Curves formed by colonies of micro-organisms growing on a plane surface

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Introduction.

In many cases, when a colony of micro-organisms such as moulds, yeasts or bacteria grows on the plane surface of a solid medium (*e.g.* agar), starting from a single cell, the colony tends to grow as an ever expanding circle. The reason for this is that every cell, if free from competition, can multiply at roughly a constant rate in all directions in a plane, limited by the fact that territory occupied by one cell cannot be occupied by another. For the purposes of the present discussion, we can assume, as a first approximation, that the whole process is two-dimensional.

It is a matter of common observation in bacteriology and mycology[1, 2] that occasionally a colony may show departure from a circular shape, due to part of it (known as a *sector*) growing at an obviously different rate from the rest. A sector originates when one cell on the growing edge of the colony begins suddenly to multiply at a faster rate than the remainder, an event due in some cases to mutation. It is also often observed that when colonies, growing near to one another in the same plane, meet, the boundaries between them are generally of very regular shapes.

This paper studies the geometry of

(1) the intersection curves between colonies,

(2) the intersection curves between colonies and their sectors,

(3) the outer growing edge of colonies and sectors.

We find that the most general intersection curve between two colonies consists of an arc of a Cartesian oval together with arcs of equiangular spirals. In special cases, the Cartesian oval degenerates into a hyperbola, a circle or a straight line; and the sector curve may be considered as a special case in which the Cartesian oval arc is absent. In the same way, we find that the outer growing edge of the sector may be thought of as a special case of the more general outer

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[1] G. Pontecorvo and A. R. Gemmell, *Nature*, **154** (1944), pp. 532-534. "Colonies of Penicillium Notatum and other moulds as models for the study of population genetics."

[2] L. E. Shinn, *Journal of Bacteriology*, **38** (1939), pp. 5-12. "Factors governing the development of variational structures within bacterial colonies."

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edge and that both consist of a circular part together with parts of involutes of the equiangular spirals.

Since this analysis does not appear to have been done before, it is hoped that it may prove useful and be further developed in the study of variation, and of interaction of variant forms, in micro-organisms.

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Figure 1.

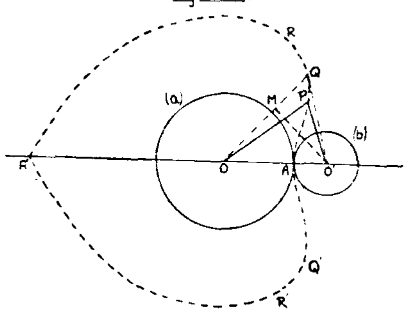


Figure 2.

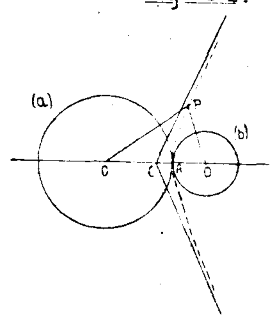


Figure 3.

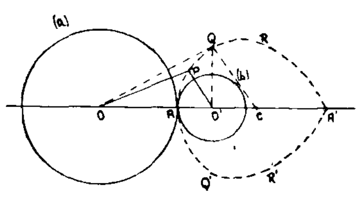
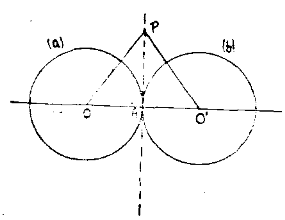


Figure 4.



General case.

Two colonies, (*a*) *and* (*b*), *grow out from two different points* O *and* O' *with different growth rates and beginning at different times.* (See Figure 1.)

Let the colonies meet at A, and let AQA' and $AQ'A'$ represent the subsequent boundary curve, which of course is symmetrical about OO'. We choose three convenient parameters which the biologist can determine without difficulty, namely p, a and v where

$$p = OA \;= \text{radius of colony } (a) \text{ at time of meeting,}$$
$$ap = AO' = \text{radius of colony } (b) \text{ at time of meeting,}$$
$$v = \frac{\text{growth rate of colony } (b)}{\text{growth rate of colony } (a)}.$$

Figure 1 is drawn for the case where $a < 1$, $v > 1$.

Let P be any point on the boundary curve, and let $OP = r$, $O'P = r'$, angle $O'OP = \theta$.

The intersection curve is formed in two stages. *At first* the growth of both colonies is radial, and we have

$$v = \dot{r}'/\dot{r} = dr'/dr. \tag{1}$$
$$\therefore \; vr - r' = \text{constant} = (v - a)\,p. \tag{2}$$

This is the equation in bipolar coordinates of a quartic curve known as a Cartesian oval[1, 2] with O and O' as two of its three foci.

