IX. *On the Hygroscopic Mechanism by which certain Seeds are enabled to bury themselves in the Ground.* *By* FRANCIS DARWIN, *M.B.*, *F.L.S.*

(PLATE XXIII.)

Read March 16, 1876.

THE object of this paper is to describe the hygroscopic mechanism by which certain seeds are enabled to bury themselves in the ground. This phenomenon as it occurs in the Geraniaceæ has already been described by Hanstein[*], and again by G. Roux[†] in the case of *Erodium*; lastly, Asa Gray[‡] briefly points out the power of burying themselves possessed by the carpels of some of the Western American species of this genus. After describing the process, he adds, "It is the same with the grain and awn of *Stipa*." I may mention that the latter note only appeared after I had completed my researches on this subject.

The species on which my observations have been made are *Stipa pennata*, *Avena elatior*, *Heteropogon contortus* (Bombay), *Heteropogon* (*Andropogon*) *melanocarpus*, (Florida), *Androscepia arundinacea*, *Anthesteria ciliata*[§] (Khasia), *Anemone montana* (from Switzerland).

It seems to me an extremely remarkable fact that the curious power of burying themselves should be exhibited by plants belonging to several distinct orders, and inhabiting various parts of the world; and that the mechanism should be essentially the same in all of them is even more remarkable.

My observations have been chiefly confined to *Stipa*; a short description of the caryopsis of this plant will explain the general method of action common to all the other fruits observed by me.

Fig. 1 represents the seed[‖] of *Stipa pennata*. It terminates inferiorly in a sharp strong oblique point (p)[¶], armed with a dense plume of barb-like hairs; $v\ k_1\ k_2\ f$ is the strong woody awn, of which the lower vertical part (v) is strongly twisted on its own axis, the appearance of the strands of a rope being given by the ribs r and r, fig. 9 (and seen in section in figs. 11 & 12), which run spirally up the awn. Above, the awn terminates in a long untwisted portion (f), bearing a series of beautiful hairs, giving its well-known feathery aspect: when the seed is dry this portion extends nearly horizontally outwards. The twisted and vertical part (v) is separated from the feathery part (f) by a curious double bend; the two angles thus formed I call the lower and the upper knee (k_1 and k_2).

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[*] Sitzungsberichte d. Niederrhein. Gesell. Bonn, 1868. See Sachs, 'Botany,' Eng. Trans. p. 841, for abstract.

[†] Annales de la Soc. Bot. de Lyon, 1873.

[‡] Silliman's Journal, Feb. 1876, p. 158.

[§] Dr. Hooker most kindly supplied me with specimens of the four last-mentioned species.

[‖] The use of this expression in place of the strict botanical term may perhaps be allowed me, on account of its greater convenience.

[¶] Said to be capable of injuring the intestines of animals which feed on the grass (Hooker's Trans. of Decaisne and Le Maout, p. 892).

The hygroscopic action of the awn may be shown by holding the seed so that the twisted axis is vertical; on wetting the awn, the feathery portion will revolve, describing a circle in a horizontal plane; the vertical part untwisting, and its strand-like ribs becoming more and more oblique (*i. e.* making a smaller angle with the axis of the awn), until at last, when the awn is thoroughly wet, it shows no signs of torsion, and the two ribs run parallel to its axis down two of its opposite surfaces. As the awn untwists, the two knees, k_1 and k_2, are obliterated (k_1 disappearing first); by this means the feather is brought into line with the twisting part, and the awn forms a long straight pliable rod, pointing vertically upwards. It follows from this, that though the end of the feather begins (at the commencement of the wetting) by describing a circle, it ultimately describes a helix.

As the awn dries again, the action is exactly reversed: the axis becomes twisted; the two knees reappear; and the feather becomes again subhorizontal.

It was this remarkable property exhibited by *Stipa* of untwisting and twisting in response to alternations of moisture and drought, which convinced my father and myself that the whole structure must be adapted to some very definite end. We concluded that this object must be that of forcing the seed into the ground (in the manner to be immediately described). The sequel gives the result of my investigation of this point.

