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What is a microscope? How the microscope has evolved over three hundred and fifty years

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Abstract. The microscope is named from the Greek *mikrós* (small) and *skopeîn* (to see). The first light microscopes were described over three hundred and fifty years ago, building on the development of lenses for the telescope. The publication of *Micrographia* in 1665 popularised the microscope and yet its technological development only really took off in the 1800s in parallel with many other technological developments of the time. Key to building microscopes reproducibly was the theoretical understanding of how the image is formed in the microscope, developed by Ernst Abbe in the 1880s as part of his collaboration with Carl Zeiss. That eventually led to the standardisation of light microscopes with the help of the Royal Microscopical Society. The electron microscope was then invented in the 1930s, building on principles already uncovered for light microscopy. The microscope has continued to evolve to help us to see even smaller and smaller objects across the physical and life sciences, and it is a key tool for many scientists. This overview briefly summarises the development of the microscope from its early origins up to the present day.

1. The first microscopes were invented over three hundred and fifty years ago.

It is not entirely clear who invented the first microscope, which depended on being able to make glass lenses of a suitable quality and then to combine them inside a set of sliding tubes to make a crude compound microscope. However, it may have been father and son, Hans and Zacharias Janssen (Middelburg, Netherlands) in around 1595, followed by several others in Europe. Robert Hooke, a trained physicist, who attended Westminster School and then Oxford, began experimenting with microscopy at about the same time that he became involved with the Royal Society. The Royal Society encouraged him to publish his findings in the well-known text '*Micrographia*' (now available online[1]) in 1665, also entitled '*some physiological description of minute bodies made by magnifying glasses with observations and enquires thereon*'. Not only does this book contain drawings of the various objects that Hooke observed under the microscope, but it also contains details of how he made his lenses for his microscope. In addition he came up with the term '*cell*' for individual units in cork (which are indeed what are now called cells) and he measured their dimensions. At the time it was a very popular book and it remains so today. Interestingly it has been reported that due to a bitter dispute between Isaac

[1] https://ttp.royalsociety.org//ttp/ttp.html?id=a9c4863d-db77-42d1-b294-fe66c85958b3&type=book

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Newton and Robert Hooke over the nature of light there is no surviving portrait of Robert Hooke, possibly because Newton had it removed from the Society[2].

Micrographia was widely read and may have helped to inspire another famous early amateur microscopist, Antonie van Leeuwenhoek (Delft, 1632-1723), to design and make a small pocket-sized microscope with a single lens (figure 1). In fact he made many microscopes (estimated to be over five hundred) with a range of magnification from x85 to x266 [1], [2]. The quality of the single biconvex lenses made from ground glass that he incorporated into these microscopes was very high, enabling him to see fine detail in multiple types of specimens. The resolving power of two microscopes currently in a museum in Leiden has been estimated to be 3.5 µm and the one in Utrecht at 1 µm. In contrast the compound microscopes of the time were generally of poorer quality with the glass lenses suffering from multiple issues such as chromatic and spherical aberrations that degraded the quality of the image, especially when used in combination. While Hooke preferred to use the compound microscope, he commented in *Micrographia* that simple (single lens microscopes) do "*make the object appear much more clear and distinct and magnifie as much as double microscopes… because the colours which do much disturb the clear vision in double microscopes is clearly avoided*", a clear reference to chromatic aberration. Leeuwenhoek first published his findings in the *Philosophical Transactions of the Royal Society* in 1673 with the help of the Secretary of the Royal Society (Henry Oldenburg) who translated his Dutch text into English (figure 1). Several more letters were subsequently published, although when Leeuwenhoek started to claim that he had seen living organisms in water samples (in 1676), there was apparently some initial scepticism. He was made a Fellow of the Royal Society in 1680.

