Phyllotaxis, the regular arrangement of leaves or other lateral organs in plants including pineapples, sunflowers and some cacti, has attracted scientific interest for centuries. More recently, there has been interest in phyllotaxis within physical systems, especially for cylindrical geometry. In this letter, we investigate transitions between phyllotactic states of soft vortex matter confined to a conical frustum. We show that the ground states of this system are consistent with previous results for cylindrical confinement and discuss the resulting defect structures at the transitions. We then eliminate these defects from the system by introducing a density gradient to create a configuration in a single state. The nature of the density gradient limits this approach to a small parameter range on the cone. We therefore seek a new surface, the horn, for which a defect-free state can be maintained for a larger range of parameters.

1 INTRODUCTION

Novel defect structures can form in systems for which the lattice structure is not commensurate with the confining geometry. A regular triangular lattice on a sphere requires twelve positive disclinations, while toroidal crystals exhibit arrangements with negative and positive disclinations on the interior and exterior of the torus respectively [1,2]. Moreover, close packed particles on curved surfaces at large enough system size exhibit additional defects in the form of grain boundary scars [3–8] or pleats [9] in order to relieve the lattice strain energy.

Under cylindrical confinement, objects including discs [10], spheres [11–15], nanoparticles [16–18] and radially repulsive point-like particles [19,20] arrange into regular structures which can be described as phyllotactic states. Phyllotaxis, most commonly used to describe the regular arrangement of leaves or other lateral organs in plants, describes the arrangement of objects into regular spirals which intersect to form a triangular tiling. Phyllotactic state transitions, often accompanied by lattice defects, are observed when an incompatibility arises between a state and the confining geometry. Circularly symmetric phyllotaxis in constant curvature spaces leads to transitions characterized by circular grain boundaries [21,22], as observed in sunflower heads [23]. Moreover, deviations from regular cylindrical confinement, by either varying the radius of the particles being packed [24] or the geometry of the system [25,28], allow transitions between phyllotactic states. Understanding these transitions, as well as the resulting defect structures at the transitions, could give important insight into phyllotactic transitions in plants, such as are observed in some cacti [29] and Agave Parryi [30], which is important for understanding plant growth.

In this study, we numerically investigate the ground states of repulsive point-like particles, modelled as vortices in a type II superconductor, confined to the surface of a conical frustum. Recent work by two of the authors [20] showed that the phyllotactic ground state for cylindrical confinement is uniquely determined by a parameter $\alpha$. The variation in circumference $c$ for the conical system leads us to rewrite the definition of alpha in Ref. [20] to $\alpha = \frac{c^2}{\rho}$, where $\rho$ is the two-dimensional vortex density, to highlight the two dimensional nature of our system. The locally expected ground state for fixed $\rho$ changes when $\alpha$ crosses a transition value between states. We observe these state changes and classify the defect structures at the transitions. Introducing a linear density gradient allows us to remove the defects and create a flowing system with a single phyllotactic state despite the changing geometry. However, $\alpha$ still varies within the system, limiting the parameters for which this approach is possible. We therefore seek out a surface, the horn, for which $\alpha$ can be kept constant and show that in this case the single state can be sustained for a wider range of parameters.

2 SYSTEM MODEL

Vortices in type-II superconductors provide an excellent platform for studying soft lattice systems due to the large range of lattice parameters for which the...
lattice is stable, as well as the possibility of controlling the density with an external magnetic field. We model a system of vortices, interacting along the surface via the standard repulsive force on the \( i^{th} \) vortex: \( \mathbf{F}_i = -f_0 \sum_{j \neq i} K_1 (|\mathbf{r}_i - \mathbf{r}_j|/\lambda) \hat{r}_{ij} \). Here the position of vortex \( i \) is denoted by \( \mathbf{r}_i \), with \( \hat{r}_{ij} \) a unit vector from vortex \( i \) to \( j \) along the surface, \( K_1 \) is a modified Bessel function of the second kind and \( \lambda \) is the London penetration depth. We set \( \lambda = 1 \) and the constant \( f_0 = 1 \) throughout. We impose a cut off radius \( r_c = 5a_0 \) to all simulations, where \( a_0 \) is the average lattice parameter in the system. For cylindrical confinement, the observed ground states are the same for the Bessel function, Yukawa and radially repulsive Gaussian potentials up to an overall energy scaling \( [20] \). We therefore expect that the results presented in this work are generic for point-like particles confined in two dimensions with repulsive pairwise interactions along the surface.

We utilise the zero Gaussian curvature of the conical frustum and consider the ‘unwrapped’ surface in the plane, with boundary conditions identifying the two cut edges as equivalent. Figure 1(a) shows a schematic of the system and the unwrapping procedure. The flattened shape has length \( L \) and spatially varying circumference \( c(l) = c_0 + l \Delta c/L \), where \( L \) is the coordinate along the slant direction of the cone, which becomes a radial coordinate in the flattened system, \( \Delta c = c_L - c_0 \), and \( c_0 \) and \( c_L \) are the circumferences at \( l = 0 \) and \( L \) respectively, as labelled in Fig. 1(a). We minimise the effect of hard boundaries at the ends of the system by attaching vortex reservoirs of fixed density to these regions and only analysing states at least a distance \( r_c \) from the hard boundaries.

