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A liquid crystal model for mitotic cell division - and the enigma of centriole involvement in mitosis in animals but not plants

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ABSTRACT

There is a strategic difference between the process of cell division by mitosis in animal cells and that in cells of higher plants. One particularly puzzling feature is the absence of centrioles in plant cells, when they appear to be of central importance in the control of the process in animal cells. It is argued that in both cases the dividing cell uses the versatility of the liquid crystalline state of the mitotic cytoplasm created by the wide-scale assembly of microtubules prior to mitosis. It is not the centrioles *per se* which are vital – it is the director field of the mesophase which is crucial – and alternative procedures have been developed by plants and animals to create this. In both cases, they can be related to known spontaneous alignment states of liquid crystalline systems.

KEYWORDS

Mitosis; centrioles; microtubules; liquid crystalline phases; director field; phragmoplast

“Centrioles present something of an enigma. Centrioles are absent from the cells of higher plants [but] when animal cells undergo mitosis they are considered by some to benefit from the presence of centrioles which appear to control spindle fibre formation and which later has an effect on chromosome separation.” [1]

Preface

When introducing the complex process of cell division in biology courses in some American universities, there was (and perhaps still is) a well-used aside to the audience which usually drew mild laughter from the students and sometimes gave rise to an exaggerated response from any member of faculty staff who happened to be present. It related to the distinction between cell division in animals and higher plants. In the former case subcellular bodies called *centrioles* appear to be of central importance. They are clearly visible, apparently organising their surroundings and directing the sequence of events which occur around them. However, in the cells of higher plants they are absent, and things appear to function perfectly well without them.

It was only necessary to give the merest hint that this would be an apt analogy for the role of Chancellor/Dean/Head of department (- or any other suitable target within the University).

Glossary

Centrioles - cylindrical, self-replicating subcellular organelles which occur in pairs, involved in microtubule growth and organisation.

Centromere - the part of a chromosome that links sister chromatids together, and where spindle fibres are attached during mitosis.

Centrosomes - (occur in animal cells only) the main microtubule organizing centres in the cell. They are composed of two orthogonally-aligned centrioles. In animal cell mitosis, they separate and migrate to form the poles of the spindle.

Chromatid - one of the two identical strands into which a chromosome separates, prior to cell division.

In vivo - within a living system.

In vitro - literally ‘in glass’ (*i.e.* a test tube) - outside the living system.

Kinetochores - multi-component complexes attached to centromere regions of chromosomes. They come into action at the end of metaphase when the bonds which have held each chromatid pair together break and the two daughter chromatids are drawn towards the opposite poles by the contraction of the microtubules.

Mesogen - a compound which is capable of forming a liquid crystalline phase.

Metaphase - the central stage of mitosis, where the chromosomes have been marshalled into the equatorial plane of the cell, but have not yet begun to separate into two chromatids.

Phragmoplast - the plate which forms in the equatorial plane of a plant cell towards the end of mitosis – and which develops in to the new cell wall between the daughter cells.

Plasma membrane - the phospholipid bilayer surrounding the cell.

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Spindle - the apparatus within the cell which organises the alignment and separation of chromosomes during cell division.

Tactoid - a Zeppelin-shaped droplet of nematic liquid crystalline material.

Tubulin - the small globular protein units, in the cytoplasm, from which microtubules are assembled.

1 Introduction

1.1. Mitosis – the scale of the problem

The process of cell division in living systems is difficult – and complex machinery has evolved to cope with it. Some idea of the magnitude of the problem can be gained by considering the dimensions of the DNA strands which have to be copied, separated and distributed equally to the two daughter cells. The numbers become literally astronomical. If pieced end-to-end the 3 billion base pairs in each human cell would give a DNA strand about 2m long (and the total DNA in all cells of a human body would extend to about twice the diameter of the Solar System). If we ignore the protein component of the chromosomes, and take the diameter of an unwound thread of DNA to be about 3nm, the length:width ratio of the strand comes to about 6×10^8 . Scaled up to distances that are easier to visualise, this would correspond to a 2 cm diameter hosepipe with a length of 12,000 km. And, remember that when a human cell divides, each chromosome has to be divided along its entire length,

into two and the halves separated without entangling themselves.

In comparison, the annual problem of unscrambling the cable of an electric lawnmower in spring, after it has spent a couple of months spontaneously entangling itself, looks trivial.

1.2. Bernal's view of the mitotic spindle

Over fifty years ago, the great polymath J. D. Bernal suggested (from observations with a polarising microscope) that, during cell division by mitosis, at the crucial stage where the nuclear membrane has dispersed the cytoplasm becomes a tactoid [2] [Figure 1](#).

At that time, tactoids as shown in [Figure 1](#), were familiar objects to anyone working on liquid crystalline systems. Zocher had encountered them in studies of liquid crystalline suspensions of vanadium pentoxide [3] and Bernal had studied the Zeppelin-shaped droplets formed by concentrated solutions of tobacco mosaic virus particles [4]. In spite of Bernal's impressive reputation, this proposal appears to have been rejected out of hand, with no serious consideration. The mitotic spindle sometimes appears to be pointed at both ends and it is more-or-less Zeppelin-shaped and sufficiently fluid to allow chromosomes be drawn through it. However, it does not have the well-defined boundary of a tactoid and was presumably thought to have too much internal structure to be directly comparable. Any resemblance was taken to be superficial and simplistic.

