Delving into Hooke's Research: Lacunae in Quills and Cell-Walls in Cork

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Summary
Hooke's discovery of the cellular nature of cork was related in his published account (Hooke 1665) to his observations of comparable features in the shaft of feather. However, quills are acellular, and his observations may be questioned on that account. An examination of quill structure shows that it has an appearance remarkably like that of sectioned cork, and scanning electron microscopy confirms that he was justified, after all, in his assumption.

Hooke's Investigations

ROBERT HOOKE (1635-1703) was born in Freshwater on the Isle of Wight during his father's ministry in the parish. In 1648 his father died, leaving the 14-year-old Robert a legacy of £100. The young Hooke went to study under Sir Peter Lely in London; from there to Westminster school; and it was here his academic abilities and quick mind became apparent. He is said to have mastered the six books of Euclid in a week of intensive study. He is also said to have learned 'to play twenty lessons on the organ, and invented thirty ways of flying'.

In 1653, he went up to Oxford and entered Christ Church as a servitor, and proceeded to gain his MA. In 1661 he recorded a short experiment on capillarity, later published in *Micrographia* (reference 1, page 10). Robert Boyle, who had used Hooke as an assistant in his work on air-pumps at Oxford, drew this to the attention of the Royal Society. So impressed were they by Hooke's work, that he was given the task of acting as curator of experiments to the new Society, and Boyle was thanked for relinquising his assistant.

In this way Robert Hooke came to London, at a crucial moment in the development of natural philosophy. His work established many of the principles which underlie what later became known as science. Hooke's work was marvellously varied and filled with prophetic insight. Thus, he regarded light as 'a very short vibrative motion' and heat as 'a property of a body arising from the . . . agitation of its parts'. But it was his work on microscopy which became best known. We remember Hooke's Law, and still teach it in schools; but likewise we celebrate *Micrographia* as one of the first great texts of the scientific era, and certainly as the single volume which set in train the study of microscopy.

Hooke's coinage of the term 'cell' was to mark a concept fundamental to the modern understanding of biological systems. He was led to the word because of the structures he saw in cork. This, the cortex of *Quercus suber*, is an unusual material with characteristic properties. Hooke listed them in order:

1. Cork is 'exceeding light a body' — *ie* has low density;
2. Liquids are not absorbed by cork, which is 'so very unapt to suck and drink in water';
3. Cork has 'such springiness' when compressed and 'swelling nature' when released.

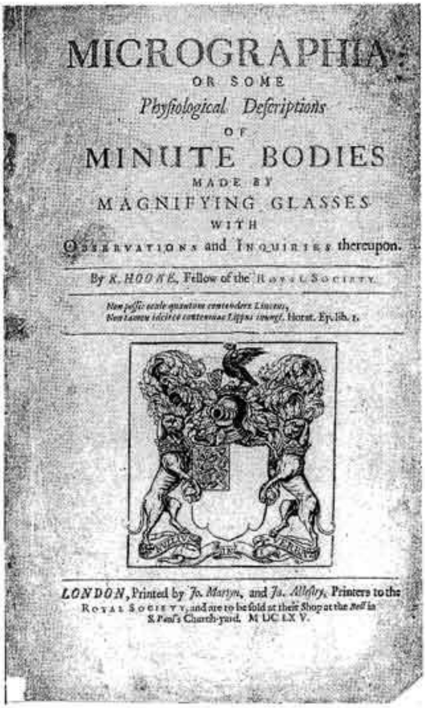

FIG. 1. The title page from a copy of Hooke's *Micrographia* in the author's library collection.

Hooke systematically related the structures he observed to these phenomena, for he noted that cork was made up of 'a great many little Boxes,' and was 'not unlike a Honey-comb'.

These he called *cells,* because they reminded him of tiny square rooms. The ratio between wall material and void accounted for the lightness of cork; the closed nature of the cells accounted for its inability to become waterlogged; and the honey-comb structure explained the ability of cork to be compressed and yet to return to its former dimensions. It is interesting that he imagined the cells to have formed by the cross-division of long, pore-like structures in the earlier stages of development:

(The cells) 'were separated out of one continued long pore, by certain Diaphragms, as is visible in Figure B'. He added that he had seen the same kind of structure in other specimens, including:

The pith of Elder, or almost any other Tree;

The inner pulp or pith of Cany hollow stalks of: Fennel, Carrots, *Daucus,* Burdock, Teazel, Fern, Some kind of Reeds.

Footnote

Other representations by Hooke of cellular structure include epidermal cells of *Urtica* and wild oat bear in transverse section (Plate 15, *Micrographia);* petrified wood (Plate 10); fungal mycelium (Plate 12); and leaf surface of *Rosmarinus* (Plate 14). Interestingly, his figures of feather structure (Plate 22) — which clearly depict the barbules — omit any portrayal of the construction of the shaft, even though three sectional view of the shaft are included in diagrammatic form.

