Further Observations on Cell-wall Structure as seen in Cotton Hairs.

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[PLATE 10.]

The present note summarises the results of observations made subsequently to the recognition of growth rings in the cell-wall,* of which a photograph in transverse section is given in Plate 10, fig. 2. These observations are all related to previous physiological studies, and most of them have been made on material of known origin, *i.e.*, dated bolls† and pure-line plot crops.

An excellent memoir on our present knowledge of the cotton cell-wall by Mr. H. J. Denham, now in course of publication, makes it unnecessary for us to deal with the historical aspects of the matter.

Methods.

- (a) The "swelling" technique has been further developed by the use of calcium thiocyanate (for which, as well as for the use of naphthamine blue as a stain, we are indebted to Mr. H. E. Williams§). Other reagents have also been found serviceable when the conditions are adjusted to produce an equilibrium state on the verge of actual solution, e.g., cuprammonium and caustic soda, alone or together, and also sulphuric acid have been largely used. The latter is exceptionally interesting as showing specific differences between various hairs in respect of the critical concentration. The artifact nature of swollen walls has been continuously borne in mind, and all observations have been returned to the unswollen state by measurements of the contractions and expansions experienced by the hair.
 - (b) Our section-cutting technique has been described elsewhere.
 - (c) The junior author devised a simple "pressure" technique, single hairs
- * W. L. B., "Existence of Daily Growth Rings in the Cell-wall of Cotton Hairs," 'Roy. Soc. Proc.,' B, vol. 90 (1919).
 - † W. L. B., "Raw cotton (Development and Properties of)," chapter 4 (London, 1915).
- † Denham, H. J., "The Structure of the Cotton Hair and its Botanical Aspects: Memoir of the British Cotton Industry Research Association," 'Jour. Textile Inst.,' vol. 13, p. 99 (1922).
- § Williams, H. E., "The Action of Thiocyanates on Cellulose," 'Jour. Soc. Chemical Industry,' vol. 40, p. 221 t (1921).
- || Denham, H. J., 'Nature,' vol. 107, p. 299 (1921); W. L. B. and H. A. H., 'Nature,' vol. 107, p. 361 (1921).

being stressed enormously, under a cover-slip, by pressing with the blade of a knife. This we have found very useful; it is evidently akin to the breaking of aeroplane timber studied by Robinson.*

- (d) The inter-relation of external convolutions and internal wall structures has been systematically examined by detailed repeated mapping along the length of single hairs.
- (e) Groups of hairs of equal length from single seeds have been similarly mapped to obtain the average distribution of convolutions in studying the change from day to day in dated samples. A very full re-examination of the daily pickings samples† has also been made in connection with this work but only slight use will be made of these results at present, as they need direct experiment on growing plants for confirmation of our interpretations.

The evidence on which we base our conclusions is very detailed and various, and to particularise every item would be extremely tedious. We have, therefore, adopted the plan of summarising our results rather after the manner of geological research; and by way of further assistance in keeping this note from undue expansion, we shall restrict ourselves to dealing with the more debateable features of hair structure as brought out by Mr. Denham's memoir, already referred to.

The Cuticle.

This we found to be distinct from the primary wall, though extremely tenuous. It possesses a spiral structure, probably showing reversals of the spirals, and quite probably identical in frequency, or even in details of pattern, with the pit spirals (see below), but the difficulty of correlating the two sets of observations is very great; Haller's method; (SnCl₂ and AuCl₃) was not successful. The spiral lines of weakness and their apparent reversals, plus the resistance of the cuticle to solvents, determine the familiar "beading" of swollen hairs. The miscalled "stomata" of De Mosenthal§ are probably primary wall-structures in essence, the cuticle being moulded to them; we doubt very much whether the cuticle is actually perforated. A granular superficial structure seen after heating (in the thiocyanate process) and staining with osmic acid seems to be due to the melting and redistribution of the wax film, which varies in amount with varieties and species of cotton around 0.4 per cent. of the hair weight.

^{*} Robinson, W., "The Microscopical Features of Mechanical Strains in Timber and the Bearing of these on the Structure of the Cell-wall in Plants," 'Phil. Trans.,' B, vol. 210, p. 49 (1920).

[†] W. L. B., "Raw Cotton," p. 112, loc. cit.

[‡] Haller, 'Chem. Zentr.,' p. 652 (1920).