If in the above-described experiment the feather is prevented from revolving while the seed is left free, the untwisting of the vertical part of the awn will make the seed rotate on its axis. In consequence of the untwisting, the vertical part of the awn from the knee (k_1) to the tip of the seed becomes longer by about 7 per cent. Therefore, if we fix a dry *Stipa*-awn in a vertical position, the seed resting freely on the ground, and the feather being prevented from revolving, on wetting the awn the seed will rotate and will be pressed against the ground. But this requires that the expansion of the awn shall not be permitted to take place in an upward direction; *i. e.* the upper extremity must be fixed to give a *point d'appui*, from which the expansion may take effect in pressing the lower extremity against the soil.

In describing the untwisting of the axis it was stated that the angles k_1 and k_2 increase as the awn absorbs water, until the whole awn is converted into a straight rod. Now in the same way that, by interfering with its movements, the rotation of the feather is transferred to the seed, so by preventing the feather from rising to its full extent the tendency of the awn to become straight results in increased pressure of the point against the ground. The seed now resembles a brad-awl in exhibiting vertical pressure on a revolving point. In order that this action may take place in its entirety, three *points d'appui* are theoretically needed, although one is practically capable of performing the duties of all. The first is required, to transfer the rotation from the feather to the seed; the second, to force the expansion resulting from the untwisting of the awn to take effect downwards; the third, to convert the tendency of the awn to straighten itself into pressure of the seed against the ground. It is evident that if an awn be placed vertically, the seed resting on the ground, so that the feather can neither rotate nor describe any great angle in a vertical plane, all the required conditions will be fulfilled.

How can this be effected in a state of nature? Prof. Hildebrand has pointed out* that the long feathery awn of *Stipa* serves as a "Verbreitungsmittel," or means of distribution. It is found that seeds dropped from a height of a few feet usually preserve a nearly vertical position, and strike the ground with their point. Moreover, if they are allowed to fall among low vegetation they are caught by the knees (k_1 k_2) or by the feather, and are fixed in a more or less oblique position, the seed resting on the ground. Many seeds would no doubt escape being entangled; and many others would be caught in unsuitable positions—suspended in the air, for instance, or making too acute an angle with the ground, or resting on some hard impenetrable body. Neverthelsss many seeds are undoubtedly caught and held fast in suitable positions. The great length of the feather (nearly 30 cm.) would render entanglement in low vegetation an easy matter; and when a seed is once entangled the hairs serve to hold it fast and prevent the wind blowing it away.

In order to ascertain what would occur under these circumstances, I made experiments of the following kind:—A vessel being filled with dry sand or light soil, two upright sticks were fixed at about a centimetre apart; and these were connected at the height of 8 or 9 cm. from the surface of the soil by a cross pin, a second one being fixed 2 or 3 cm. higher up. The *Stipa*-seed is then placed with its point resting on the soil, and its feathery awn passed through the loophole between the two supports and the two cross pins. The whole is now placed under a bell glass lined with wet blotting-paper. This is better than wetting the awn directly; for in touching it with a wet brush it is possible to push it into the soil without being aware of it, and in syringing it the soil may become too much wetted. In order to dry the awn it is merely necessary to remove the glass; thus by alternations of dryness and moisture the awn is made to twist and untwist, just as it would under the changing hygrometric conditions of dew and sunshine in a state of nature. The amount buried may then be measured with a pair of compasses. It is very important to estimate the amounts buried, by measuring from the surface of the soil to the top of the *seed*, and not to any marked point in the awn; for in the latter case the measurements will be obviously inaccurate, owing to the lengthening and shortening of the awn.

All the movements of the awn are far more conveniently studied when the seed is fixed and the feather free to rotate; and in taking the times of rotations &c. I have found it best always to employ immersion in water in preference to exposing the awn to a damp atmosphere; for by the former means a constant amount of moisture is secured, and in nature the awn must be frequently exposed to an amount of moisture practically equivalent to immersion.

A dry *Stipa*-awn plunged into water at the temperature of the room began to rotate within a second of its immersion, and untwisted at the rate given in the following table:—

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* Verbreitungsmittel der Gramineen-Früchte, Bot. Zeit. 1872, No. 49.

Turn.	Completed in	Turn.	Completed in
	M. S.		M. S.
No. 1	2 30	No. 6	1 30
2	2 0	7	1 45
3	1 45	8	2 10
4	1 35	9	3 20
5	1 25	10	

Thus the rate increases up to the 5th revolution, and then diminishes quickly.

