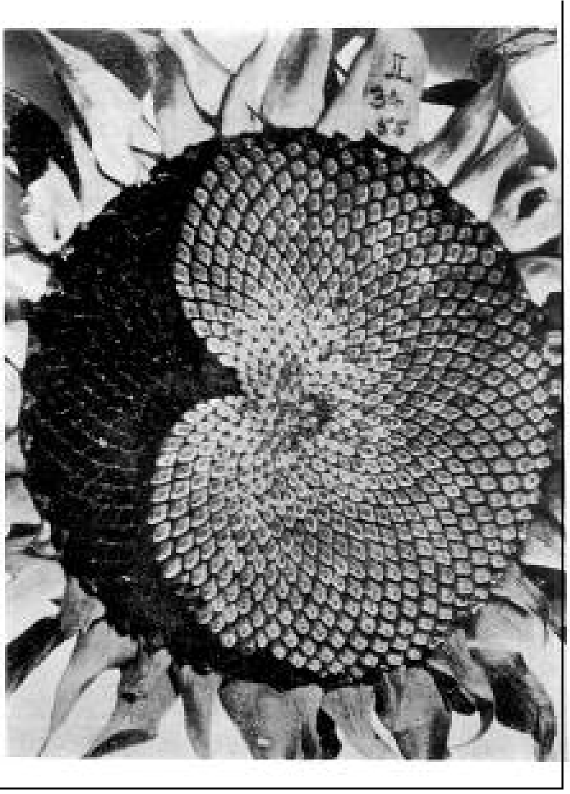
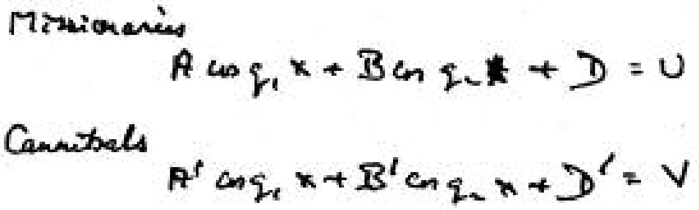


Figure 3 From AMT/C27/14. © PN Furbank



Missionaries

$$A \cos q_1 x + B \cos q_2 [illegible] + D = U$$

Cannibals

$$A' \cos q_1 x + B' \cos q_2 x + D' = V$$

Figure 4 A hexagonal lattice (AMT/K/3/1). © PN Furbank.

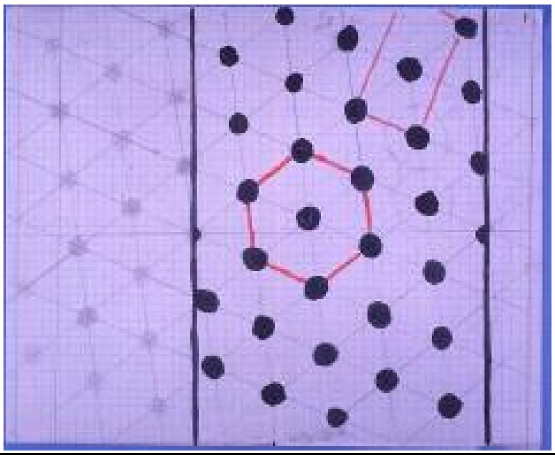


Figure 5 An early geometrical theory of phyllotaxis, from Bravais and Bravais (1837).