[§] De Mosenthal, H., "Observations on Cotton and Nitrated Cotton," 'Jour. Soc. Chem. Ind.,' vol. 23, p. 292 (1904).

The Primary Wall.

Various details of our evidence confirm the view that this wall, even when adult, is a different cellulose from that of the secondary wall. Further, we have seen reason to believe that until growth in length has passed its maximum rate, the cellulose (as distinct from the cuticle) has a different composition from that which it has assumed when the secondary thickening begins. We ourselves, for convenience, called this early stage "pre-cellulose," and we have since learned* that the general problem is now being investigated by Priestley. Accidentally, our preparations have shown the secondary cellulose completely dissolved, but the primary wall, spirally marked, untouched.

The pit spirals of the secondary wall (see below and figs. 5-7) are continuous through the primary wall, and possibly even to the cuticle spirals (vide supra). Thus it would seem that the law of Predetermination† plays an important part in the cotton hair, and the bearing of this on our convolution maps will be described later.

The objects discovered and excellently photographed by De Mosenthalt we propose to designate as the "slow spirals." Their nature is obscure, but they are evidently a kind of pitted corrugation in the outer surface of the primary wall, to which the cuticle moulds itself. The sides of the trough in which the elliptical craters lie often project beyond the surface of the hair, and are thus discernible in profile. These slow spirals are particularly easy to see in fuzz hairs, but are probably present to some degree along all parts of every hair, lint (fig. 3), or fuzz, for they flash out momentarily during swelling with critical-strength sulphuric acid, even though not visible previously. The spiral shows frequent reversals (fig. 3). The relation of this spiral to the pit spirals, in respect of pitch, direction, and reversals, has been studied in detail, and we have satisfied ourselves—with some regret for an untenable hypothesis—that they are sometimes independent of one another. We have no evidence that the slow spiral pattern is pursued into the formation of the secondary wall, unlike the pit spirals, nor even that it represents any textural modification (as distinct from modification of surface or thickness) in the primary wall itself, excepting that when a hair has been "tendered" by acid it shows a saw-tooth form of cracking, the long slope coinciding with pit spirals

^{*} Discussion in Section K on the "Quantitative Analysis of Plant Growth," 'British Association,' 1921.

[†] W. L. B., "Predetermination of Fluctuation, a Preliminary Note," 'Proc. Cambridge Phil. Soc., May, 1914.

[‡] Loc. cit. W. L. B., "Analyses of Agricultural Yield," Part III, 'Phil. Trans.,' B, vol. 208, p. 157 (1917–18).

and the short resembling slow spirals (fig. 4). However, as we have satisfied ourselves that these spirals are not invariably opposed in direction, the fact may not be relevant, though it does suggest a chemical polarity.

These slow spirals are thus somewhat mysterious objects, and we must wait for direct growth experiments to elucidate their nature. In passing, we may note that the distortions produced by swelling make the quick pit spirals simulate them very closely (fig. 8), a circumstance which led us to much confusion at first.

The Secondary Wall.

One of us has formerly described the growth rings,* while many observers have figured and commented on the existence of spiral markings in the wall and on its inner surface especially. The occurrence of somewhat elusive simple pits has also been described from fresh material by the senior author,† and the probable existence of an internal spiral structure has been suggested in various forms by non-botanical writers.‡ We are now in a position to co-ordinate all these observations and views.

By means of the simple "pressure" method, it is possible to "develop" a spiral series of cracks throughout the length of a hair, with little distortion, which can then be mapped in detail (fig. 6), and related to a previous charting of the external form of the hair (vide infra). Such a pressed hair dissolves much more quickly in swelling reagents, presumably from the greatly increased free surface, and possibly also (since lower concentrations will attack it), because the flank of the patterned and orientated cellulose aggregates is, so to speak, exposed. When swollen, only a complex structure resembling basket work is produced (fig. 5), and it was the spasmodic occurrence of this in slides given us by Mr. Williams which started the present research.

By mapping the simple pits in fresh greenhouse material, for which we are indebted to Mr. Vernon Bellhouse, and then mapping their spiral cracks, we have satisfied ourselves that the pits are simply abnormally wide intervals between otherwise contiguous spirals. It is therefore possible that any plant cell-wall which shows simple pitting may possess spiral structures similar to that of the cotton hair. We would also call attention to the structures in wood cell-walls described by Robinson, who describes and figures these

^{*} W. L. B., "The Existence of Daily Growth Rings in the Cell-wall of Cotton Hairs," 'Roy. Soc. Proc.,' B, vol. 90.