Let Q, Q' be the points on the Cartesian oval such that $O'Q$ and $O'Q'$ are tangents. After these points are reached, the growth of the second colony is no longer radial, since cells on its outer edge begin to grow round the arcs QR and $Q'R'$.

To locate the points Q, Q' where the change occurs, let angle $OQO' = \alpha$; and let ϕ be the angle between OP and the tangent at P to the boundary curve.

Then we know that

$$\cos\phi = dr/ds, \tag{3}$$

and at the point Q,

$$\phi = \alpha, \text{ and } ds/dr' = 1. \tag{4}$$

Hence, from (4), (3) and (1)

$$\sec\alpha = dr'/dr = v. \tag{5}$$

This determines α and the boundary curve follows the Cartesian oval until angles OQO' and $OQ'O'$ reach this value. (Here we have assumed that $v > 1$. If $v < 1$, OQ instead of $O'Q$ is tangential when $\cos\alpha = v$.)

Let $OQ = r_1$, $O'Q = r_1'$, angle $QOO' = \theta_1$; and let $O'M$ be the perpendicular from O' to OQ. From triangle OQO', we have

$$r_1^2 + r_1'^2 - 2r_1 r_1' \cos\alpha = OO'^2.$$
$$\therefore \; r_1^2 + r_1'^2 - 2r_1 r_1'/v = p^2(1 + a)^2. \tag{6}$$

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[1] A. B. Basset, *Elementary Treatise on Cubic and Quartic Curves*, Cambridge, 1901, p. 172.

[2] H. Lamb, *Infinitesimal Calculus*, Cambridge, 1921, p. 320.

Also, from equation (2),

$$v\, r_1 - r_1' = p\,(v - a). \tag{7}$$

Eliminating r_1', we obtain

$$r_1^2 (v^2 - 1) - \frac{2\, r_1 p}{v} (v - a)\,(v^2 - 1) + p^2 [\,(v - a)^2 - (1 + a)^2\,] = O. \tag{8}$$

Also, using equations (5) and (7),

$$\cos\theta_1 = \frac{OM}{OO'} = \frac{r_1 - r_1' \cos a}{p\,(1 + a)} = \frac{v\, r_1 - r_1'}{v\, p\,(1 + a)} = \frac{v - a}{v\,(1 + a)}. \tag{9}$$

The larger of the two roots of equation (8) gives the correct value for OQ. This can be verified by applying the sine formula to triangle OQO' in which θ_1 and a have already been determined.

After Q and Q′ are reached, we have in place of equation (1)

$$\left.\begin{aligned} v &= \dot{s}/\dot{r} = ds/dr = \sec\phi. \\ \text{Hence}\qquad \phi &= \text{constant} = a, \end{aligned}\right\} \tag{10}$$

which shows that QRA' and $Q'R'A'$ are equiangular spirals[1] round O. Their polar equations are

$$r = r_1\, e^{(\pm\theta - \theta_1)\cot a}, \qquad \text{where } \sec a = v. \tag{11}$$

(If $v < 1$, the spirals will be described round O'.)

Special Cases.

1. *Two colonies grow out from O and O′ at the same rate but beginning at different times.*

In this case, $v = 1$, and equation (2) becomes

$$r - r' = (1 - a)\, p. \tag{12}$$

Hence P traces out one branch of a hyperbola with foci at O and O'. If $a < 1$, it is the branch nearest O' (see Figure 2), since $r - r'$ is always positive.

The right side of equation (12), taken positively, gives the length of the transverse axis of the hyperbola. If we call it $2A$, and call the eccentricity e, we have

$$2A = |\,1 - a\,|.\, p,$$

and

$$2Ae = OO' = (1 + a)\, p.$$

Hence

$$e = (1 + a) / |\,1 - a\,|, \tag{13}$$

and if $2\,\omega$ is the angle between the asymptotes,

$$\cos\omega = 1/e = |\,1 - a\,| / (1 + a). \tag{14}$$

[1] H. Lamb, *loc. cit.*, p. 307.

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Putting $v = 1$ in equations (5), (8) and (9), we find $a = 0$, infinite roots to equation (8) and $\cos\,\theta_1 = (1 - a)\,/\,(1 + a)$. Hence for the hyperbola, ω corresponds to θ_1 in the general case.