The lower bend or knee is obliterated in from $20'$ to $30'$; the awn becomes completely untwisted in from $\frac{3}{4}$ to 1 hour; in doing so it increases in length by about 7 per cent.; a well-grown awn measures from the point of the seed to this lower bend 70 mm. dry, 75 wet. The upper knee disappears in periods of time which are rather variable, and lie between two and three hours. The movement which takes place as the awn untwists or twists is a combination of two rotations: the first is that due to the torsion of the vertical portion of the awn (50–55 mm.) from the lower knee down to the seed; the other rotation is due to the torsion of the short portion (15–18 mm.) between the knees. This latter axis is carried round quite independently of its own torsion, by the torsion of the long vertical axis; thus the portion k_1 k_2 (fig. 1) describes a cone about an axis of rotation which is continuous with v; and, again, owing to the torsion of the part k_1 k_2, the feather is made to rotate, describing a figure of rotation having a line continuous with k_1 k_2 for its axis. We have seen that the feather is usually nearly horizontal when dry, and vertical when wet (the seed being held vertically in both cases); it follows that in passing from the wet to the dry state the tip of the feather does not describe a regular helix, as would be the case if there were only one bend, but a complex figure varying with the varying relations between the rotations due to the two axes v and k_1 k_2. The rotations due to the untwisting of k_1 k_2 are slow (7–13 minutes); and since but two revolutions are possible, owing to the shortness of this part, their effect is not always great on the revolutions due to the untwisting of the vertical axis, which are from 13 to 16 in number. The rotation of the awn is best studied by fixing the seed while the upper end is allowed to revolve; and by the experience gained in this way it is possible to understand what occurs in the experiments on artificial burying where the awn is fixed while the seed is free to rotate. When an awn has been placed for several hours in the damp chamber, fixed in the kind of support described, it will not always be found to have buried itself. I have often found that the point of the seed has been dragged across the soil into which it should have thrust itself; and in these cases it has happened that the seed has been pushed down over the edge of the vessel, so that it would have tended to bury itself if the soil had been of a larger area. It is this dragging motion which I believe to be produced by the torsion of the short axis between k_1 and k_2 (fig. 1); for just as, when the awn is free, irregular movements are impressed on its rotation, so the tendency to irregular rotation is transferred to the seed when the awn is fixed. In other cases the experiment is successful, and the seed is found buried to a certain depth; the sand is often found disturbed close around the point, owing, no doubt, to the irregularity of the rotatory motion of the awn. The following measurements give the amounts buried in three cases during a single wetting:—

I.

3 P.M.—A seed of 16 mm. length, resting with its point on damp sand.
5 P.M.—14 mm. of seed projecting above soil.
9 A.M. (still wet).—10 mm. „ „
Amount buried 6 *mm.* (2 of them in 2 hours).

II.

5 P.M.—12 mm. of seed projecting.
9 A.M.— 7 mm. „ „
Amount buried 5 *mm.*

III.

11.0 A.M.—6 mm. of seed projecting.
3.15 A.M.—2 mm. „ „
Amount buried 4 *mm.*

On removing the bell glass—that is, on substituting a comparatively dry for a damp atmosphere—the awn begins at once, *i. e.* in less than one second, to twist in the opposite direction to the hands of a watch; and as the drying proceeds all the above-mentioned movements are reversed. The following are the times in which the first six revolutions were made in once instance:—

Turn.	Completed in	Turn.	Completed in
	M. S.		M. S.
No. 1	13 0	No. 4	2 30
2	9 0	5	6 0
3	5 0	6	7 30

the movement being slow at first, then becoming quicker, and then slow again.

The lower knee (k_1) becomes perceptible in from 5 to 10 minutes, the upper knee (k_2) begins to be perceptible in from 10 to 15 minutes. The whole process of drying cannot be said to be thoroughly complete under two hours (in an ordinary room in winter); but the movement during the second hour is extremely slow, and practically almost unimportant.

When the drying-process is finished an examination of the seed will show that one of three things has occurred:—

(i.) The upward traction which results from the return of the awn to its former dry condition frequently pulls the seed out of the soil, especially if the sand used in the experiment is dry.

(ii.) The seed may, however, be able to withstand the upward traction.

(iii.) It may actually be found to be buried deeper than it was at the commencement of the drying-process.

The following measurements give the amount buried in three instances during a single drying:—

I.

6.45 P.M.—9 mm. of seed projecting above surface.
8.15 A.M.—7 mm. ,, ,,
Amount buried 2 *mm.*

II.