[†] W. L. B., "Raw Cotton," fig. 12 and p. 78.

[†] Vide Denham, Memoir, B.C.I.R.A., loc. cit.

[§] Williams, vide supra.

^{||} Robinson, loc. cit.

so-called slip planes as being interrupted by the fragile middle lamella, which seems improbable unless these "slip-planes" are pre-existent. The spasmodic occurrence of swollen spirals in thiocyanate preparations merely showed an erratic anastomosing series, but with the cuprammonium and soda mixture, and better still with critical sulphuric acid (circa 1.540 sp. gr.), the nature of these anastomoses was evident; the wall is then seen to consist of about a hundred spiral fibrils—a screw of a hundred threads—all approximately identical, except in one respect. This exception consists in the frequent presence of two spirals, within the series, which stain more deeply than the others with naphthamine blue. They do not seem to be otherwise different from their neighbours in any way, and as they seem always to lie at the ends of the major axis of the collapsed cell-wall, they might be merely stressproduced artifacts. On the other hand, one of them may disappear by approaching the other, the interval between them changing. Thus, the appearance shown in swollen hairs is altered from a symmetrical double screw (figs. 8, 9) to an asymmetric one, and thence to a single-thread screw, as we pass along the hair. This is not compatible with artifact origin, and it would seem that for some reason unknown two fibrils, lying diametrically opposite one another, are somewhat different from the others. We have noticed similar bifurcation and re-union in the spiral thickening of protoxylem vessels in other plants.

The question of the relationship between these radial boundary surfaces and the tangential growth-ring boundaries next arises. Numerous attempts to demonstrate the matter clearly in transverse section have largely failed; and some considerations relating to free surface, cohesion, and the like, make it rather unlikely that these two sets of structures could ever be thus demonstrated perfectly and simultaneously in the swollen state. We also suspect that the shearing stress of the razor edge may produce molecular disturbances which alter the reactions of the cellulose. Partial demonstrations of the existence of these radial boundaries have frequently been obtained, but rarely (fig. 1) comparable with the growth-ring demonstration of fig. 2. We thus have to depend on optical longitudinal sections, and by this means have satisfied ourselves in exceptionally good preparations that the spirals are arranged in layers, each layer constituting a single growth-ring.

The cotton hair cell-wall is thus an elaborate structure, laid out on a simple plan. In the first instance, a spiral pattern seems to be laid out in the primary cell-wall and cuticle; this, it should be noted, must happen while the hair is growing in length. The deposits of secondary cellulose, as growth-rings, do not obliterate this pattern, but follow it most strictly. Thus, a radial (spiral) structure persists through the concentric deposits. The simple pits

of any cell, equally with those of cotton hairs, are, after all, merely a special case of the same procedure, while an analogy may be found in the medullary rays of timber.

Our partial elucidation of this structure has already thrown light on some physical properties of the hair. Abnormal hairs are often found in which, to a greater or less extent, the spiral structure is visible without any "development." Our colleague, Mr. Slater, in the Physical Section of this Department. has, in some preliminary studies, found the flexibility of such hairs to be highly abnormal, such hairs standing in the same relation to normal hairs, as strands of yarn compared with solid wires of celluloid. We have mentioned our opinion that the razor edge may produce molecular disturbances in the cellulose. Akin to this is a remarkable phenomenon discovered by the junior author, reminiscent of the results described by Griffith* with quartz rods. If a hair has been pressure-treated to develop the pit spirals without re-agents and then is subjected to stress in longitudinal extension, no alteration is noticeable until the hair breaks; after breaking, however, little or no trace of the pit spirals is left in any part of the hair. We have failed to obliterate the spiral cracks by any tension without actual breakage, and it would seem that, as in Griffith's work, a molecular disturbance is needed, which the back-lash of the break provides.

Dimensions and Constitution of a Pit Spiral Fibril.