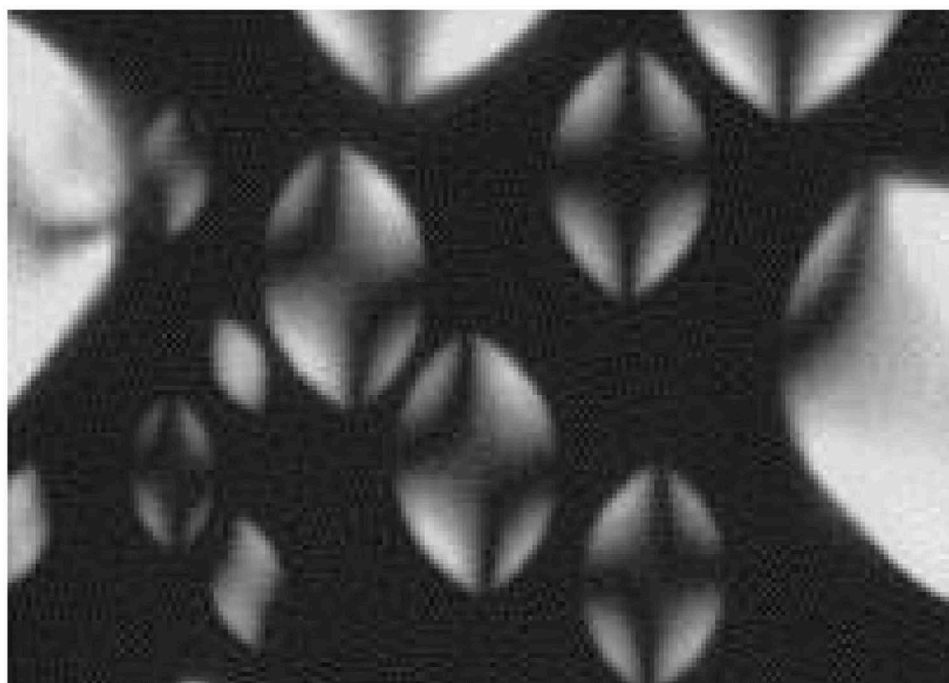


Figure 1. Tactoids of a suspension of vanadium pentoxide, viewed between crossed polarisers. (2).

However, in the light of considerably more knowledge of the processes involved in cell division, and of the self-ordering properties of liquid crystalline phases, it would appear that there may be more than a grain of truth in the suggestion – and that, although the spindle is not a tactoid, it is argued that it is essentially composed of material in a liquid crystalline state.

1.3. The enigma

This paper discusses the distinction between the forms of mitosis in animal and plant cells and in particular focusses on the long-standing puzzle concerning the role of sub-cellular units termed centrioles – which appear to be central controlling features in one case but which are absent in the other. It will be argued that in both cases the liquid crystalline state of the cell contents is of paramount importance and that the various global states adopted by cells during mitosis involve director field patterns which can be spontaneously adopted by liquid crystalline systems *in vitro*.

2. Liquid crystalline systems

2.1. Nature's sensitive phase

To identify a phase as being in a liquid crystalline state is considerably more than simply describing its appearance. It implies a package of concomitant properties. When Peter Collings and Mike Hird wrote their introductory book *Liquid Crystals* [5] they followed the title with the words *Nature's Sensitive Phase*. If you had to choose three words to summarise the properties of liquid crystalline mesophases you could not do much better than these.

Liquid crystalline systems are sensitive to more-or-less every physical factor that could affect their structure – and in general, they are considerably more sensitive than any other state of matter to changes in :-

- Temperature
- Concentration of the major components.
- Concentration of small amounts of minor additives – especially chiral dopants, where low concentrations can lead to major structural changes.
- The shape of the containing vessel – and its surface treatment.
- Electric and magnetic fields of moderate strengths.

Note that, to a greater or lesser extent, all of the above factors are exploited in the design of modern liquid crystal displays.

The oligomers, precursors and fragmented specimens of virtually every biological polymer: collagen, cellulose,

actin, DNA and RNA can give a liquid crystalline suspension in solutions above a threshold concentration [6]. And the liquid crystalline state of aqueous solutions of microtubules has been well-characterised [7].

2.2. The self-ordering properties of nematic liquid crystalline phases

2.2.1. In a tube

The 'cellular' optical texture sketched in Figure 2 is spontaneously adopted by samples of nematic material contained in a clean glass tube, when the isotropic liquid is allowed to cool. It can be observed in both thermotropic and lyotropic systems [8] – and is not particularly sensitive to the dimensions of the container.