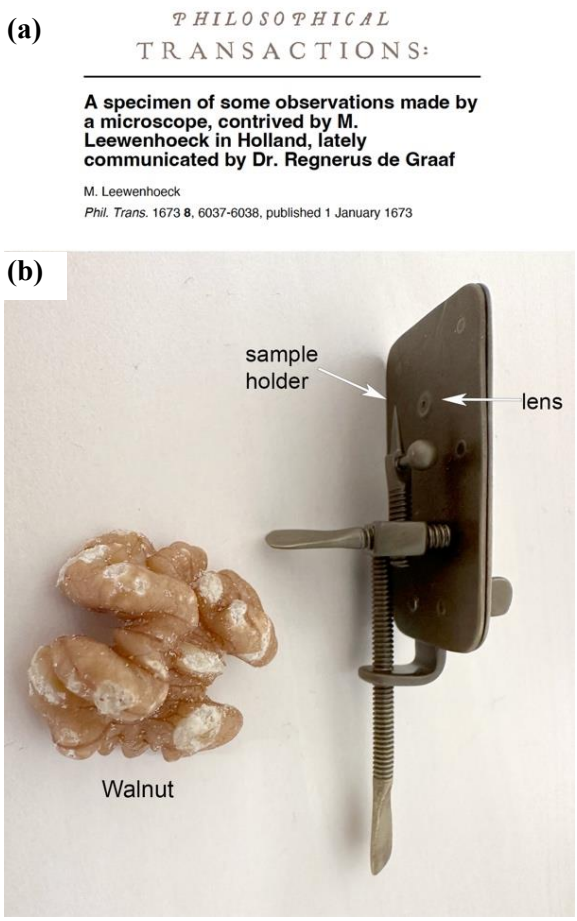

Figure 1. The Leewenhoek microscope. **(a)** The title of the first letter published in the Royal Society Journal, *Philosophical Transactions* in 1673 (available online at https://royalsocietypublishing.org/journal/rstl). **(b)** A replica Leewenhoek microscope next to a walnut to give an idea of its small size. The sample to be viewed would be placed on top of the pin as indicated by the arrow and viewed through the lens from the other side of the microscope. The screws adjusted the position of the sample so it could be viewed easily.

[2] https://royalsociety.org/blog/2010/12/hooke-newton-and-the-missing-portrait/

2. Microscopy developments into the 1800s

Microscopes continued to be of much interest over the next few centuries. However, each microscope was made individually using empirical knowledge and as a result of this trial and error approach, microscope quality varied considerably. No-one had yet managed to overcome the various aberrations that the early microscopes suffered from. However, in the 1700s and into the early 1800s several people started to make achromatic lenses that overcame chromatic aberration, firstly for telescopes. In the early 1730s Chester More Hall, a barrister and amateur astronomer and optician, made use of new types of glass that were starting to be manufactured. He observed that combining a convex lens made from flint glass (lead containing) with a second, concave lens made from crown glass (soda-lime) appeared to overcome chromatic aberrations and he used this approach in his telescopes [3].This idea was later taken up by John Dollond, who incorporated the idea into his telescope and presented his findings to the Royal Society [4] in 1757. Sometime later this idea was applied to microscope lenses, mostly likely by Jan and Harmanus van Deijl (1738-1809) of Amsterdam, who eventually published their work in 1807 [5]. However, all of these lenses had a relatively low magnification and still suffered from spherical aberrations. Eventually Joseph Jackson Lister, using a combination of theory and experiment, solved the problem and presented his findings to the Royal Society in 1830 [6]. These ideas were taken up and implemented by microscope manufacturers such as Andrew Ross, who worked closely with Lister. Incidentally Ross also invented the first type of objective correction collar, which overcomes additional aberrations introduced by using a glass coverslip over the object being imaged. This effect is nicely demonstrated in an online tutorial which the reader can try[3]. With Lister he also came up with a design for a microscope stand in 1839 that was used for many years going forward (figure 2).