Taking 0.4μ as the thickness of a substantial growth-ring, and allowing 100 spirals to the ring in a hair whose original cell diameter was 15μ , and its mean wall diameter considerably less, gives us 0.4μ square as the approximate cross-sectional area of one Pit Spiral Fibril. Its length is apparently that of the hair. Without undue speculation it is evident that we are here approaching molecular dimensions, the probable size of the cellulose molecules being such that some number of them between 1,000 and 100 would constitute the cross-sectional area of one such pit spiral. There is even the slight possibility that in these pit spiral fibrils we have reached the limits of morphology and are examining a chemical (or colloido-chemical) unit. For other reasons, however, we rather incline to the view that "cellulose," even in a pit spiral fibril, is a complex of more than one kind of cellulose molecule.

Origin of the Pit Spiral Structure.

It seems clear to us that this secondary wall structure is a predetermined one, and that, paradoxically, we must therefore look to the period of growth

^{*} Griffith, A. A., "The Phenomena of Rupture and Flow in Solids," 'Phil. Trans.,' A, vol. 221, p. 163 (1920).

[†] Griffith, loc. cit.

in length to determine the causation of such abnormalities in it as we have mentioned. Physiological work in this direction, under glass, is contemplated. But this leaves unsolved the more fundamental problem, as to why even the primary wall should be thus patterned and heterogeneous, consisting of structures which can sometimes be mechanically broken apart, which are possibly only united by a molecular film of water, and which show (when enormously swollen and stained with naphthamine blue) granular lines alternating with clear zones (fig. 8).

Until a late stage we were not certain whether the slow spirals were not always opposed in direction of rotation to the pit spirals, and a working hypothesis was adopted which combined Church's results* on the fundamental geometric structure of the cell with a general idea of protoplasmic circulation, and with some earlier studies of growth in a fungus hypha by one of us.† This hypothesis, though now entirely speculative, may yet be of interest. It postulated the existence of two "growth centres" mutually exclusive or polar in their inter-relations, as a rule; these controlled the longitudinal extension of the cell by intussusception, and their micro-bio-chemical operations were rhythmic, as in Liesegang ring-formation. It was unlikely that such a system would build forward along a straight line, hence revolution was postulated, sometimes right-handed, sometimes left-handed (fig. 3), under the influence of accident or environment or even of stereo-isomerism. revolution of the builders produced the spiral form, their rhythmic operation the successive fibril phases; and molecular predetermination, akin to crystallisation, produced fibrillar continuity.

When it became clear that the slow spirals were not the trails of these "growth centres"—since their direction was not invariably opposed to that of the pit spirals—the hypothesis became mere speculation.

It does, however, remain clear that there is a fundamental geometric structure in the cell wall, though our hope of confirming and extending Church's main conclusion has at present failed.

The Protoplasmic Débris.

We have only to mention that this is of assistance in swelling technique as a rough guide to the amount of longitudinal contraction.

The Convolutions.

We now come to a much observed feature of the cotton hair, about which nothing definite has been published, whether in respect of their effect on

^{*} Church, A. H., "Phyllotaxis in Relation to Mechanical Laws" (Oxford University Press, 1904).

[†] W. L. B., "Temperature and Growth," 'Ann. Bot.,' 1909.

spinning properties, or on the physical properties of the hair, or of their origin. The senior author has regarded them* as a necessary consequence of the simple pits in the wall, with modifications caused by wall-thickness variations, and we can now extend this to include the pit spiral structure, which should completely explain the convoluted form of the collapsed dead hair.

Actually, however, the explanation is not yet complete. Mapping pit spiral against convolutions, in any one piece of hair (fig. 10), there is a general similarity, but by no means exact identity. It is probable, however, that if we could construct scale models of the wall structure (growth rings and pit spiral fibrils) in the form of semi-rigid tubes, and then cause them to collapse, we should find that local variations of texture, packing, interfibrillar friction, wall-thickness and hardness, etc., would produce similar discrepancies to those we have observed, and we venture to think that the existence of convolutions can be explained in this way, if we include the reinforced spirals already mentioned, whose presence makes the "arch" structure unsymmetrical.