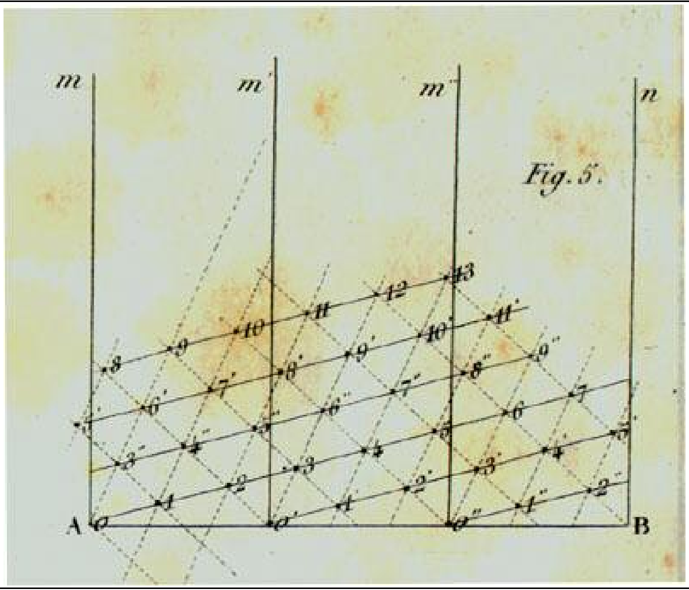
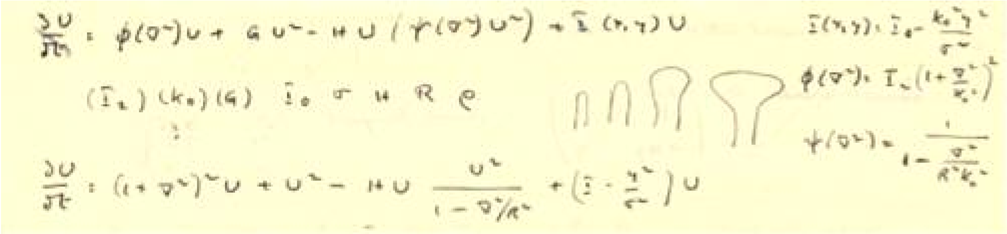


Figure 6 A version of the morphogenesis equation allowing for growth in the apical meristem region and the possibility of dynamic phyllotaxis. Also (below the first line) a list of the numerical parameters which must be specified to allow computational solution. From AMT/C/27/28. © PN Furbank.



$$\frac{\partial U}{\partial t} = \phi(\nabla^2)U + GU^2 - HU\left(\psi(\nabla^2)U^2\right) + I(x,y)U$$

$$I(x,y) = I_0 - \frac{k_0^2 y^2}{\sigma^2}$$

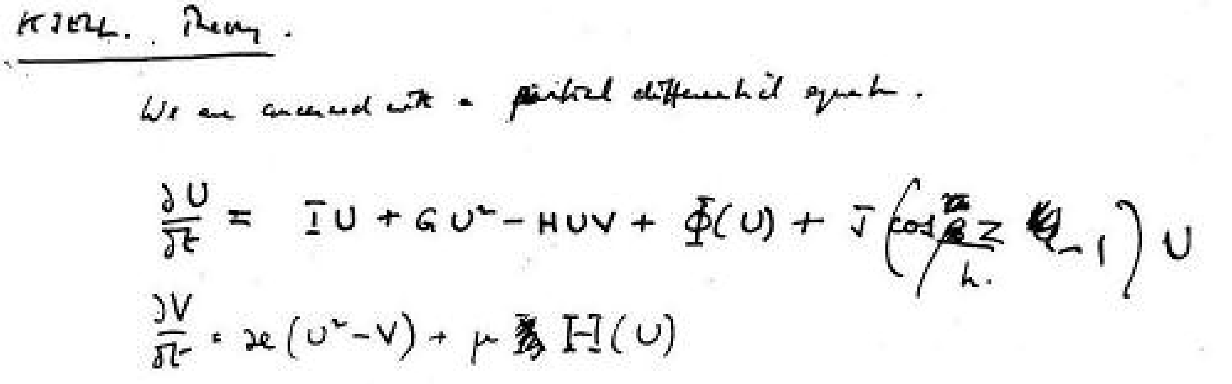
$$\phi(\nabla^2) = I_2\left(1 + \frac{\nabla^2}{k_0^2}\right)^2$$

$$\psi(\nabla^2) = \frac{1}{1 - \frac{\nabla^2}{R^2 k_0^2}}$$

$(I_2)\ (k_0)\ (G)\quad I_0\quad \sigma\quad H\quad R\quad \rho$

$$\frac{\partial U}{\partial t} = (1 + \nabla^2)^2 U + U^2 - HU\frac{U^2}{1 - \nabla^2/R^2} + \left(I - \frac{y^2}{\sigma^2}\right)U$$

Figure 7 KJELL theory. From AMT/C/27/25, beginning a series of developments designed to allow the dynamic growth equations of Figure 6 to be calculated by computer. © PN Furbank.