The explanation for this texture appears to be straightforward. It is a consequence of the boundary conditions. If we take the alignment at the glass/mesophase interface to be normal, and then extend the pattern into the bulk of the sample, the molecules become increasingly congested as the axis is approached and the splay distortion energy increases. In order to relieve this stress, the sample adopts the pattern shown in (2c) which is sometimes, picturesquely referred to as *escaping into the third dimension*. This entails a significant bulk movement of material in a direction parallel to the axis. For an elongated single domain, this becomes a difficulty. Stress in the sample is relieved by it spontaneously dividing into a number of 'cells' of more or less (but not necessarily precisely) the same length, pointing alternately left and right as shown in (2e).

If solid, elongated inclusions of colloidal dimensions are introduced into systems of this kind, they are sometimes able to distribute themselves more or less randomly throughout the bulk of the sample but aligning parallel to the local director field – as shown in Figure (2b). (And this has been used as a way of verifying that the molecular alignment is that inferred from polarising microscopy.) Larger particles tend to settle along the unique axial line, (2c) particularly at the positions where the local director best matches the epitaxial alignment at the particle surface (2e).

2.2.2. In a spherical droplet

A second well-studied example of spontaneous pattern formation in a simple liquid crystalline system is that within a spherical droplet of nematic mesophase, where the boundary conditions can be changed merely by changing the temperature.

The process shown in Figure 3 has been elegantly described and discussed by Lavrentovich [9]. It commences with a spherical tactoid, (formed when the surface tension is strong enough to overcome the tendency of a nematic droplet to form a Zeppelin shape). The

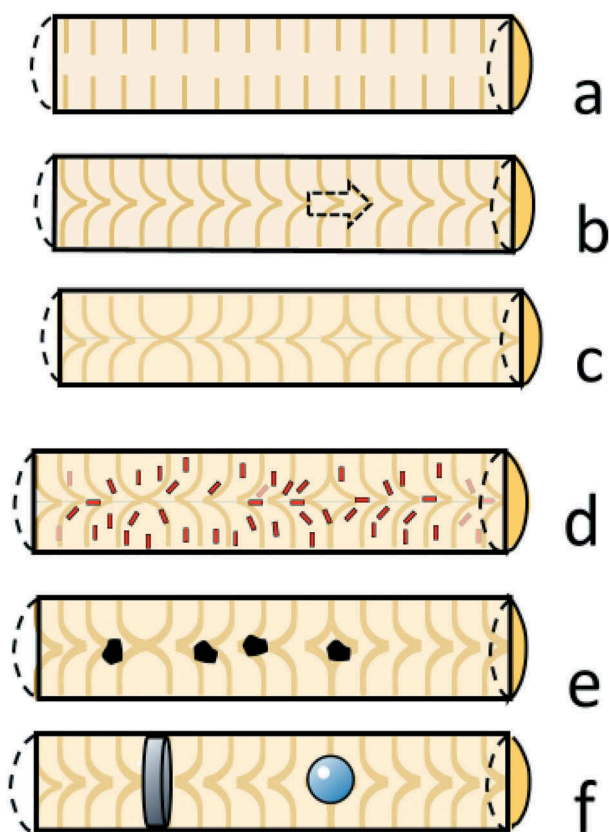


Figure 2. The spontaneous alignment of a nematic sample in a glass tube. (a) At a clean glass surface, the mesophase takes up a normal alignment. (b) When this is extended inwards, the congestion which builds up causes the director field to curve towards the axis (*escaping into the third dimension*). However, if all of the distortion lies in the same direction, this would entail an energetically costly bulk displacement of material. (c) This is alleviated by the sample breaking into cells, of approximately the same length, facing alternately to the left and right. (d) In some instances, small elongated inclusions can disperse themselves throughout the sample, taking up the alignment of the local director field. (e) Larger inclusions have been found to assemble along the axis. (f) One would expect that tailor-made inclusions, of the appropriate dimensions and surface treatment, would place themselves at corresponding positions, fitting into the director field, like a hand into a glove.

entire surface is covered with tangentially-aligned mesophase. Reorganisation of the droplet structure is caused by reducing the temperature, which alters the boundary alignment from tangential to radial.

When the preferred epitaxial alignment begins to change, what one might call the structural inertia of the system makes immediate global realignment difficult. The small numbers of molecules at the poles themselves are already normal and they form the nucleus of a growing domain of axially aligned material. Molecules near to the equator have no such nucleus and respond more slowly.