States are identified according to their phyllotactic notation, described by the integers \( (P, Q, R) \). The indices \( Q \) and \( R \) correspond respectively to the minimum number of steps along the two lattice vectors with the largest and second largest components in the periodicity direction required to form a closed loop around the circumference from a chosen start point. The effective number of lattice rows around the circumference is \( P = Q + R \). Figure 1(c) shows an example of the unwrapped system with the lattice vectors labelled. Lines of orange arrows indicate a minimum step sequence to loop the circumference and determine the state. For example, the \( (4, 2, 2) \) state (Fig. 1(c), right) requires 2 steps along the \( b \) vector followed by two steps along the \( a \) vector. See Ref. [20] for details of how to determine the lattice vectors. Alternatively, we can consider the lattice points as the intersections of spirals formed by continuously following the direction of a single lattice vector. As an example, one set of spirals for the \( (4, 2, 2) \) state is highlighted on the right of Fig. 1(c). There are two spirals in the direction shown, indicated by the light and dark blue arrows. The phyllotactic notation is determined by counting the number of times spirals of each orientation intersect a chosen circumference.

3 GROUND STATE STRUCTURES ON A CONICAL FRUSTUM

We first examine the ground states of the system by maintaining a fixed vortex density \( \rho \). The dimensionless parameter \( \alpha = c^2 \rho \) therefore increases quadratically with \( l \). Locally, we expect the system to adopt the known ground state for the local \( \alpha \) value \( [20] \) (see Supplementary Table 1 for a table of states and their corresponding \( \alpha \) values). As \( \alpha \) crosses a transition value, we expect the state to transition on the cone.

We numerically search for the zero-temperature system ground states for different \( \alpha \) values using both Monte Carlo (MC) and molecular dynamics (MD) algorithms (see Methods). Due to the small range of energies for which some states are the ground state, we use two methods to ensure we find all states. We find that our results are consistent for the two methods. The values of \( L, c_0, \Delta c \) and \( \rho \) are chosen so that the resulting variation in \( \alpha \) leads to a single transition point near to the centre of the system. If the variation in \( \alpha \) is too large, the transition points will be too close together and not all states will be observed. We note that for cylindrical confinement, some states exhibit a transition in which the lattice vectors change but the three-index phyllotactic notation does not. We do not include these transitions in this investigation due distortions of the states on the conical surface making the states too difficult to distinguish.
Figure 1: Ground state structures on a conical frustum. (a) Schematic of the conical system and cutting procedure to form the unwrapped shape. The red and blue edges are identified as equivalent. (b)-(c) Example transition between the (3,3,0) and (4,2,2) states depicted in (b) on the conical surface and (c) on the unwrapped surface with the top and bottom edges identified as equivalent. In (c) the Voronoi cells are shown for all vortices. Vortices with six nearest neighbours are shown in black while those with five or seven nearest neighbours, which together form dislocations, are shown as red squares and blue diamonds respectively. The lattice vectors for each state are indicated by the labelled orange arrows. Paths of orange arrows from bottom to top indicate possible shortest paths along lattice vectors to traverse the circumference, which can be used to determine the phyllotactic notation. The alternating light and dark blue stripes on the right side highlight the two spirals formed by following the b lattice vector for the (4,2,2) state. (d) Local density $\rho$ for this transition, calculated as the inverse of the Voronoi cell area, plotted as a function of scaled distance $X = l/L$. The vertical dashed line at $X = 0.32$ indicates the location of the transition, which also corresponds to a region with some local variation in the density. (e) Variation of $\alpha = c^2 \rho$, which dictates the preferred state, within the system. The best fit line has the equation $\alpha(X) = 10.7 + 2.0X - 0.2X^2$. The dashed horizontal gray line is for the expected transition value $\alpha = 12$. The vertical line at $X = 0.67$ shows the $X$ value for which the local $\alpha$ value is 12, calculated using the best fit line while the vertical line at $X = 0.32$ corresponds to the position of the transition. The calculated local $\alpha$ value at the transition is 11.4.
Using these techniques, we have observed all expected transitions between phyllotactic states which appear sequentially as $\alpha$ is increased over the range $4 \leq \alpha \leq 95.3$. As an example, the transition between the $(3,3,0)$ and $(4,2,2)$ states, which is predicted to occur at $\alpha = 12$ is shown in Fig. 1(b)-(c), where Fig. 1(b) shows the state on the conical surface while Fig. 1(c) shows the flattened state. The system parameters are $L = 50, c_0 = 6.0$ and $\Delta c = 0.5$. Transitions are mediated by lattice defects in the form of dislocations. These are vortex pairs in which one has five (red square) and the other has seven (blue diamond) nearest neighbours instead of the usual six neighbours. The Voronoi cells, which indicate the regions closer to a given point than any other point, are shown for all vortices in Fig. 1(c).