KJELL. Theory.

We are concerned with a partial differential equation.

$$\frac{\partial U}{\partial t} = IU + GU^2 - HUV + \Phi(U) + J\left(\cos\frac{\pi z}{h} - 1\right)U$$

$$\frac{\partial V}{\partial t} = \varkappa(U^2 - V) + \mu H(U)$$

Figure 8 Left: Probable solution of a reaction-diffusion equation of the form (*). One of the earliest (1951-1954) known pieces of computer graphics in biology. From AMT/K/3/8. Right: Enlargement of AMT/K/3/8 showing individual grid points as pairs of base 32 digits @=0, / =1, …V = 30, £=31), lowest significant digit first, and contoured on the basis of the most significant digits. © PN Furbank

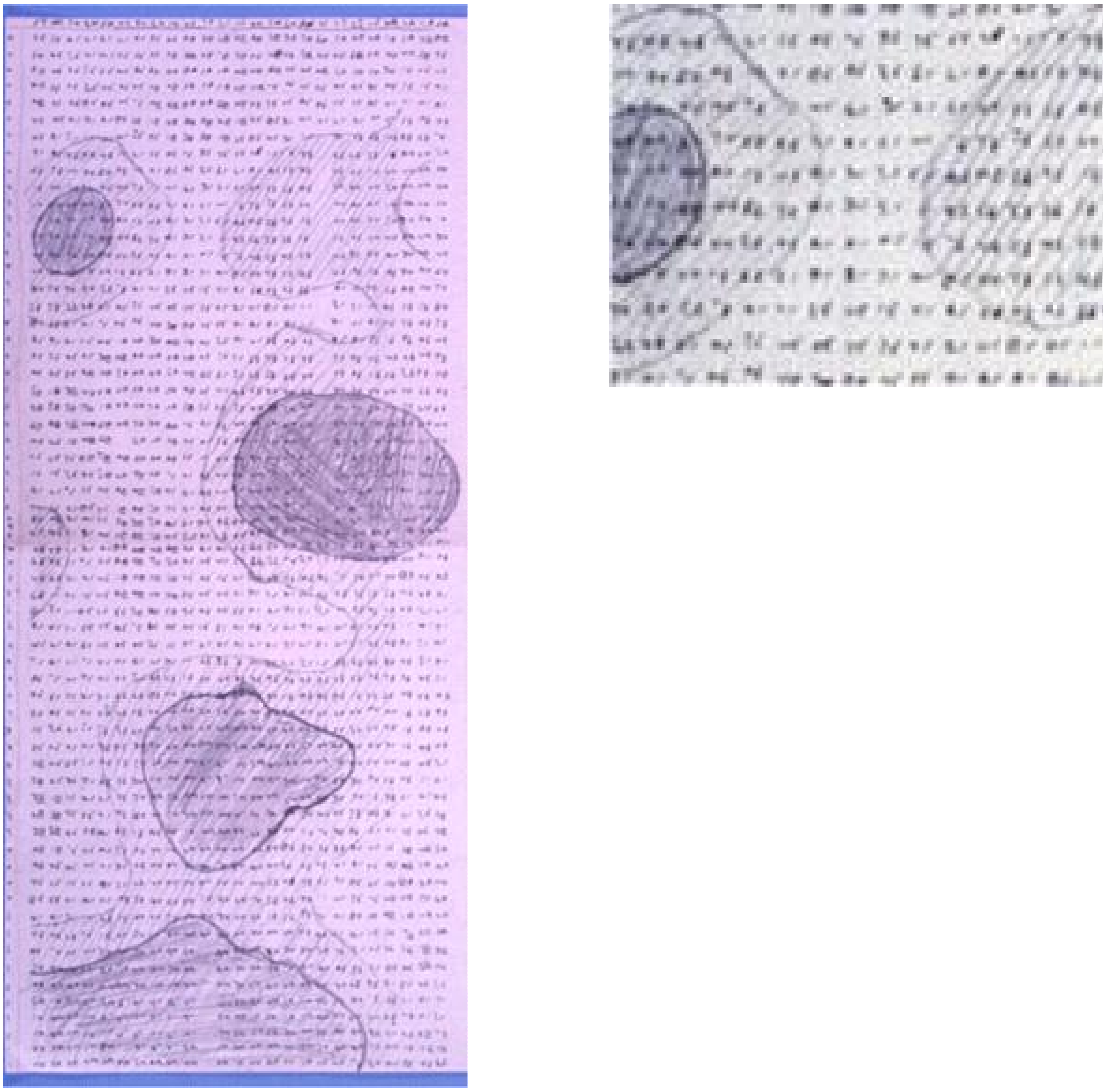


Figure 9. A bifurcation tree for possible phyllotactic evolutions. From AMT/MAN/4. © PN Furbank.

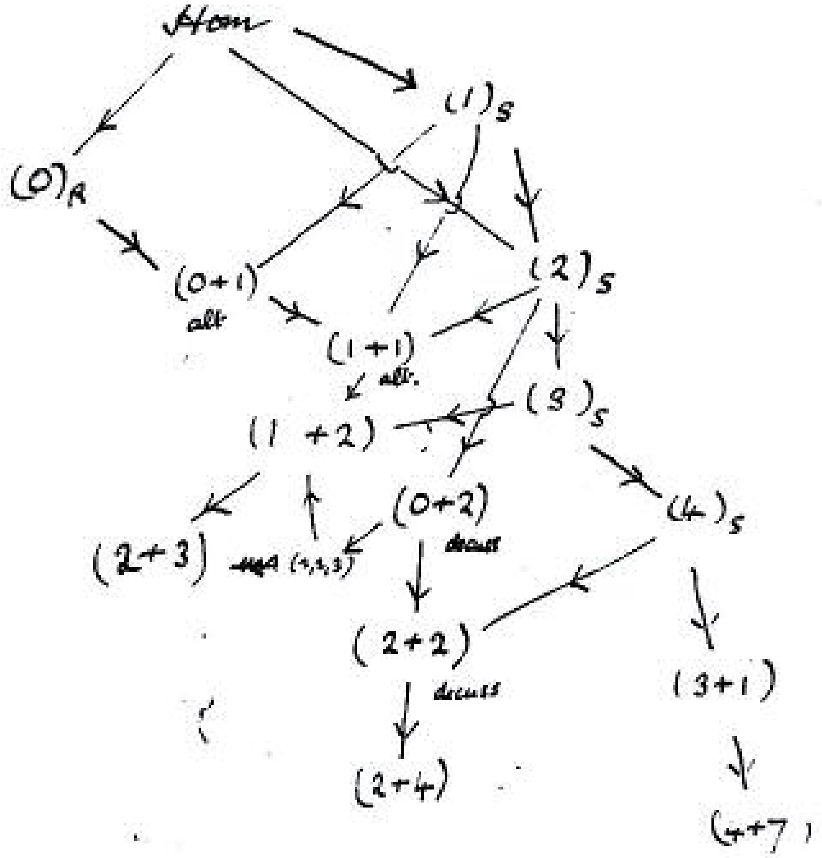


Figure 10 From AMT/MAN/M/8. Parastichy transitions annotated by Turing with likelihood of occuring. © PN Furbank

(0+2) → (1+2)	*An unlikely move*
(0+2) → (2+2)	*Quite possible, with [indecipherable]*
(0+2) → (2+3)	*Quite poss. and favoured by a / component (eg some zygomorphy)*
(1+1) → (2+2)	*Almost inevitable*
(2+2) → (2+4) *(2+2) → (2+3)*	*In competition. (2+2) → (2+3) is favoured by 5 < 6, but (2+2) → (2+4) by 6=2+4. Latter probably favoured by fast [unreadable] of conc.*
(1+2) → (2+3)	*Requires a breakdown process. Can probably only fail by too quick growth, leading to stationary patterns?*

Figure 11 Possible sphere packing parameters as a function of geometry. Detail from Figure II of Tafel II of van Iterson (1904). © Kluyver Laboratory for Biotechnology Archives of Delft University (www.beijerinck.bt.tudelft.nl); used with permission.