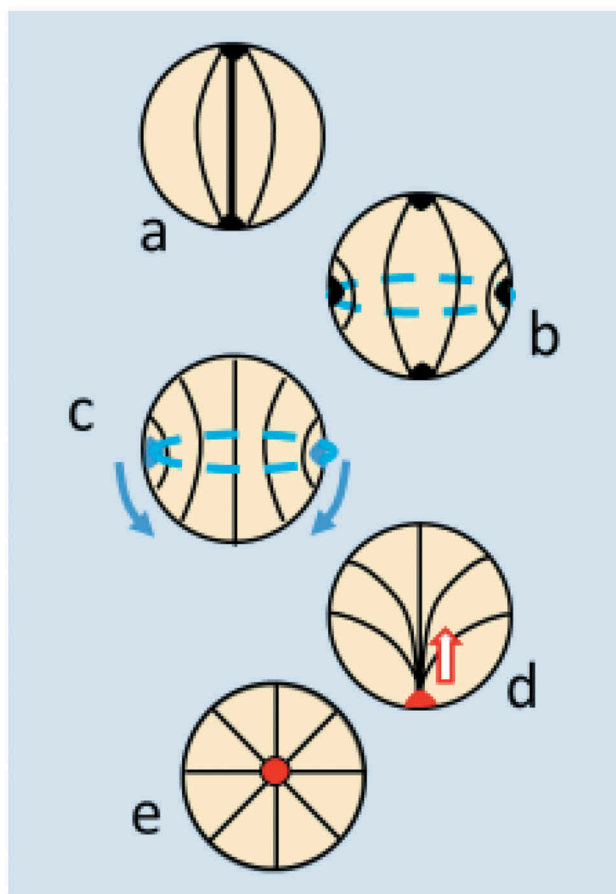


Figure 3. Topological dynamics of defects in a nematic spherical droplet suspended in a glycerine-lecithin continuum. By lowering the temperature of the sample, one changes the director orientation at the surface of the droplets, from tangential (a) to normal alignment (e). The starting structure is a spherical tactoid with monopoles, indicated in black, at the top and bottom (a). The first stage is the formation of a disclination line (in this case, a *boojum*) around the equator indicated in blue (b) and (c) and its migration to the bottom of the droplet, where it shrinks into a hedgehog (d), indicated in red. The final stage is the withdrawal of the hedgehog from the surface into the centre of the droplet (e). Redrawn from Lavrentovich [9].

Their lowest energy option is to form a toroidal ring as shown.

At the start there were two unique points in the director field. These were a pair of half-hedgehogs, one placed at each pole. At the final stage there is a single full-hedgehog at the centre of the droplet. Although the initial and final stages have high symmetry, there is no easy topological pathway to be made between the two equivalent low-symmetry routes – i.e. whether the equatorial disclination band moves upwards, or downwards (as shown in these sketches). Since, in the final state, the hedgehog ends in the centre of the droplet it makes no difference to the outcome which route is taken.

These examples illustrate a concept which will be invoked in the remainder of this article. Inclusions within a liquid crystalline host phase are in principle able to align and position themselves at particular sites within the director field. Or to express it more succinctly, they appear to 'know' where to go to and which way to move, when the conditions change.

3. Optical microscopy of mitosis

3.1. The structure and polarity of microtubules

Early studies of cell biology were dependent almost totally on information obtained from optical microscopy. And the power of this technique depended on the availability of suitable selective stains. For example, the section used for preparation of the micrograph of onion root tip cells in various stages of mitosis in Figure 4(a) [10] has been treated with haematoxylin (a stain based on an ancient textile dye derived from logwood).¹ This has selectively stained the chromosomes black and made them clearly visible. [Note that the term *chromosome* was not intended to imply that these objects were naturally coloured. It was used because they could be coloured with a stain.]

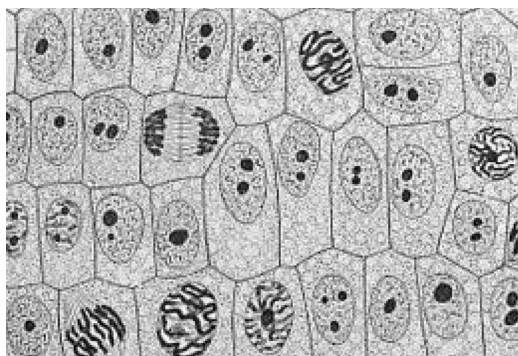
3.1.1. Microtubules

The 'resting' cell (i.e. one not engaged in cell division) contains large numbers of dimeric tubulin units dispersed in the cytoplasm. When the process of mitosis begins, these aggregate, producing microtubules. (Figure 5). These assemblies are polar (in the sense of the word as used by crystallographers) with all of the molecular units pointing the same way. This directionality is critical to the functioning of microtubules in mitosis (and in their other roles in cell biology). The two ends of a microtubule have been arbitrarily labelled (+) and (-). [Note that this designation has nothing to do with any electrostatic charge the ends may carry.]

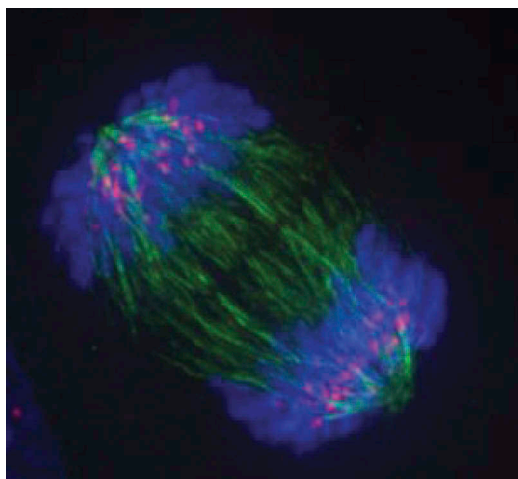
In terms of their physical properties microtubules are like zip fasteners. Intact microtubules are strong and can resist appreciable stress – provided their ends are protected. But the whole microtubule can be easily unravelled by pulling it apart at an unprotected end.