This, however, leaves a major problem to solve, to wit, the reason why the pit spirals, and hence the convolutions, vary their pitch and direction. On grounds of convenience, we have studied the convolutions rather than their causative spirals, and while no definite conclusions have yet been reached, a number of suggestive observations have been made on the daily pickings material,† which consists of fruit-capsules (bolls) opening on ninety successive days:—

- (a) On counting the number of convolutions in a unit length at the middle of the hair (fig. 11, heavy line), we found the average number changing from day to day, as in the case of other hair properties, indicating that environmental changes affected the convolutions. Similar results were given by counting at other *loci* (fig. 11), and by taking the percentage distribution as between these various *loci* (fig. 12).
- (b) Extending these measurements by mapping the convolutions along the whole length of the average hair (fig. 13), there were indications that the locus of any feature (e.g., a low number of convolutions) shifted its position along the hair on successive days. The earlier the day of boll opening the further removed was the particular feature from the base of the hair, thus indicating that the environmental determinant of convolution form must have operated while the hair was still growing in length. Our evidence is based on too slight data to be conclusive in itself, but it will be noticed that it confirms

^{*} W. L. B., "Raw Cotton," pp. 79 and 147, loc. cit.

⁺ Vide supra.

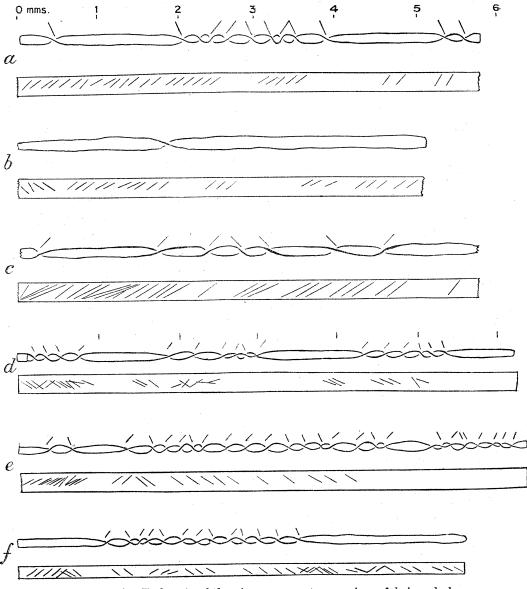
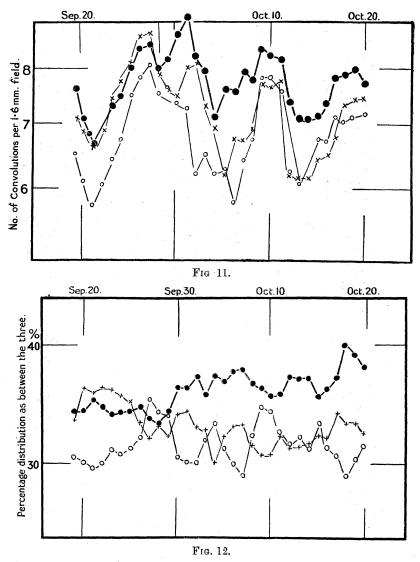


Fig. 10—a to f.—Each pair of drawings represents one piece of hair and shows:—above—the position of the convolutions with slanting lines drawn to indicate the direction at each turn; below—direction of slope of pit spirals, as determined at various points after pressing. Length corrected to original value. Exceptionally discrepant pieces have been selected for reproduction.

our conclusions already drawn from microscopic work, and thus increases their probability.



Figs. 11 and 12.—From capsules opening on successive days in the daily pickings series (q.v.) five seeds were taken each day at random, and twenty hairs of similar length from each of these five were arranged with their bases in line. The number of convolutions included in a microscope field of 1.6 mm, was then determined at three loci along the hair, respectively, 5, 15 and 25 mm, from the base. The curves as shown are the three-point means of the original data, each point thus representing the average of 300 hairs. The data are further analysed in fig. 12 in order to discriminate between general fluctuation common to the whole length of the hair, as indicated in fig. 11, and the existence of differential fluctuation in various parts, due to determinations taking place at different times during development. The logarithmic plotting shows that the latter fluctuation is quite marked, though its amplitude is reduced by a half.