We measure $\alpha(l)$ within the system and find that the transitions occur at $\alpha$ values consistent with predictions. Plots of the local $\rho$ and $\alpha$ values for the state in Fig. 1(b) and (c) are shown in Fig. 1(d) and (e) respectively. As expected, $\rho$ is constant while $\alpha$ increases with $l$. Both plots show spreading in the data around the transition point. In general, small deviations between expected and actual $\alpha$ values at transitions are observed. In the example in Fig. 1(d), the expected transition is at $\alpha = 12$ (horizontal dashed line) while the actual transition occurs at $\alpha = 11.4$. These deviations are likely due to the competing energetics of lattice strain and defect formation as well as the way in which the states form during the annealing process and finite-size effects in the $l$ direction.

We observe a range of distinct defect patterns at the transitions: single dislocations, separated pairs of dislocations, grain boundary scars, and domain walls. In the case of one or two single dislocations, as shown in Fig. 2(a)-(b) for the $(5,4,1)$ to $(5,5,0)$ and $(7,7,0)$ to $(8,6,2)$ transitions respectively, the defects are completely surrounded by vortices with six nearest neighbours. Grain boundary scars are lines of two or more adjacent dislocations at the transition, an example of which is shown in Fig. 2(c) for the $(6,6,0)$ to $(7,4,3)$ transition. Finally, a domain wall, in which a line of dislocations spans the entire circumference, is shown in Fig. 2(d) for the $(5,5,0)$ to $(6,3,3)$ transition.

By inspecting the defect patterns observed, we find phenomenological rules to predict the number and arrangement of defects present. Transitions between pairs of states with general notation $(2R, R, R)$ and $(Q, Q, 0)$ give domain walls. In these cases, the $c$ lattice vectors of the pair are orthogonal. Similarly, transitions between pairs of states with general notation $(2R + 1, R + 1, R)$ and $(Q, Q, 0)$ lead to grain boundaries. In these cases, the large angles between the $c$ lattice vectors mean that it is not possible to transition from one state to the next with only a small rotation of the lattice. In both cases, the competing structures are not compatible so the transition requires defects to span much or all of the circumference.

Furthermore, we find a rule to predict the number of defects at transition $n_d$. We observe $n_d = |R_< - R_> |$, where $R_<$ ($R_>$) is the smallest phyllotactic index of the state with the lower (higher) $\alpha$ value at the transition. This is explained by noting that the $R$ index corresponds to the lattice vector with the largest component along the periodicity direction or, equivalently, the steepest set of spirals forming the state. Due to the periodicity constraint, this is the most confined of the three lattice directions and therefore controls the value of $n_d$.

Figure 2: Example defects at transition points between states. (a) $(5,4,1)$ to $(5,5,0)$ transition mediated by a single dislocation. (b) $(7,7,0)$ to $(8,6,2)$ transition gives two dislocations. (c) $(6,6,0)$ to $(7,4,3)$ transition gives a grain boundary consisting of three dislocations. (d) $(5,5,0)$ to $(6,3,3)$ transition requires a grain boundary formed of three dislocations which spans the entire circumference.
4 MAINTAINING A SINGLE LATTICE
STRUCTURE WITH A
DENSITY-DRIVEN FLOW

Having confirmed that the local $\alpha$ value determines the local ground state, we can design a configuration in a single defect-free state. We introduce a density gradient, equivalent to a magnetic field gradient, to counteract the increasing circumference and minimise variation in $\alpha$. In this section we demonstrate that designing such a configuration should therefore be possible, and discuss the limitations of this approach.

We implements a source-sink density-driven flow scheme using MD methods by attaching reservoirs maintained at fixed vortex number to the ends of system, following the methods detailed in Ref. [32] (also see Methods). Maintaining the reservoirs at different densities creates a density gradient, inducing vortex flow towards the lower density (see schematic, Fig. 3(a)).

Due to the very small opening angle of our conical frustum ($\sim 1^\circ$), we treat the boundaries between the reservoirs and the system as straight lines in the plane, rather than as arcs of circles. The expected density profile can be determined by approximating the discrete flow as continuous and solving the steady state diffusion equation with fixed densities $\rho_0$ and $\rho_L$ at $x = 0$ and $L$ respectively, where $x \approx l$ is the Cartesian coordinate in the plane. The resulting density profile is given by $\rho(x) = \rho_0 + x\Delta \rho/L$, where $\Delta \rho = \rho_L - \rho_0$. Consequently, $\alpha$ is approximately cubic in $l$. For small enough $\Delta c$ and $\Delta \rho$, it should therefore possible to maintain the range of $\alpha$ values within a single state.