At first sight, this looks like a biological design fault, but, (as described below) it is a crucial property, which is exploited in the workings of the molecular machinery of mitosis.

Because of their polarity, the growth rates at the two ends of a lengthening microtubule are very different. Even in a microtubule which is apparently maintaining a constant length, there is a dynamic (rather than static) equilibrium where tubulin units are being added at one



a



b

Figure 4. (a) A section of onion root tip, showing cells at various stages of mitosis (stained with haematoxylin [10]). The staining of sections of tissue with haematoxylin has been a widely-used technique in cytogenetic studies. (At the metaphase stage chromosomes are at their most clearly visible state, and can be most easily identified and counted.) However, it can give a false impression of the events taking place, because it does not identify the other major cytoskeletal species present, such as microtubules, actin fibrils or cellulose microfibrils. In fact, concentrated regions of microtubules (around centrioles for example) tend to appear as pale featureless areas. (b) A cell at late anaphase, stained with a mixture of modern fluorescent dyes [10]. These stain selectively: microtubules are yellow and chromosomes blue, with their centromere regions in pink.

end whilst they are detaching at the other – leading to a tread-milling process. If the microtubules are growing in response to some biochemical trigger, with a concentration gradient present, those growing in a particular direction can be favoured over those growing the opposite way – ultimately producing a polar microtubule array. (If such a feat could be reproduced in a non-biological system, a new regime of liquid crystal device technology should be possible.)

4 Mitosis

In overview, mitosis is the part of the cell cycle during which the nucleus divides, resulting in two daughter

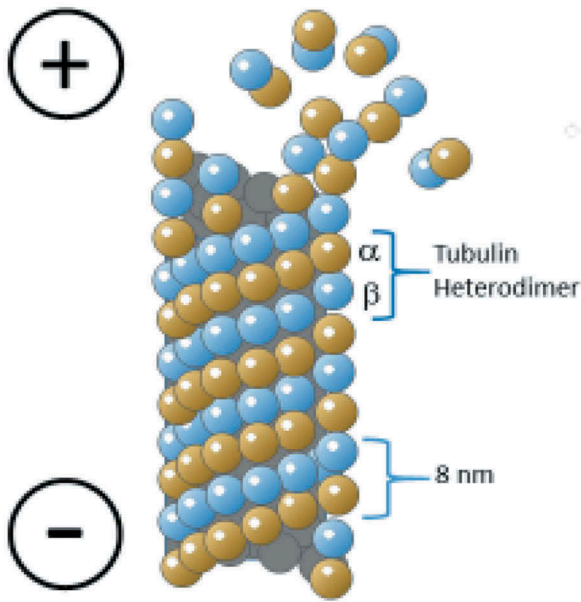


Figure 5. The microtubule.

The α/β heterodimers assemble to form hollow cylinders. In these, the dimers all point in the same direction giving the microtubule a polarity. The two ends are distinct, with different rates of growth, and are recognised by different parts of the mitotic machinery. This sketch shows a microtubule fraying the (+) end, with dimer units breaking away.

nuclei that are identical to that of the mother cell – containing the same genetic material, distributed within two identical sets of chromosomes.

4.1. Mitosis in animal cells

The central stage in mitosis is termed metaphase. This is pictured in Figure 6. It occurs when the chromosomes have been condensed (wound up to form compact bodies) and