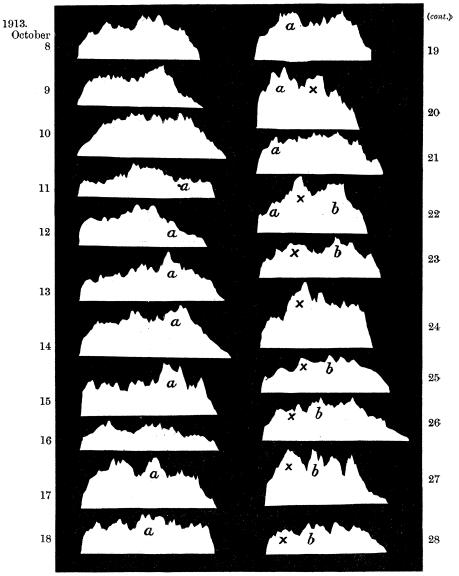


Fig. 13.—Average distribution of convolutions from day to day along the whole length of the hair. Data obtained by taking twenty hairs from the same square millimetre of one seed chosen at random each day. These hairs, being roughly of the same length, were arranged with their bases in line and the number of convolutions in a 1-6 mm. field measured at intervals of successive half millimetres. In five cases, where only twelve hairs were measured, the scale of the distribution curve has been corrected accordingly. The letters a, x and b are placed on some of the curves to indicate the general tendency which appears to be shown, though indistinctly, by the various modes, in shifting backwards towards the base as the date of opening of the capsule becomes later. Base of hair at left hand of each curve.

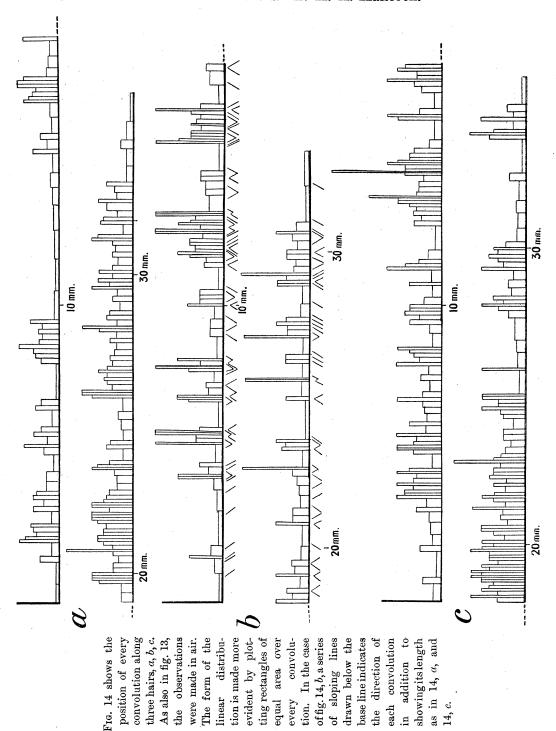
The actual data were obtained by selecting usually twenty hairs of equal length on each day over a sequence of thirty days, and counting the convolutions in successive intervals of 1.5 mm. from base to tip; they thus comprise some 20,000 measurements, but statistical considerations make it evident that they need to be greatly extended in order to be conclusive, and in practice it should be found easier finally to attempt the proof by means of direct physiological experiment and by observations of the pit spirals.

A fairly close correspondence was indicated as between the general form of the hair-length growth curve (formerly ascertained)* and the shift of any convolution-form *locus* from day to day.

(c) A renewal of a former attempt was also made, in order to see whether any forms or markings could be found along the length of the hair which would correspond for linear extension to the daily marks of the growth-rings in secondary thickening. The system of convolution mapping was extended to measure the length and direction of every separate convolution. measurements were then plotted as shown (fig. 14), using rectangles of equal area for each one, the bases of which were equal to the convolution length, and in this form of plotting it is very evident that the convolution sequence along any one hair is at least wave-like. Phases of steep-pitched and short convolutions alternate with phases of slow and long convolutions. discrepancies between convolutions and pit spirals seem to happen chiefly in the latter phase, which also seems, as might be expected, to contain more convolution reversals (fig. 14, b). The number of peaks (short convolution phases), in the curve, seems to tend towards correspondence with the number of days (about 25), during which the hairs used in these observations (daily pickings samples) were growing in length.

Here, again, no rigid conclusion can be drawn, but the facts are certainly very suggestive of a daily environmental effect, acting by predetermination on the convolutions through the pit spiral patterning of the primary wall.

- (d) We have not forgotten the probability that mutual pressure inside the growing capsule, together with the curling grouping which the hairs thereby take up, may influence both pit spiral and convolution, but we anticipate that this will be found subsidiary to the other causes indicated.
- (e) A source of error in other observations made on material which had been acted upon by softening and swelling re-agents should be noted. When the wall cellulose is softened with the hair held in slight tension, the convolution spiral may become mechanically unstable and instantaneously jump to a new conformation, the hair becoming a cylindrical helix, like an



"Ayrton spring." This change is apt to complicate observations on wall structure.