We determine $\rho_0$ and $\rho_L$ from a chosen target value $\alpha_0$ for vortices entering and exiting the system. The value of $\alpha_0$ is chosen to be away from transition values to allow the reservoirs to maintain the desired state. After steady state is reached, which typically takes around $10^5$ time steps, a single state is maintained throughout the system provided that the variation in $\alpha$ is small enough for the state to be maintained.

Using the parameters $L = 50$, $c_0 = 6$ and $c_L = 7$ and sampling a range of $\alpha_0$ values, we have observed all of the expected configurations which are ground states on the cylinder from (2,2,1) through to (7,7,0) at $\alpha = 57$. For higher $\alpha$ values, the states become more unstable to fluctuations in the system and are much more difficult to maintain. Figure 3(b)-(d) show snapshots of the density-driven flow scheme for three examples: (b) the (4,2,2) state in a system with $\alpha_0 = 13$, (c) the (6,4,2) state with $\alpha_0 = 32$, and (d) the (7,7,0) state with $\alpha_0 = 57$. In each case, the vortex location is shown in black while their expected locations, relative to the red reference point, are shown in orange. The larger $\Delta c$ and therefore $\Delta \rho$ values are used with a state that is able to accommodate a larger $\alpha$ variations in order to highlight the deviations from constant $\alpha$. We therefore seek a system for which the value of $\alpha$ can be held constant.

5 SURFACE WITH CONSTANT $\alpha$

The nature of the density-driven flow scheme means that for small deviations from cylindrical confinement $\rho(z) = \rho_0 + \Delta \rho z$, where the $z$ axis is the axis of revolution. We solve for the profile $c(z)$ which gives a constant value of $\alpha = \alpha_0$. This leads to a horn-shaped surface with

$$c(z) = \sqrt{\frac{\alpha_0}{\rho_0 + \Delta \rho z}} \equiv \frac{c_0}{\sqrt{1 - \eta z}},$$

where $c_0$ is the circumference at $z = 0$, $\eta = -\Delta \rho / \rho_0 > 0$, and the length is scaled so that $0 <
Figure 3: Maintaining a single state by inducing a density-driven flow. (a) Schematic of the source-sink density-driven flow scheme. (b) (4,2,2) state with target value $\alpha_0 = 13$, (c) (6,4,2) state with $\alpha_0 = 32$, and (d) (7,7,0) state with $\alpha_0 = 57$. For (b)-(d), the colour gradient in each case indicates the density from highest (red) to lowest (blue). The direction of flow is towards the region of lowest density. (e) Local density variation with scaled distance along the system $X = l/L$ corresponding to the snapshot in (b) with a linear fit line (red line) plotted. (f) Local variation in $\alpha$ with distance along the system, corresponding to the snapshot in (b). The red line gives a cubic fit for the local $\alpha$ value.
We perform MD on the surface by numerically solving for the geodesics connecting pairs of vortices. The distance between a pair is the length of the geodesic and the forces act along the tangent vectors to the geodesics. As per the conical system, we attach source and sink reservoirs to maintain the required density gradient. See the Supplementary Information for details of the equations and techniques used for MD in this case. We choose the parameters $r_0 = 0.02$ and $\eta = 0.56$ so that the circumferences at $z = 0$ and $z = 1$ are equivalent to those for the cone example in Fig. 4(a).

To verify our results, we need to know the expected vortex locations for constant $\alpha$ on the surface. At a given value $z = \tilde{z}$, the expected local lattice vectors are those for a cylinder with circumference $c(\tilde{z})$. Since $\alpha$ uniquely determines the lattice vectors of the state, and is constant on the surface, the local lattice vectors are always in the same direction relative to the periodicity direction $\hat{\theta}$. Following the direction of the local lattice vectors therefore traces out curves known as loxodromes, for which the tangent vector forms a constant angle relative to $\hat{\theta}$ (see Supplementary Information for derivation). The intersection points of these curves indicate the expected vortex locations. An example snapshot of the horn system is depicted in Fig. 4(b), while Fig. 4(c) shows the same snapshot flattened onto the plane. In both images, the vortex locations are indicated in black. They are expected to sit at the intersection points of the plotted curves (shown as white points), determined relative to the blue reference point.

The vortex locations for the horn in Fig. 4(b)-(c) are closer to their expected locations than those for the cone depicted in Fig. 4(a). We quantify the deviation between the expected and actual vortex locations for the cone and horn snapshots in Fig. 4(d). We plot $g(\sigma/d) = \sigma^2/d^2$, where $\sigma$ is the distance between a vortex and its expected location and $d$ is the distance between the vortex and the reference point. For the horn (blue points) we observe that $g(\sigma/d)$ is very close to zero, as expected for a constant $\alpha$ system, while for the cone (orange points) there is a clear upward trend in $g(\sigma/d)$ as $d$ increases. We therefore conclude that the horn system is displaying a state of constant $\alpha$.

Using the horn system for simulation is limited by the density variation within the system, and therefore the variation in the horn radius, due to the vortex interaction strength. If the variation is too large, vortices in the dense region will interact very strongly while those in the least dense regions may be far enough apart that the interactions are almost negligible. There are also large computational costs in simulations due to the time required to calculate distances along the curved surface.