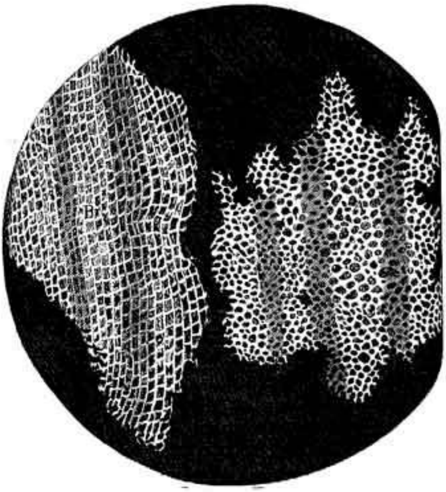

FIG. 2. The historic sections of cork were published as the eleventh plate of *Micrographia*. Compare with the electron micrographs, Figs. 6 and 8.

These are well-known and significant descriptions, and they accurately portray the appearance he observed by preparing fine sections of hand-cut plant material. The portrayal of cork in *Micrographia* (see Fig. 2) indicates how good he was as a microtomist, and the reprise of his techniques by Leeuwenhoek a decade later is a practical reminder of how fine such early sections could be (Ford 1981). They enable us to refute the views that such early experiments involved little finesse, or that the pioneer microscopists paid relatively little attention to obtaining excellent preparations from the specimens available.

Cork in context

Although Robert Hooke coined the term 'cell' during his work on cork, he had actually figured them in previous work. His order from the Royal Society to provide a regular series of microscopical demonstrations was dated 15 March 1663. The first of his presentations took place on 8 April 1663, and was a demonstration of the microscopical appearance of moss.

The specimen (see Fig. 3) showed a waisted sporangium, tapering leaflets with the presence of a fine terminal portion, and a conspicuous mid-rib in each leaflet. It may portray *Tortula muralis* Hedw., the wall screw moss, which was abundant in London where it grows on walls. The most interesting point to which attention should be directed is the clear representation of the cellular nature of the leaflets. Their distribution and proportion is well depicted. It was in this beautiful and innovative portrayal that Hooke first observed the living cells with which we are now familiar.

Hooke's demonstration of cork came a week later, on 13 April 1663. Interestingly, he does not in his description refer back to his prior observations, but confines himself to analogous structures found in sectioned material. And

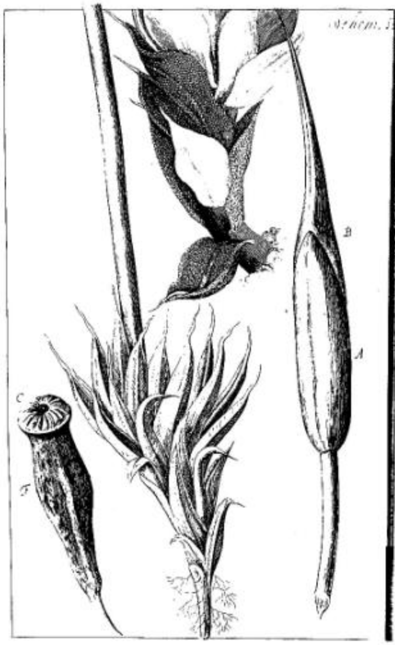

FIG. 3. Scheme [= plate] 13 of *Micrographia* illustrated Hooke's studies of a wall moss, probably *Tortula muralis* (see text). This was the first of his drawings to portray living cells.

in this section of *Micrographia* he introduces the parallel observation of similar structures in the shaft of a feather. It is easy to dismiss this as a mistake, but Hooke is careful to emphasise that the feather specimens were different in some key respects.

> 'I ghess this pith which fills the Feather, not to consist of abundance of long pores separated with Diaphragm, as Cork does,' he writes on p. 115 of *Micrographia,* 'but to be a kind of . . . hardned froth, or a *congeries* of very small bubbles consolidated in that form, into a pretty stiff as well as tough concrete. . . .'

This passage (reproduced in facsimile in Fig. 4) shows that Hooke believed he was observing similar structures in the shaft of the feather to those he had seen in hand-cut plant material, though it also indicates that he perceived the quill to differ in some organisational respects.

Scanning Electronmicroscopy

Freeze-fractured cork was prepared for scanning microscopy by double-sided tape mounting and conventional gold sputtering. The quill was hand-cut using a disposable scalpel and was mounted and gold coated in the same way. In making correlated micrographs, care was taken to see that the visible features

Footnote

The term *congeries,* from the Latin *congere* = to carry together, was defined by the Oxford English Dictionary as 'a collection of things merely massed or heaped together; a mass, heap'.

Nor is this kind of Texture peculiar to Cork onely; for upon examination with my *Microſcope*, I have found that the pith of an Elder, or almoſt any other Tree, the inner pulp or pith of the Cany hollow ſtalks of ſeveral other Vegetables: as of Fennel, Carrets, Daucus, Bur-docks, Teaſels, Fearn, ſome kinds of Reeds, *&c.* have much ſuch a kind of *Schematiſme*, as I have lately ſhewn that of Cork, ſave onely that here the pores are rang'd the long-ways, or the ſame ways with the length of the Cane, whereas in Cork they are tranſverſe.