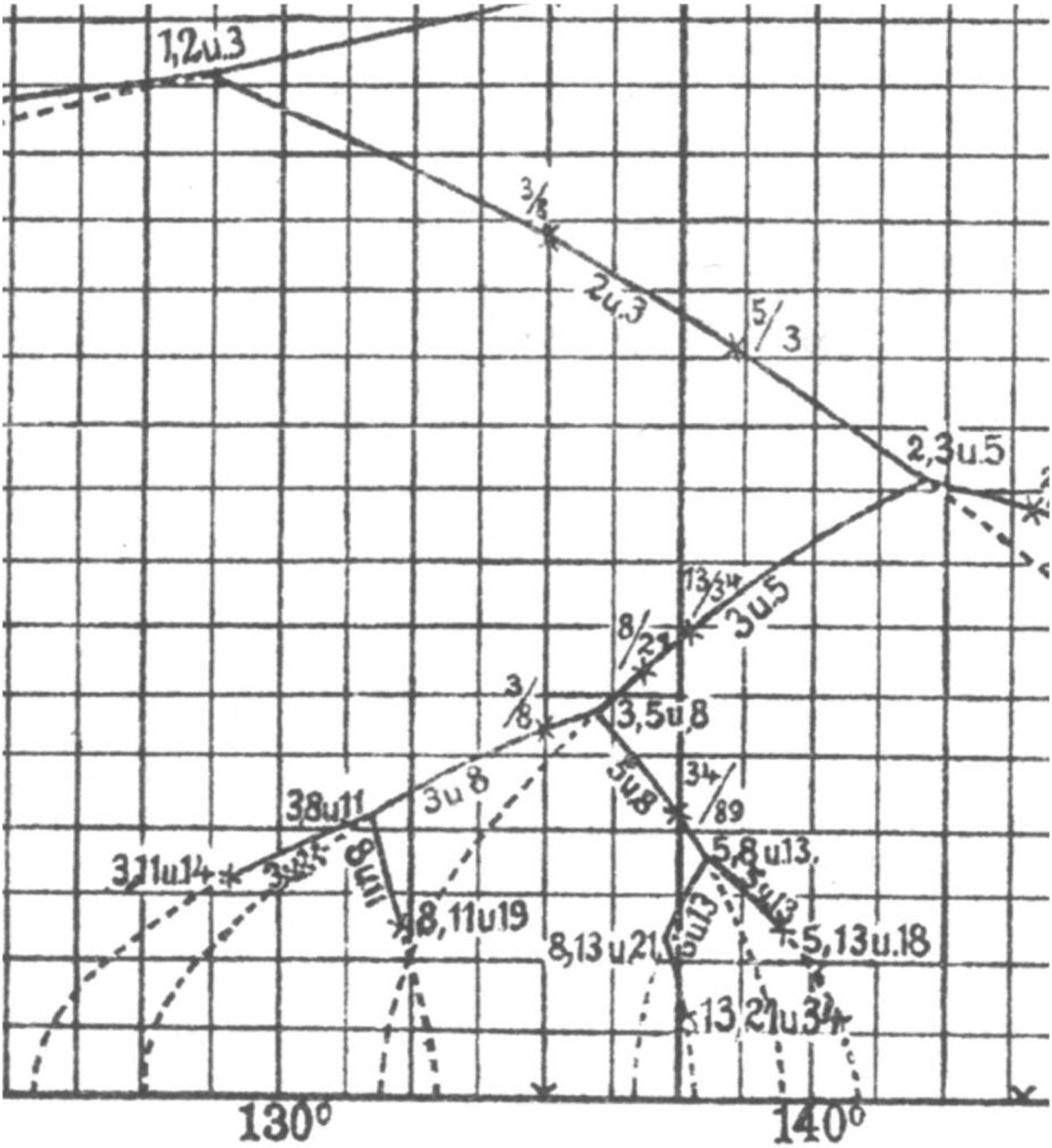
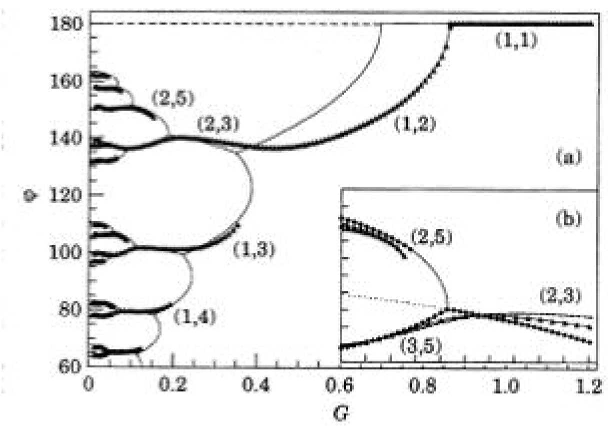