6 CONCLUSIONS

We have demonstrated the adaptability of the vortex lattice in both static and dynamic regimes when confined to a geometry that is not commensurate with the local lattice ground state, as well as the importance of the dimensionless quantity $\alpha$ in controlling this behaviour. By fixing the density, the ground state displays transitions between phyllotactic states as $\alpha$ crosses a transition value. The number of defects at the transition can be described by a phenomenological rule. By inducing a density gradient in opposition to the changing circumference, we have created defect-free structures in which the entire system is in a single state. However, on the conical surface $\alpha$ still varies so this approach is limited to small $\Delta c$ and $\Delta \rho$. We therefore sought a surface, the horn, for which the value of $\alpha$ could be kept constant with our chosen density profile and demonstrated that in this case the vortices flow in a state of constant $\alpha$.

More generally, we note that the method presented for constructing a configuration with constant $\alpha$ on the surface using loxodromes can be applied to all surfaces of revolution, such as in the example of the (7,6,1) state tiling the surface of revolution of the curve $y(x) = \cos x + 2$ about the $x$ axis in Fig. 4(e). Tilings of this type, where all sites are six-fold coordinated, are possible for all surfaces of revolution of the profile $y(x)$ revolved about the $x$ axis for which $y(x) > 0$ for the range of $x$. 

$z < 1$.
Figure 4: Comparison between cone and horn systems. (a) Flattened cone in the (4,2,2) state. Black circles show vortex positions in a snapshot of the simulation. The intersections of the grey curves, marked with orange circles, indicate the expected vortex locations for the system at constant $\alpha$ relative to the red reference point. (b) Horn surface plot and (c) unwrapped horn system in the (4,2,2) state at comparable system size and density to (a). Actual vortex locations are shown in black while the expected vortex locations, relative to the blue reference point, are shown as white circles, which sit at the intersections of the loxodrome curves. (d) Deviation of vortex positions from expected location normalized by distance from the reference point, plotted relative to the distance from the reference point. The plot corresponds to the images in (a)-(c) for the cone (orange) and horn (blue) respectively. (e) (7,6,1) state of constant $\alpha$ tiled on the surface of revolution of the curve $y(x) = \cos x + 2$ about the $x$ axis.
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**AUTHOR CONTRIBUTIONS**

H.S.A., A.A.T. and N.K.W. designed the investigation. H.S.A. and A.A.T. performed simulations. H.S.A., A.A.T. and N.K.W. analysed the results and wrote the manuscript.

**METHODS**

**Ground state structures on a conical frustum**

Monte Carlo (MC) and molecular dynamics (MD) techniques were used to find the ground states on the cone. We follow the Metropolis prescription for MC integration by annealing a pseudo-randomly generated starting vortex configuration initially at high temperature down to zero temperature. Snapshots of the systems are compared and the state with the lowest internal energy is selected as the numerically solved ground state. We perform MC minimisation for $100 \leq N_v \leq 256$, where $N_v$ is the number of vortices, for $4.0 \leq c_0 \leq 10.5$ with $\Delta c = 0.5$ and $L = 50$. Using this range of parameters, we have observed all transitions in the range $4 \leq \alpha \leq 42.1$.

MD is performed by numerically solving the overdamped Langevin equation for the motion of each vortex up to the imposed cut-off radius $r_c = 5a_0$, where $a_0$ is the lattice parameter. We control temperature through implementation of a thermostat and slowly anneal a pseudo-randomly
generated initial configuration at high temperature into the ground state. The system is created with $L = 50$, $c_0 = 6.0$ and $\Delta c = 0.5$ as the typical values. These parameters allow for enough variation in $\alpha$ that there is a single transition point within the system. For higher $\alpha$ transitions, typically $\alpha > 50$, we instead use $\Delta c = 0.1$ and $L = 30$ due to the higher density of the lattices involved in the transitions. Other choices of $c_0$ and $\Delta c$ have been investigated to verify they are consistent with the results presented here. Using this method we have investigated densities large enough to observe all transitions in the range $4 \leq \alpha \leq 95.3$.

**Density-driven flow on a conical frustum**

The vortex reservoirs are created to be larger than $r_c$ and all vortices are added and removed from the source and sink respectively at the ends of the reservoirs in order to ensure there are minimal effects on the dynamics within the system. Vortices are added into the source reservoir at pseudo-random locations in a region close to the outside edge of the system. The vortices within the reservoir form into a particular state which then flows into the system. As the state is formed within the source, there are occasions where defects may form in the structure and escape into the system. This noise flows through the system and the expected state is the persistent structure. If a clean state entirely free from the possibility of defect structures entering from the source is desired for a different application, steps can be taken to produce a more ordered source reservoir. Positioning the vortices at their expected positions for the state of interest within the source helps to eliminate the chance of defects persisting and escaping the source.