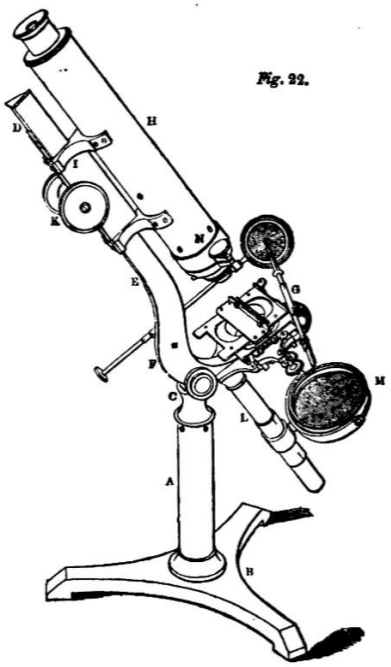

Figure 2. Ross's microscope as described in c. 1839[1]. A is a solid pillar screwed into a solid tripod (B) with a strong joint (C) on which the whole instrument turns such that it can be horizontal or vertical or any intermediate angle. D, E, F and G are moveable, and comprise one solid casting with F to G comprising a thick pieced plate with the stage and appendages. H is the compound body attached to D, E and moves up and down by a rack and pinion (controlled by K) to control focus. The circular stem (L) under the stage holds a mirror (M) that reflects light through the aperture in the stage. The lower end of H contains the object glass (microscope objective) in a tube which can slide in and out of the main body, and is held in place by a screw.

These novel developments in microscope technology led Edwin Quekett, Andrew Ross and fourteen other men including Joseph Jackson Lister (the father of the surgeon Joseph Lister) to found the Microscopical Society of London in 1839, the world's oldest microscopical society [7]. It was granted its royal charter and became the Royal Microscopical Society in 1866. The main goal of the Society was the advancement of the microscope. It began to publish its own journal focused on microscopy, founded

[3] https://www.microscopyu.com/tutorials/adjustment-of-objective-correction-collars

by Daniel Cooper, called *The Microscopic Journal and Structural Record* in 1841. Most papers in that journal were focused on the use or improvement of the microscope. After Daniel's death aged just 26, two year later the journal changed its name to the *Transactions of the Microscopical Society of London*, then the *Quarterly Journal of Microscopical Science* and finally became the *Journal of Microscopy* in 1878. The introduction to the first issue, published in January 1841, written by Daniel Cooper provides an interesting overview of microscopy at that time [8]. A further insightful look into the history and then current thinking in microscopy in the early 1800s was also published by John Quekett (Edwin's brother), a Professor of Histology in 1852 [9].

The new achromatic lenses started to be widely adopted into new microscopes and then used to examine plant and animal cellular structure, the beginnings of the science of histology. However, the resolution of these microscopes was still limited to about 1 µm. To put this into context the typical diameter of a mammalian cell is approximately 20-40 µm. Not only that but each microscope was made on an individual basis, which meant the performance of each microscope varied widely. While some theory was starting to be used to improve microscopy, a major step forward arose from the collaboration between Ernst Abbe and Carl Zeiss. Ernst Abbe was a trained mathematician with a PhD from Göttingen who then became a Lecturer in mathematics, physics and astronomy at the University of Jena, aged just 23. Carl Zeiss was a machinist and instrument maker, who ran a factory and small shop that sold eyeglasses, telescopes, microscopes and so on in Jena. Zeiss wished to manufacture microscopes that were similar in quality to each other and he appointed Abbe as an optical consultant in 1866, who later became a full partner in the firm and then the sole owner in 1888 after Zeiss died.