The Fuzz Hairs.

In a previous communication,* one of us has pointed out that fuzz and lint appear to be identical in all respects, except that growth in length is inhibited in fuzz, while growth in wall thickness is restricted in the lint. None of the present observations have revealed any further differences. In many cases we have found it convenient to try out new methods, or hypotheses, on the fuzz hairs before attempting to apply them to the more delicate lint.

Conclusions.

- 1. A spiral fibrillar radial structure exists in every growth-ring of the cell-wall of the cotton hair.
- 2. The simple pits of the cell-wall are a special case of this general structure.
- 3. The pattern of the spiral appears to be predetermined during growth in length.
- 4. This pattern is preserved through all the growth-rings of the secondary wall thickening.
- 5. The number of fibrils in cross section of one hair is of the order of 1,000 upwards.
- 6. The pattern (direction, reversal, and pitch) of these spirals seems to be the major determinant of the externally visible convolutions of the hair.
- 7. There are indications that the unknown cellulose-aggregates, which compose any one spiral fibril, have a definite geometric conformation, suggestive of stereo-isomerism.
- 8. Attempts to elucidate the cellulose-structure further, as by X-rays, will probably have to take account of this spiral fibril arrangement.

While assistance in various ways has been given by our colleagues in the Experimental Department of the Fine Cotton Spinners' and Doublers' Association, to whose Executive Directors we are indebted for permission to publish this account, we would wish especially to acknowledge the interest and assistance of Dr. Mary Cunningham. The influence of Dr. H. E. Williams in re-energising this inquiry has already been acknowledged, while the independent development of work along similar lines by Dr. S. C. Harland and Mr. Denham, at the Shirley Institute, has been of indirect assistance.

^{*} W. L. B., "The Existence of Daily Growth Rings in the Cell-wall of Cotton Hairs," loc. cit.

DESCRIPTION OF PLATE.

Figs. 1 to 7 inclusive, are all photographed with Spencer 4 mm. objective and $10 \times$ eyepiece.

Fig. 1.—Transverse section of Sakel hair, possibly accidentally pressed, and slightly swollen with sub-critical strength sulphuric acid; showing radial (spiral) cracks.

Fig. 2.—Transverse section of same cotton as fig. 1. Section lightly pressed, then swollen with critical strength sulphuric acid; showing growth rings.

Fig. 3.—Ordinary Sakel hair mounted in liquid paraffin, untreated. (Denham and Harland's method.)

Fig. 4.—Hair of Sakel cotton boiled in dilute HCl, and pressed.

Fig. 5.—Hair of Sakel cotton pressed heavily in 8 per cent. caustic soda.

Fig. 6.—Hair pressed in naphthamine blue. Spiral structure entirely due to pressure

Fig. 7.—Hair of Sakel cotton pressed lightly in an adjusted mixture of cuprammonium and soda.

Figs. 8 and 9 are photographed with Spencer 16 mm. objective only, and 10 × eyepiece.

Fig. 8.—Hair swollen with calcium thiocyanate, showing double thread spiral.

Fig. 9.—Hair of Sakel cotton stained with iodine, but not otherwise treated; showing double pit spirals.

Observations on the Distribution of Fat-Soluble Vitamines in Marine Animals and Plants.

By Johan Hjort, D.Sc., For.Mem.R.S.

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(From the Biochemical Laboratory, Cambridge.)

The Norwegian fishery investigators have for many years been engaged in the study of the growth of fish, mainly the herring and the cod. By means of microscopical study of the scales of the fish it has been possible to determine the age of each individual fish, and by means of the assumption, which has been verified within certain limits, that there is a proportion between the length of the scale (l_s) and the length of the fish (l_f) (i.e., $l_s/l_f = \text{constant}$), it has been possible to calculate the "growth curve" of the fish in different years of its life, and in different seasons of the year. The results of this work, which have been summarised up to the year 1914,* proved that the growth of the said fish in the Norwegian waters was confined to a few spring—and summer—months only, and that the growth of the fish entirely ceases during

^{*} Johan Hjort, "Fluctuations in the Great Fisheries of Northern Europe," 'Rapports et Procès-verbaux du Conseil International,' vol. 20, Copenhagen (1914).