**Density-driven flow on a horn-shaped surface**

We follow the methods used on the conical system as closely as possible, making adaptations to account for the curved surface where necessary. As for the conical system, we impose a cut-off radius of $5a_0$ for interactions. The density gradient means that the separation between vortices varies with position. We therefore choose the value of $a_0$ to be the expected lattice parameter at $z = 0.5$. Details of the methodology used for molecular dynamics on the horn surface are given in the Supplementary Information.
Supplementary Information

A \( \alpha \) VALUES AT TRANSITIONS

Table 1 states the transition values \( \alpha_T \) at which the lattice state transitions into the given phyllotactic state as the value of \( \alpha \) is increased from \( \alpha = 0 \). The transition values are calculated for the case of cylindrical confinement. This table is a reproduction of results presented previously in Ref. \[20\], extended here to \( \alpha = 100.824 \).

| \( \alpha_T \) | State       | \( \alpha_T \) | State       | \( \alpha_T \) | State       |
|--------------|-------------|--------------|-------------|--------------|-------------|
| 0            | (1, 1, 0)   | 30           | (6, 3, 3)   | 68.0683      | (9, 5, 4)   |
| 2            | (2, 1, 1)   | 31.7613      | (6, 4, 2)   | 71.604       | (9, 6, 3)   |
| 4            | (2, 2, 0)   | 34.0042      | (6, 5, 1)   | 73.3         | (8, 8, 0)   |
| \( 8\sqrt{3}/5 \) | (3, 2, 1) | 38.7034      | (6, 6, 0)   | 75.7325      | (9, 7, 2)   |
| \( 9.1912 \) | (3, 3, 0)   | 504/\sqrt{143} | (7, 4, 3)   | 80.7751      | (9, 8, 1)   |
| \( 12 \)     | (4, 2, 2)   | 43.9001      | (7, 5, 2)   | 85.4282      | (10, 5, 5)  |
| 14.4506      | (4, 3, 1)   | 47.2565      | (7, 6, 1)   | 87.1823      | (10, 6, 4)  |
| 16.7283      | (4, 4, 0)   | 416/3\sqrt{7} | (8, 4, 4)   | 89.5129      | (10, 7, 3)  |
| \( 160/3\sqrt{7} \) | (5, 3, 2) | 56           | (7, 7, 0)   | 92.3081      | (9, 9, 0)   |
| \( 23.0966 \) | (5, 4, 1)   | 58.4359      | (8, 6, 2)   | 95.341       | (10, 8, 2)  |
| 26.5641      | (5, 5, 0)   | 62.8623      | (8, 7, 1)   | 100.824      | (11, 6, 5)  |

Table 1: Transition values \( \alpha_T \) for which the system adopts the given phyllotactic state as the value of \( \alpha \) is increased.

B MOLECULAR DYNAMICS ON THE HORN

We parameterise the horn surface using cylindrical coordinates \( (r, \theta, z) \), with positions on the surface described by \( r = (r(z) \cos \theta, r(z) \sin \theta, z) \). The surface has a profile

\[
r(z) = \frac{r_0}{\sqrt{1 - \eta z}}
\]

where \( r_0 = c_0/(2\pi) \) is the radius at \( z = 0 \) and \( z \) is the fractional distance along the length of the surface, such that \( 0 < z < 1 \), and \( \eta > 0 \).

Throughout this section subscripts \( z \) or \( \theta \) indicate a derivative with respect to that variable, while subscripts \( i \) and \( j \) are used to index particular vortices. It is useful to note the following relations

\[
\begin{align*}
r_z(z) &= \frac{r_0 \eta}{2(1 - \eta z)^{3/2}} = \frac{\eta}{2r_0^3}r(z)^3 \\
r_{zz}(z) &= \frac{3r_0 \eta^2}{4(1 - \eta z)^{5/2}} = \frac{3\eta^2}{4r_0^5}r(z)^5.
\end{align*}
\]

In order to do molecular dynamics, we need to know the geodesics on the surface between pairs of points. The distance \( d_{ij} \) between a pair of vortices is the length of the geodesic connecting the pair along the surface,
a derivation for which is given in the following section. We numerically solve for the geodesics and calculate $d_{ij}$ for each pair within the cut-off radius.

The net force on a chosen vortex in a given time step is the sum of the individual forces acting upon it. We set a distance length scale $a_0$ as the length of the lattice parameter for the expected state at $z = 0.5$, i.e. $f_{ij} = -f_0 K_1(d_{ij}/a_0)$, where $f_{ij}$ is the magnitude of the force on vortex $i$ due to vortex $j$. The distance $\delta d$ moved by a vortex is restricted to a small value through the choice of the value of time step $\delta t$. We therefore approximate that the vortex moves a distance $\delta d$ along the tangent vector to the net force, which is approximately parallel to the geodesic along the direction of the net force over the distance $\delta d$.