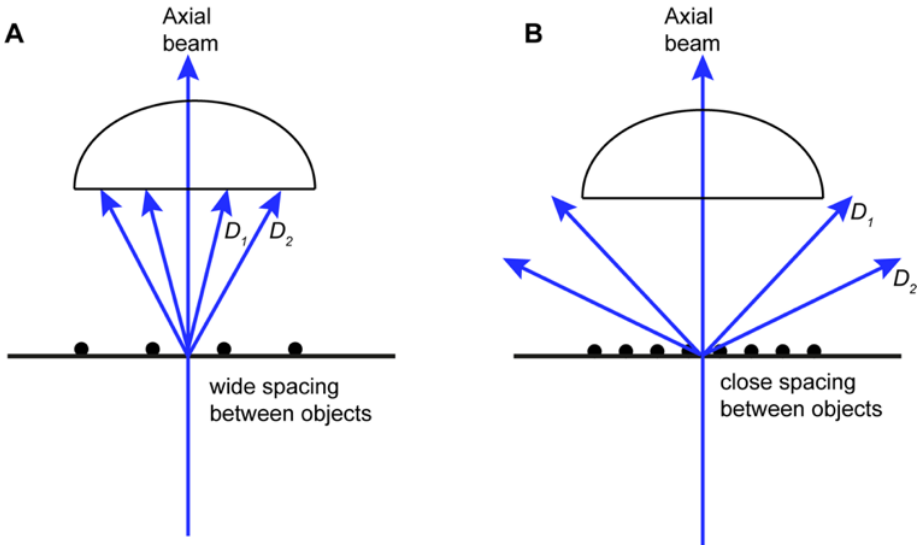

Figure 3. Diffraction in the microscope. When light passes through objects separated by a wide spacing, the objects give rise to a series of diffracted rays (D_2, D_2, …) of light either side of the main axial (illuminating) beam. The closer together the objects the wider the separation of the diffracted beams. The aperture of the objective lens needs to be large enough to be able to capture the diffracted beams in order to resolve fine detail.

Critically Abbe was able to use his knowledge of mathematics and physics to work out the theory of how the image is formed in the microscope and to test this experimentally. He outlined his theory in an extensive paper in 1873 published in a German journal [10], later translated into English by Henry Fripp and published in the *Monthly Microscopical Journal* [11], [12] as two separate papers in 1875. Abbe demonstrated how the aperture of lenses was critical irrespective of magnification to seeing fine detail in objects. He showed how the microscope lens must be able to capture not only the axial light rays, but also the diffracted beams (figure 3). Thus, the larger the aperture of the lens, the better its ability to

resolve fine detail: specifically the formation of a "virtual" image, the '*peculiar deviations of rays of light from their normal course*' (diffracted light), the varied 'refrangibility' (refraction) of different colours, that there is a limit to the 'amplification' or absolute power of the microscope that cannot be overcome, and most importantly that the smaller the linear dimensions of details '*the larger must be the angle of aperture of the objective*'. He also noted that the use of 'immersion' rather than 'dry' can provide a gain in 'amplification', that is, the use of immersion lenses can increase the aperture.

Abbe described the general principles of image formation in the microscope in his original German paper, but not in his famous equation. He defined the aperture in a paper, written in English and published in the *Transactions of the Royal Microscopical Society* in 1881 [13], and clearly stated his formula for the relationship between resolving (or separating power), numerical aperture and wavelength in a subsequent paper (figure 4) [14]. Abbe had a strong relationship with various members of the Royal Microscopical Society and particularly with John Ware Stephenson, the Treasurer of the Society at the time, with whom he regularly corresponded. One of their topics of conversation was the use of immersion, which led to Abbe reconsidering its role in microscopy and particularly its role in enlarging the aperture, leading to a subsequent publication in the *Journal of Microscopy* about this in 1879 [15]. Importantly his work led to the production of microscopes by Zeiss that were standardised, made reproducibly and thus performed in a predictable way.

The smallest dimensions which are within the reach of a given aperture are indicated with sufficient accuracy by taking the limit of the resolving or separating power of that aperture for periodic or *regular* structures, i. e. the minimum distance apart at which given elements can be delineated *separately* with the aperture in question. The numerical expression of that minimum distance is

$$\delta = \tfrac{1}{2}\frac{\lambda}{a},$$

where a denotes the numerical aperture and λ the wave-length of light; a fair average is obtained for the latter element (with observations with the eye and white light), by taking $\lambda = 0{\cdot}55\ \mu = 0{\cdot}00055$ mm.; i. e. the wave-length of green rays

Figure 4. A snapshot of Abbe's formula as published in the *Journal of Microscopy* in 1882 [14].