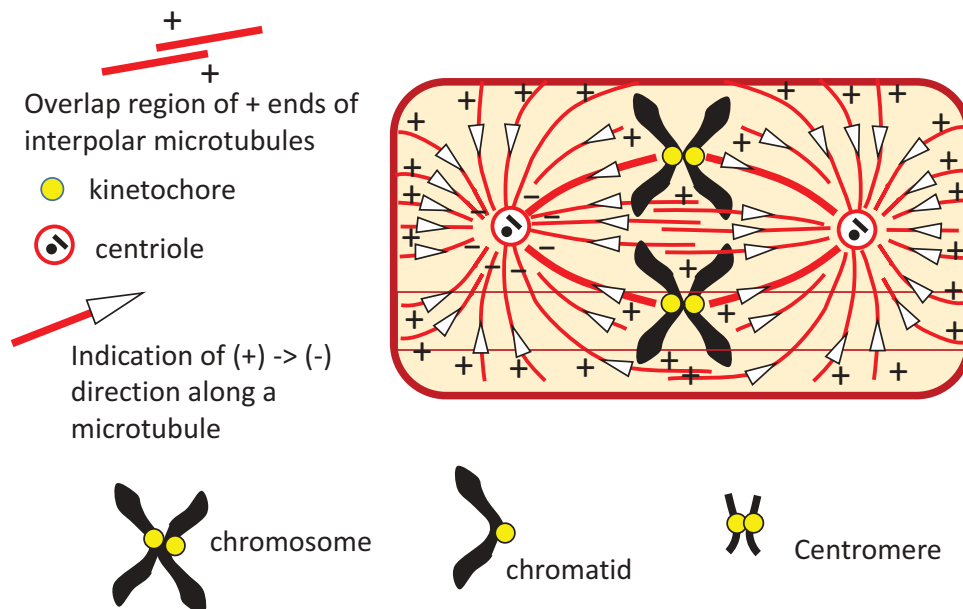
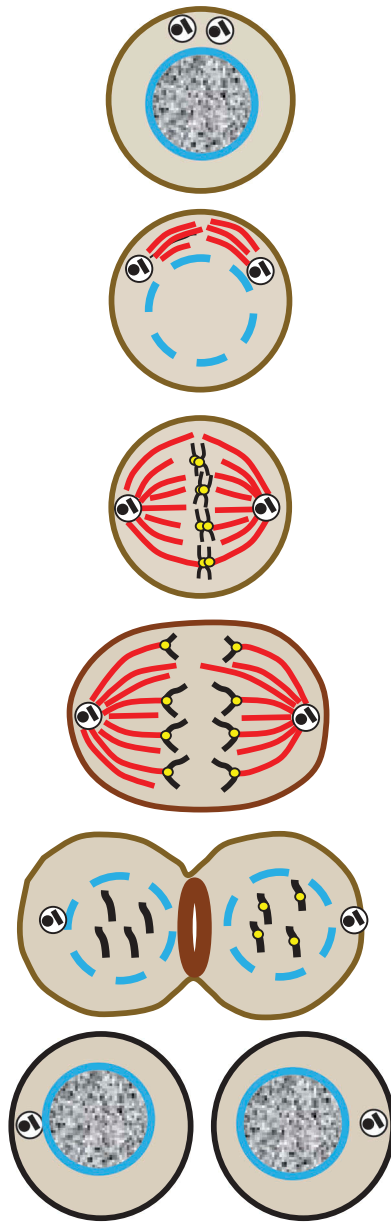


Figure 6. The state of an animal cell at metaphase.

are assembled in the equatorial plane of the cell. They are ready to be split into identical halves which will be drawn to opposite ends of the cell. This figure stresses the role of microtubules in mitosis. Note their polarity and the bonded overlap of the (+) ends in the equatorial region, which maintains the structure of the spindle.

A stylised sketch of the complete process of mitosis in animal cells is given in Figure 7. Note the apparently central role of the centriole pairs, occupying positions at the poles of the spindle and drawing the daughter chromatids towards themselves to begin the culmination of mitosis. This sequence of sketches could be termed the 'classical' picture of mitosis as represented in almost a hundred years of reviews and textbooks. It is drawn largely from sections stained with haematoxylin, and emphasises the 'important' items, i.e. the chromosomes. What it does not show is the toroidal equatorial ring of microtubules and actin fibrils only discovered in the 1960s, sketched in Figure 8. This appears in the later stages of mitosis, and contracts like a sphincter muscle, pinching off the daughter cells.

The establishment of the mitotic spindle has been described as 'a fine balancing act'. (Prosser and Pelletier ref). The delicate stability of the microtubule is essential for the 'search and capture' process. There are alternate periods of growth and contraction of the microtubules. If an extending microtubule can find a centromere and attach itself, its vulnerable (+) end is protected and it is then safe during the next phase of retraction. The forwards and backwards dance of microtubules continues until all kinetochore microtubules are anchored onto a centrosome at one end and a centromere at the other. Only then can the next stage of mitosis take place



Interphase The nucleus is distinctly visible but the chromosomes within it are not.

Prophase The chromosomes are condensed and the nuclear membrane has been dissipated.

Metaphase Fully-coiled chromosomes are lined up in the metaphase plate.

Anaphase Each chromosome has divided into two chromatids, which are being drawn to towards opposite poles.

Telophase

The chromosomes have reached the poles and are beginning to unwind. A ring of actin fibres and microtubules is contracting in the equatorial plane, and nuclear envelopes are reforming.

The chromosomes have unwound and are no longer visible. Division into two identical daughter cells is cells approaching completion.

Figure 7. Mitosis in animal cells (figures redrawn from [10]).

4.2. Mitosis in plant cells

The sketches in [Figure 9](#) outline the sequence of stages in the mitosis of higher plants.

There are glaring differences between these and the corresponding sequence described above, for animal cells. There are two major differences:-

- (1) In plants there are no centrioles – no distinct structures defining pole positions – just a rather amorphous region which appears to be a site of microtubule aggregation. Instead, the centre of activity appears to be the equatorial plane of the
- cell. Before the prophase stage begins, an equatorial band of microtubules appears, (resembling the actin-containing band which occurs towards the final stages of animal cell mitosis), which appears to direct the alignment of what passes for a spindle in plant cells.
- (2) After the metaphase stage has been reached a major structuring process takes place, with a sandwich of microtubules extending outwards from both sides of the central equatorial plate, and parallel to the central axis, as sketched in