The pith alſo that fills that part of the ſtalk of a Feather that is above the Quil, has much ſuch a kind of texture, ſave onely that which way ſoever I ſet this light ſubſtance, the pores ſeem'd to be cut tranſverſly; ſo that I gheſs this pith which fills the Feather, not to conſiſt of abundance of long pores ſeparated with Diaphragms, as Cork does, but to be a kind of ſolid or hardned froth, or a *congeries* of very ſmall bubbles conſolidated in that form, into a pretty ſtiff as well as tough concrete, and that each Cavern, Bubble, or Cell, is diſtinctly ſeparate from any of the reſt, without any kind of hole in the encompaſſing films, ſo that I could no more blow through a piece of this kinde of ſubſtance, then I could through a piece of Cork, or the ſound pith of an Elder.

FIG. 4. Hooke noted a structural distinction between cork and quill material in his discussion. From pp 115-116 of *Micrographia*.

were orientated similarly and were displayed at magnifications which made the salient features dimensionally compatible. This entailed utilising a final magnification of the quill material that varied between × 1.5 and × 3.0 that of the cork preparation. An accelerating voltage of 10 kv was used throughout.

At × 100 the cells of cork were clearly visible, and their regular alignment should be noted. An appearance of transverse septa across a tubule is conveyed. Quill at × 150 reveals a comparable structure, though a more random distribution of the cell-like components is apparent.

Cork at × 500 showed the box-like configuration clearly, and may be compared with Hooke's original etching. Note crystals of oxalate, a metabolic by-product, on the cell walls. At × 1000 comparable structures are seen in the quill material, and fibrous substructure is apparent. Pitting is visible on the septa.

At high magnification, the typical cork cell appearance makes a striking comparison with the quill. Septa pitting is visible in the feather, a consequence of the method of keratin secretion during the growth of the quill. This draws to our attention the only error made by Hooke. He considered the septa of the quill to be 'without any kind of hole in the encompassing films, so that I could no more blow through a piece of this kind of substance, than I could through a piece of Cork. . . .'

Since the pores are generally less than 1 μm in diameter, and the majority are around 0.2 μm, Robert Hooke might be forgiven for failing to resolve them with an early compound microscope. However he might have paid closer attention to the properties of quill. The shaft of a feather can be easily deformed, and only the rigidity of the outer layers helps it return to its original form. Air passes easily through the walls of the compartments in the shaft of the quill, and in this respect it behaves quite differently from a fragment of resilient cork.

But, though this detailed criticism remains, the comparison between the septate nature of a feather and the cellular construction of cork was well made by Robert Hooke. The quill shaft looks as though it might be cellular, even though we now know it cannot be.

FIG. 5. Oblique longitudinal section of feather shaft shows a quasi-cellular septate structure, well described by Hooke. × 150.

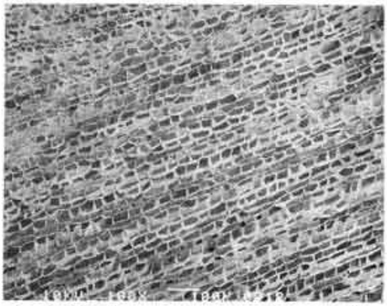

FIG. 6. Cellular structure of cork revealed at × 100 in a freeze-fractured preparation. Compare with Hooke's engraving, Fig. 3.

FIG. 7. The higher magnification of × 100 shows the light, open construction of the feather. Note fine fibrous strands, and septate 'cellular' appearance.

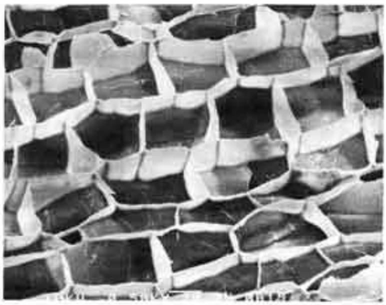

FIG. 8. The room-like appearance of cork referred to by Hooke is clearly visible at × 500. Note too the appropriateness of his allusion to transverse walls dividing a long, pore-like tubule.

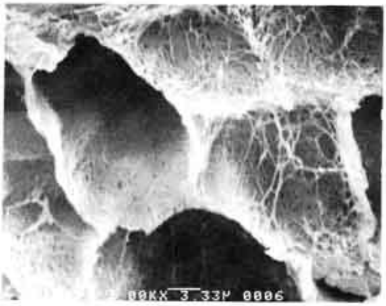

FIG. 9. At higher magnification (× 3000) the feather shaft shows more clearly as a non-cellular, septate structure. Fine pitting is visible on the septa, with pores approximately 0.2 μm in diameter being present in abundance.

FIG. 10. Cork cell walls at × 1000 show the 'honeycomb' divisions observed by Hooke. Excretory oxalate deposits are visible as elongated crystalline deposits on the cell walls.

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Final page to be posted just as soon as we can locate a copy.