3. Microscopy developments in the 1900s

The theory of image formation in the microscope gradually became accepted together with the importance of the aperture in resolution. Many other improvements were made including further improvement of apochromatic lenses, partly with the help of Otto Schott in development of new forms of glass, also working with Zeiss. These new lenses were important in obtaining the best resolution obtainable with the light microscope (~250 nm) and after a few trials became well established in the manufacturing process towards the end of the 1880s. Today the numerical aperture of the best air lens is around 1.0 and that for oil immersion lenses is 1.4, although a few specialist lenses go up to a numerical aperture of around 1.49. Abbe and Zeiss succeeded in making a lens with a numerical aperture of 1.63 in 1889 [3], although it used naphthalene monobromide as the immersion liquid and the refractive index of the sample had to be at least 1.6 for successful image formation.

By the end of the 1900s most microscopes were no longer made by hand, but machine-made and mass produced. This led to the need for standardisation of microscopes. Users wanted to exchange parts such as objectives between different microscopes, which meant that they had to be able to use the same screw thread and the lenses needed to be able to perform in the same way on different microscopes. The Royal Microscopical Society led the way in introducing standards that were widely adopted by microscope manufacturers across the world. Other developments included the introduction of binocular

microscopes and improved methods for illuminating specimens using brightfield illumination. In the 1930s, Frits Zernicke invented phase contrast, for which he won the Nobel Prize in Physics in 1955. This technique has been particularly useful for imaging living cells, which have very little natural contrast. Dyes such as haematoxylin and eosin[4] have long been used in histology, as have other methods including silver staining developed in the late 1800s by Camillo Golgi to see neurons.

Fluorescence microscopy [16] was first described by George Stokes in 1852 [17], following on from William Herschel's observation that a solution of quinine emitted a faint blue light when illuminated under certain conditions. Quinine is present in tonic water, and a quick demonstration of fluorescence is easily made using tonic water and a laser pointer emitting blue light. Fluorescent xanthene dyes were discovered in the mid-1800s and many such as fluorescein and rhodamine are still commonly used today [18]. With the advent of generating antibodies that recognise specific proteins in the laboratory in the 1950s and specifically the generation of hybridomas, which can be used to make large amounts of monoclonal antibodies using cultured cells [19], it became clear that if antibodies could be fluorescently labelled, they could be used to identify where specific proteins were located within cells. However, in fluorescence microscopy, fluorescent dyes are excited by light with a wavelength appropriate for the dye of interest and emit light at a longer wavelength. The challenge for microscopy was to block the excitation fluorescent light from the final image in order to be able to clearly see only the emitted light. A leader in this area was Bas Ploem [20], who invented the epi-illumination cube used in fluorescence microscopes, which contains a filter to block excitation light from reaching the eyepiece.

Fluorescence microscopy is now a key technique for most life scientists and has also led to revolutionary developments of the light microscope. One of the first was the invention of confocal microscopy, a scanning laser method that reduces out of focus light with many contributors towards its development including Colin Sheppard, Amarjoyti Choudhury, Tony Wilson, Fred Brakenhoff, Bill Amos and others. Initially of no commercial interest to companies such as Zeiss the confocal microscope is now one of the most commonly used type of fluorescent microscope. Laser scanning optical systems and the beginnings of confocal microscopy featured in the early research efforts of Stefan Hell, who went on to invent one of three major types of super-resolution fluorescent microscopy approaches termed STED (stimulated emission depletion microscopy), nicely described in his Nobel Prize Biographical Sketch[5]. In this approach the scanning excitation laser beam is accompanied by a doughnut-shaped depletion beam, which sends fluorescence molecules into their dark state (de-excites them), reducing the size of the emitted fluorescent spot, effectively turning closely separated objects that are not resolvable into widely spaced ones which are. This approach was eventually published in 2000 [21]. It generally improves resolution by at least five-fold compared to a confocal microscope and has recently been developed further into MINFLUX, which can achieve 1 nm resolution [22], a resolution 250x better that a standard fluorescence microscope.