**B.1 Determining the distance between two particles - boundary value problem**

The distance between two points is determined by numerically calculating the length of the geodesic connecting the pair. Depending on the state on the surface, there may be occasions where either $\theta(z)$ or $z(\theta)$ is singular. As such, geodesic equations for both $\theta(z)$ and $z(\theta)$ must be known so that if one has a singularity, the other can be used.

**B.1.1 Solving for $\theta(z)$**

We determine the equation satisfied by the geodesic $\theta(z)$ on the surface. The line element $ds$ is given by

$$ds = \sqrt{dr^2 + r^2 d\theta^2 + dz^2}$$  \hspace{1cm} (B.4)

$$= dz \sqrt{r_z^2 + r^2 \theta_z^2 + 1}$$  \hspace{1cm} (B.5)

$$\equiv dz f$$  \hspace{1cm} (B.6)

where we have dropped the functional dependence $r = r(z)$ for brevity.

The geodesic must satisfy the Euler-Lagrange equation for $\theta$, leading to:

$$0 = \frac{d}{dz} \frac{\partial f}{\partial \theta_z}$$  \hspace{1cm} (B.7)

$$= \frac{2rr_z \theta_z + r^2 \theta_{zz}}{\sqrt{1 + r_z^2 + r^2 \theta_z^2}} \frac{r^2 \theta_z(r_z r_{zz} + rr_z \theta_z^2 + r^2 \theta_z \theta_{zz})}{(1 + r_z^2 + r^2 \theta_z^2)^3}$$  \hspace{1cm} (B.8)

Using that $\sqrt{1 + r_z^2 + r^2 \theta_z^2} > 0$, we can multiply out the denominator to give

$$0 = (2rr_z \theta_z + r^2 \theta_{zz})(1 + r_z^2 + r^2 \theta_z^2) - r^2 \theta_z(r_z r_{zz} + rr_z \theta_z^2 + r^2 \theta_z \theta_{zz})$$  \hspace{1cm} (B.9)

$$0 = r \left[ r(1 + r_z^2) \theta_{zz} + r^2 r_z \theta_z^3 + (2r_z(1 + r_z^2) - rr_z r_{zz}) \theta_z \right]$$  \hspace{1cm} (B.10)

We make use of Eqs. (B.1)-(B.3) leading to

$$0 = \left( 1 + \frac{\eta^2 r_z^2}{4r_0^2} \right) \theta_{zz} + \frac{\eta^4 r_0^2}{2r_0^2} \theta_z^3 + r^2 \left( \frac{\eta}{r_0^2} - \frac{\eta^3 r_0^2}{8r_0^4} \right) \theta_z$$  \hspace{1cm} (B.11)

Substituting in for $r(z)$ then leads to the equation satisfied by the geodesic $\theta(z)$

$$0 = 2(1 - \eta z)(1 - \eta z^3 + \eta^2 r_0^2 \theta_{zz} + 4\eta r_0^2 (1 - \eta z)^2 \theta_z^3 + \eta(2(1 - \eta z)^3 - \eta^2 r_0^2)) \theta_z$$  \hspace{1cm} (B.12)
Equation (B.12) can be solved numerically, with boundary conditions given by the positions of the two vortices, to find $\theta(z)$ and $\theta_z(z)$. The distance $d_{ij}$ between vortices $i$ and $j$ is then the length of the geodesic and is determined by numerically integrating

$$d_{ij} = \int ds = \int_{z_i}^{z_j} dz \sqrt{1 + r_z(z)^2 + r(z)^2 \theta_z(z)^2}.$$  \quad (B.13)

### B.1.2 Solving for $z(\theta)$

We repeat the process from the last section, this time solving for the geodesic $z(\theta)$. In this case the line element $ds$ is given by

$$ds = d\theta \sqrt{r(\theta)^2 + z_\theta(\theta)^2} = d\theta \sqrt{\frac{r_0^2}{1 - \eta z} + z_\theta^2 + \frac{r_0^2 \eta^2 z_\theta^2}{4(1 - \eta z)^3}} \quad (B.14)$$

$$= d\theta \sqrt{\frac{r_0^2}{1 - \eta z} + z_\theta^2 + \frac{r_0^2 \eta^2 z_\theta^2}{4(1 - \eta z)^3}} \quad (B.15)$$

$$= d\theta g \quad (B.16)$$

Solving the Euler-Lagrange equation for $z$ gives

$$\frac{\partial g}{\partial z} = \frac{d}{d\theta} \frac{\partial g}{\partial z_\theta} \quad (B.17)$$

$$\frac{\partial g}{\partial z} = \frac{3 \eta^3 r_0^2 z_\theta^2}{4(1 - \eta z)^3} + \frac{\eta r_0^2}{4(1 - \eta z)^3} \quad (B.18)$$