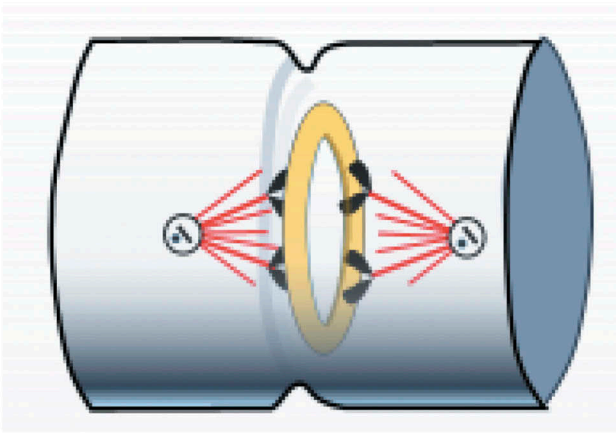


Figure 8. A more detailed sketch of the contractile ring of microtubules, actin and myosin fibres, formed during the telophase stage of mitosis in animal cells. This first forms a furrow to develop around the equator of the cell, as shown, and then squeezes the two daughter cells apart.

Figure 10. In the final stage, instead of being pinched off by a toroidal ring of ‘muscle’ the daughter cells are separated by the construction of a new cell wall, which forms from the phragmoplast a coagulation of material brought to the equatorial plane of the cell. The assembly of the new cell wall begins in isolation at the centre and spreads outwards until it reaches and fuses with the old wall.

5. Discussion

Plant and animal cells both undergo mitotic cell division. Their main difference is how they form daughter cells

during the final stages of the process. Animal cells form a furrow around the mid- plane of the cell, which deepens until it divides the cell into two identical daughters. Plant cells cannot do this, since they require a rigid, load-bearing cell wall to withstand turgor pressure. Instead, a new wall is established, extending across the mid-plane of the cell. In animal cells, the establishment and operation of the mitotic spindle appears to be under the control of the two centriole pairs – but there are rare animal organisms which can operate without centrioles and occasional instances where a mutation has caused them to be absent. In such cases it is found that the procedure of mitosis can take place, but it may give rise to a daughter cell with genetic defects of some kind.

In general, it could cause a genetic catastrophe if the process of dividing chromosomes into separate chromatids were not completed before they start to be drawn towards the poles, and incorrect DNA sequences were to be passed on to the next generation (although chromosome doubling in evolutionary trees presumably originated in rare events of this kind which were not destructive of the cell). There are built-in checkpoints incorporated into the biochemistry of mitosis, to prevent such things happening and it is important that mistakes be identified, and remedied as quickly as possible. This must require a sensitive trigger mechanism to enable mitosis to be aborted immediately. Microtubules have evolved to live on the edge of stability and it is perhaps not surprising that animal cells have become dependent on the assistance of centrioles to operate mitosis without mishaps.

Since Bernal’s time, evidence has built up to support his picture of the liquid crystalline state of the mitotic

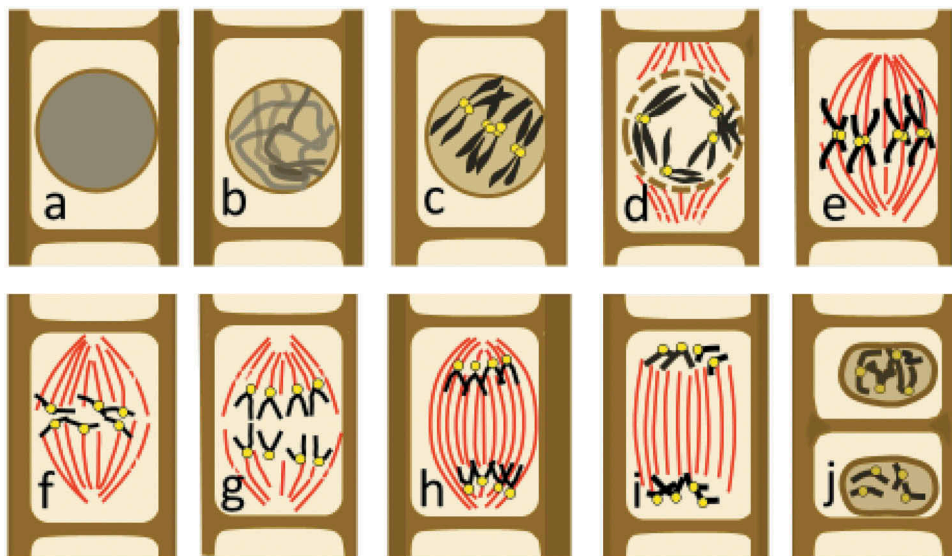


Figure 9. This series of sketches outlines the sequence of stages in the mitosis of higher plants.

Note that this figure is redrawn from an old illustration (pre 1960) [10] and does not show the pre-prophase band or the phragmoplast (c.f. Figure 10).