The discovery of green fluorescence protein (GFP) by Osamu Shimomura, Douglas Prasher and Martin Chalfie, and the ability to fuse the coding sequence for this protein to that for proteins of interest and then express the GFP-fusion protein in living cells [23] has driven live cell imaging to uncover the dynamics of protein behaviour. New variants with different colours (Roger Tsien and others [24]) has meant multiple proteins can be imaged at the same time. A version of GFP, which does not emit light until it is illuminated (photoactivatable GFP) developed by George Patterson and Jennifer Lippincott-Schwartz [25] was used to develop a second super-resolution microscopy approach called PALM (photoactivatable light microscopy) [26]. Like STED this technique engineers conditions in which only a small subset of fluorophores emit light at any one moment in time because the majority of the paGFP molecules are in the dark state and thus not emitting light. These fluorescent spots are sufficiently spatially resolved that their positions can be identified with nanometre precision. By collating a large number of sequential images in which different paGFP molecules emit light into a single image, a super-resolved image is generated with an approximately ten-fold improvement in resolution (~ 20nm) over

[4] https://www.histology.leeds.ac.uk/what-is-histology/H_and_E.php
[5] https://www.nobelprize.org/prizes/chemistry/2014/hell/biographical/

wide-field microscopy. A related approach developed at the same time (STORM: stochastic optical reconstruction microscopy) [20] used combinations of dyes rather than fluorescent proteins and this was then developed further into dSTORM, which only requires a single dye [27]. A third super-resolution approach (structured illumination microscopy) was also developed at about the same time [28]. This approach illuminates the sample with a pattern and the improved resolution, which depends on interference effects between the sample and the pattern of illumination, provides a two-fold improvement in resolution.

Following on from developments in light microscopy was the important development of the electron microscope. The resolution of the light microscope is limited by the wavelength of light, however, the wavelength of electrons is much smaller. As resolution depends on wavelength the ability to make a microscope that uses electrons rather than photons to generate the image thus promises much higher resolution. The discovery that the behaviour of electrons can be considered as waves in which their wavelength depends on the mass and momentum of the particles was demonstrated by Louis de Broglie in his PhD research in the 1920s (published in his thesis '*On the Theory of Quanta*')[6]. Next Dennis Gabor discovered that magnetic fields could be used to make electron lenses in 1927 and while he did speculate on making an electron microscope (EM) [29], the EM was then developed by Bodo von Borries, Max Knoll and Ernst Ruska [30]. Von Borries did not receive the initial credit he deserved as Ruska published their work '*On Progress in the Construction and Performance of the Magnetic Electron Microscope*' in *Zeitschrift fur Physik* in 1933 independently. Nonetheless Ruska and von Borries worked with Siemens to develop the first electron microscope. Electron microscopes have since become key tools across the life, material and physical sciences with recent developments in cryo-EM for biology enabling researchers to resolve structures with atomic resolution [31].

What about the roles of women in microscopy? Women were either excluded or overlooked from many scientific developments in the 1800s and this extended to microscopes. However, there is no doubt that women were interested and did contribute as described in a fascinating article, which notes that women were eventually elected as Fellows of the Royal Microscopical Society in 1884 and work from women began to be published [32], although women were not able to attend all meetings and activities until 1910. The contributions from women to this area of research has changed dramatically in the last twenty to thirty years with women making major contributions to the development of super-resolution microscopy techniques, for example [33].

In summary the microscope has come a long way since its first outings over three hundred and fifty years ago. Current new developments in microscopy are arriving thick and fast. It is an exciting time to be a microscopist with every new thing that we are able to observe using the wide range of microscopes available to us every bit as exciting as the first observations of minute objects such as the flea in Hooke's time, and long may it continue.

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