2. *Two colonies grow out from O and O' at different rates but beginning at the same time.*

In this case, $a = v$ and Figure 3 is drawn for $a = v < 1$. Equation (2) becomes

$$r'/r = v. \tag{15}$$

The curve QAQ' is therefore an arc of a circle (the Circle of Apollonius). It can easily be shown that the circle has its centre at C where $OC = \dfrac{p}{1 - v}$, and that its radius is $\dfrac{p\,v}{1 - v}$. O and O' are inverse points with respect to the circle; hence, if OQ and OQ' are tangents to the circle, angle $OO'Q$ is a right angle. The values of θ_1 and r_1 are then easily obtained.

As in the general case, the mode of growth changes when Q and Q' are reached and the curve continues as an equiangular spiral round O'. Its equation is

$$r' = r'_1\, e^{(\pm\psi - \pi/_2)\cot a}, \tag{16}$$

where $\psi =$ angle $A'O'R$ and $\cos\,a = v$.

3. *Two colonies grow out from O and O' at the same rate and beginning at the same time.*

Here, equation (2) becomes $r = r'$. Thus, the boundary curve is the straight line through A perpendicular to OO'. (See Figure 4.)

4. *Sector.*

We now consider a final special case which occurs when O' lies on the circumference of colony (a), and where the new growth then begins from O' at a greater rate than that of colony (a). (See Figure 5.)

Here, $v > 1$ and $a = 0$. Equations (10) of the general case apply to the whole of this boundary curve which is therefore made up of two equiangular spirals round O with equations

$$r = p\, e^{\pm\theta\cot a}, \qquad \text{where } \sec a = v. \tag{17}$$

The outer growing edge.

A study of the form of the outer growing edge of colony (b) for the general case gives the following results:

Until the points Q and Q' are reached, the growing edge of colony (*b*) is a circle or part of a circle, centre O'. Thereafter, it consists of part of a circle together with parts of involutes of the equiangular spirals QRA' and $Q'R'A'$. Figure 6 shows this in successive stages, the colony (a) with the smaller growth rate being ultimately swallowed.

When the point R has been reached on the spiral QRA', the boundary b_2 of (b) consists of a circular arc TS (radius $O'S = O'Q + \text{arc}\, QR$) together with a portion SR. The latter is an involute of QR since the tangent UV is equal in length to the arc VR.

The angle subtended at O' by the circular parts remains constant after Q and Q' are reached. In the special cases 1 and 3 (Figs. 2 and

Figure 5.

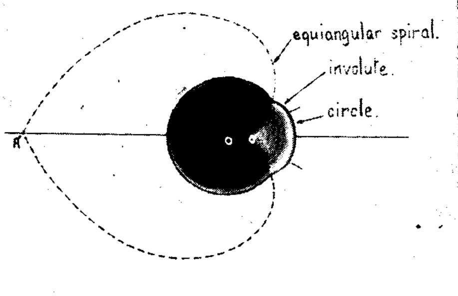
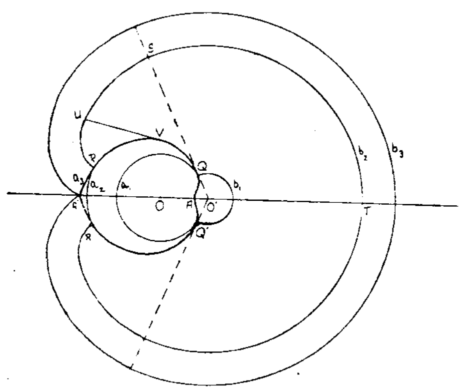


Figure 6.



4), the points Q and Q' are never reached; hence the growing edges remain circular. In the special case 4 (Fig. 5), Q and Q' coincide with O' and the angle subtended at O' by the circular part $=$ the angle of intersection of the equiangular spirals at $O' = 2\,\alpha$.

It can be shown without difficulty that the intrinsic equation of the involute curve is of the form

$$s = r_1 \sec \alpha \, e^{(\theta_2 - \theta_1)\cot\alpha} \, [\psi - \tan \alpha \, (1 - e^{-\psi \cot \alpha})],$$

where $\theta_2 = O'OR$; and that, referred to rectangular axes through O, the involute through R has the parametric equations

$$x = r \cos \theta + s \cos (\theta + \alpha), \qquad y = r \sin \theta + s \sin (\theta + \alpha),$$

where r, θ and s refer to the equiangular spiral, that is,

$$r = r_1 e^{(\theta - \theta_1)\cot\alpha}, \qquad s = (r_2 - r) \sec \alpha, \qquad r_1 = OQ, \qquad r_2 = OR.$$

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