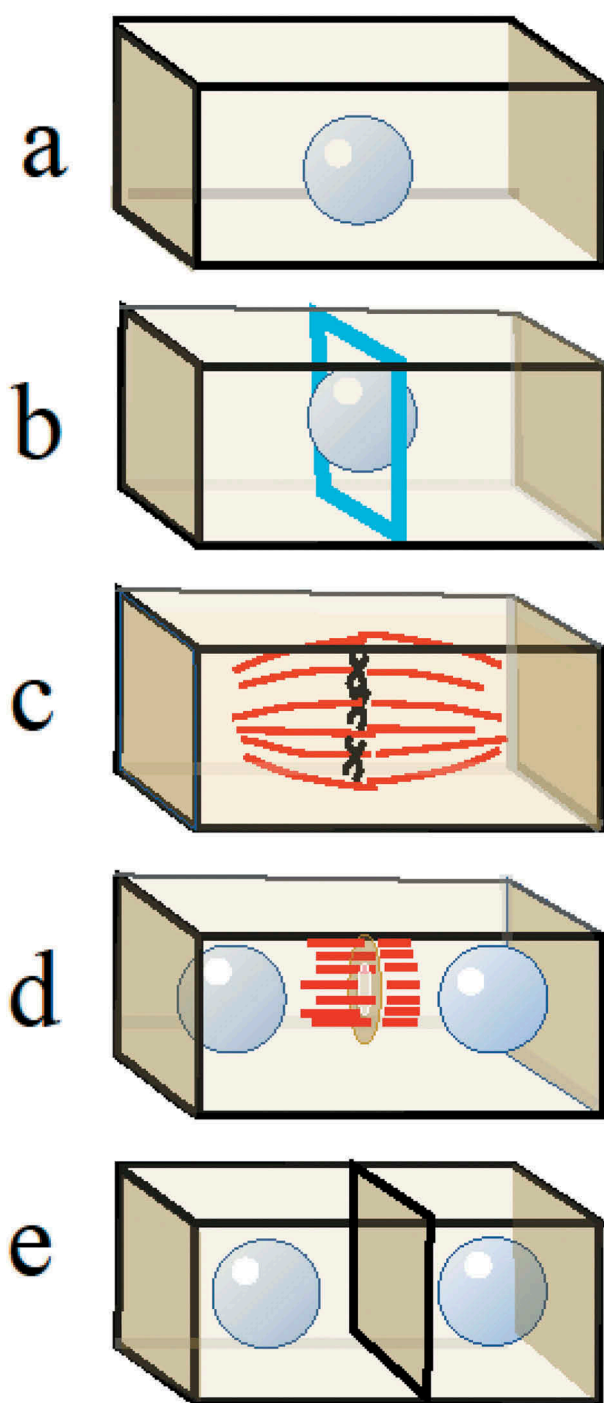


Figure 10. The stages of mitosis of a plant cell, showing the features revealed by modern staining techniques, which were not apparent in earlier haematoxylin-stained specimens. The blue rectangle in (b) represents the preprophase band and the central region in (d) represents the beginning of assembly of the phragmoplast.

cell. Studies *in vitro* have shown that a concentrated solution of microtubules assumes a liquid crystalline state, electron microscopy has shown parallel arrays of microtubules in cells and selective stains have indicated the way in which the distribution of microtubules changes throughout the various stages of mitosis.

The convincing structural similarity between the director field patterns of a nematic tactoid and the mitotic spindle has been augmented by more recent observations of the equally striking similarity between the transient toroidal equatorial rings found in nematic droplets and in animal cell mitosis (once) and plant cell mitosis (twice). I argue that these observations, coupled with the fluid nature of the materials concerned, point unequivocally to the presence of liquid crystalline phases.

In a sense the wheel has turned full cycle. One after another of the early workers who first saw liquid crystalline materials under a light microscope were struck with the ease with which they spontaneously formed patterns which flowed and grew and shrank away. Virtually all of them from Virchow onwards were led to consider seriously that these phases might actually be alive [11].

6. Conclusion

The question of how plant cells can undergo mitosis in the absence of centrioles no longer looks so enigmatic. Microtubules are the key unit in the mitotic machine for separating and directing the genetic material, and they can be directed in other ways. The rigid, load-bearing plant cell wall makes a closure like that in the final stage of animal cell mitosis impossible. An alternative way of aligning microtubules was required – with plants using the equatorial plane instead of the centriole pole.

Liquid crystalline phases are virtually unknown in what might be termed *current mainstream cell biology*. However, there is a convincing level of correspondence between the spontaneously-formed structures of liquid crystalline systems and the various stages of mitosis. Bearing in mind the known liquid-crystal forming properties of microtubules *in vitro*, this appears to justify the view that the liquid crystalline state is of central importance in explaining the topology of mitosis, and other instances, where subcellular units ‘know’ where to position themselves within a cell.

Note

1. From the 17th century until the 19th, the red heartwood of the logwood tree, (*Haematoxylum campechianum* (Blood wood) was a major source of commercial dyes. The timber was imported from central America into Europe in large quantities and used to produce stains for fabrics and leather – in a range of colours from purple to grey and black, depending on the treatment. For over a century it has been used as a stain for biological specimens, and is still routinely used as a histological stain in medicine – commonly in conjunction with eosin.

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Disclosure statement

No potential conflict of interest was reported by the author.

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