$$\frac{d}{d\theta} \frac{\partial g}{\partial z_\theta} = \frac{\eta^2 r_0^2 z_\theta^3}{4(1 - \eta z)} + \frac{3 \eta^3 r_0^2 z_\theta^2}{2(1 - \eta z)^2} + 2 z_\theta + 2 \eta \left( \frac{\eta^2 r_0^2 z_\theta}{2(1 - \eta z)^2} + 2 z_\theta + 2 \eta \right) \times \left( \frac{3 \eta^3 r_0^2 z_\theta^3}{4(1 - \eta z)^4} + \frac{\eta^2 r_0^2 z_\theta}{(1 - \eta z)^2} + \frac{\eta^2 r_0^2 z_\theta}{2(1 - \eta z)^3} + 2 z_\theta \right) \left( \frac{\eta^2 r_0^2 z_\theta}{4(1 - \eta z)^3} + \frac{r_0^2}{1 - \eta z} + \frac{z_\theta^2}{2} \right)^{-3/2} \quad (B.19)$$

Simplifying this leads to the equation for the geodesic for $z(\theta)$:

$$0 = 2(1 - \eta z) \left( 4(1 - \eta z)^3 + \eta^2 r_0^2 \right) z_\theta + \eta \left( \eta^2 r_0^2 - 8(1 - \eta z)^3 \right) z_\theta^2 - 4 \eta r_0^2 (1 - \eta z)^2 \quad (B.20)$$

Equation (B.20) can be solved numerically to find $z(\theta)$ and $z_\theta(\theta)$. The distance $d_{ij}$ between a vortex pair is once again the length of the geodesic and is determined by numerically integrating

$$d_{ij} = \int ds = \int_{\theta_i}^{\theta_j} d\theta \sqrt{r(\theta)^2 + z_\theta(\theta)^2 + r_\theta(\theta)^2} \quad (B.21)$$

### C DETERMINING THE EXPECTED VORTEX LOCATIONS ON THE HORN

We derive the equation for the curves which define the edges connecting vertices in the tiling of the horn surface. The vertices at which these curves intersect define the expected locations of vortex sites. The curves, known as loxodromes, always have their tangent vector at a fixed angle relative to the parallels and
meridians of the surface. For the surface of revolution of the curve $r(z)$ about the $z$ axis, parameterised in cylindrical coordinates as $\mathbf{r} = (r(z) \cos \theta, r(z) \sin \theta, z)$, a set of orthonormal unit vectors along the surface can be defined as

$$\hat{e}_\theta = \begin{pmatrix} - \sin \theta \\ \cos \theta \\ 0 \end{pmatrix}, \quad \hat{e}_v = \frac{1}{\sqrt{1 + r_z^2}} \begin{pmatrix} r_z \cos \theta \\ r_z \sin \theta \\ 1 \end{pmatrix}$$ (C.1)

where, in this section, subscript $z$ denotes a derivative with respect to $z$. The parallels of the surface are the lines of constant $v$ (or equivalently $z$) and the meridians are the lines of constant $\theta$. The angles of the curves are determined by the chosen value of $\alpha$.

A curve $\gamma(z)$ for which the tangent vector is always at some fixed angle $\beta$ relative to the meridians must always be parallel to the curve

$$\hat{\beta} = \cos \beta \hat{e}_v + \sin \beta \hat{e}_\theta.$$ (C.2)

Solving $\hat{T} = \hat{\beta}$, where $\hat{T}$ is the unit tangent vector to $\gamma(z)$ means that $\gamma(z)$ must satisfy

$$\frac{1}{\sqrt{1 + r_z^2 + r_z^2 \gamma_z^2}} \begin{pmatrix} r_z \cos \gamma - r \gamma_z \sin \gamma \\ r_z \sin \gamma + r \gamma_z \cos \gamma \\ 1 \end{pmatrix} = \frac{\cos \beta}{\sqrt{1 + r_z^2}} \begin{pmatrix} r_z \cos \gamma \\ r_z \sin \gamma \\ 1 \end{pmatrix} + \sin \beta \begin{pmatrix} - \sin \gamma \\ \cos \gamma \\ 0 \end{pmatrix}$$ (C.3)

where $r(z)$ and $r_z(z)$ are defined in Eqs. (B.1) and (B.2) respectively.

Solving for $\gamma_z(z)$ leads to

$$\gamma_z(z) = \pm \tan \beta \frac{\sqrt{1 + r_z(z)^2}}{r(z)}.$$ (C.4)

This expression is true for the loxodromes on any surface of revolution with a shape profile $r(z)$. We integrate this expression on the horn with the boundary condition that $\gamma(z = 0) = 0$ to give the solution

$$\gamma(z) = \frac{1}{3} \tan \beta \left[ \sqrt{1 + \frac{4}{\eta^2 r_0^2}} - \sqrt{1 + \frac{4(1 - \eta z)^3}{\eta^2 r_0^2}} - \tanh^{-1} \left( \sqrt{1 + \frac{4}{\eta^2 r_0^2}} \right) + \tanh^{-1} \left( \sqrt{1 + \frac{4(1 - \eta z)^3}{\eta^2 r_0^2}} \right) \right].$$ (C.5)