Figure 12 All possible parastichy pairs can occur, but only one branch is continuously reachable from the simplest symmetric case. Thin lines: theoretically possible parastichies; triangles: observed parastichies found in numerical simulations from various starting conditions. From Douady and Couder (1996). © Academic Press COPYRIGHT NOT CLEARED



Endnotes

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[1] A bibliography of Turing's work, published and unpublished, is maintained by Andrew Hodges at www.turing.org.uk; details on work relevant to morphogenesis including sources used in this paper is at www.swintons.net/jonathan/turing.htm; see also the Turing Digital Archive http://www.turingarchive.org

[2] The website http://www.math.smith.edu/~phyllo/ is one good starting point for more background.

[3] Hodges (1992) pp207-208.

[4] Hodges (1992) p372; Allaerts (2003) is one of the more recent commentators on Turing's more metaphyiscal motivations.

[5] AMT K.1.78; letter to JZ Young 8 Feb 1951

[6] Quoted in Hodges (1992) p437, letter to M Woodger February 1951.

[7] AMT D.4; letter to R Gandy Nov 23 (prob 1952)

[8] Letter from AM Turing, 28th May 1953, cited in Coxeter (1972).

[9] AMT A.8; letter from R Gandy to MHA Newman.

[10] cf Murray p376-378.

[11] Under suitable boundary conditions, other patterns such as stripes are possible.

[12] AMT/C/24/68.

[13] Turing (1992) p.62. Turing is not the only writer on mathematical phyllotaxis to adopt this tone.

[14] Turing (1992) p72

[15] In AMT/A/7 and Newman (1955).

[16] Turing (1992) p72

[17] AMT/C/24/68.

[18] Most of the text of this paper can be found in Turing (1992), pp 119-123. An alternative version, closer to the manuscript, can be found at my website.

[19] Turing (1992) p75

[20] This dates it to post summer 1952: see Hodges p476.

[21] At Manchester University (www.chstm.man.ac.uk/nahc/). Turing papers are in NAHC/TUR/C2 and C3.

[22] MAN/M/1. This is my foliation, details at Swinton (2003).

[23] Bennett (1996), p65

[24] There are some simple dappling patterns in the 1952 paper. There are more sophisticated computer solutions to the morphogenetic equations in the archive, but they do not explicitly demonstrate Fibonacci structure. For more details see Swinton (2003).

[25] Letter from AM Turing, 28th May 1953, cited in Coxeter (1972).

[26] Eg MAN/N/7

[27] Hodges (1992) p492.

[28] p321 of Waddington (1970).

[29] Email from Vidyanand Nanjundiah, 20th March 2003; Professor Nanjundiah believes Wardlaw talked on this topic at a 1974 Mosbach Colloquium.

[30] The subsequent literature of phyllotaxis is substantial, and I have been primarily guided by the various surveys in Jean and Barabe (1998) for this section.

Figures