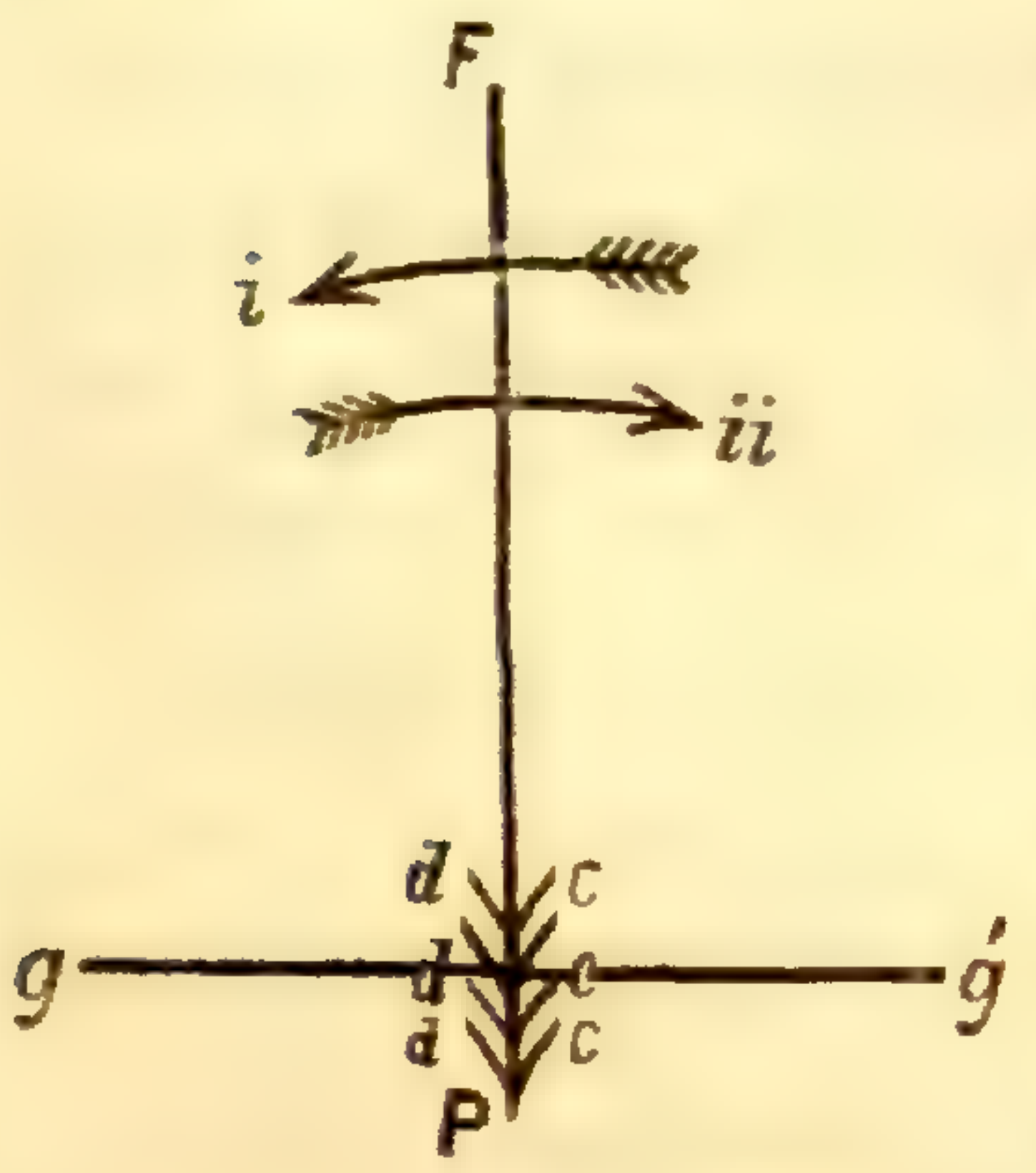
11.30 A.M.—12½ mm. projecting above surface.
1. 2 P.M.—10 mm. ,, ,,
Amount buried 2½ *mm.*

III.

9 A.M.—10 mm. projecting above surface.
11 A.M.— 6 mm. ,, ,,
Amount buried 4 *mm.*

In investigating the burial of the seed caused by drying, it must first be remarked that the plume of hairs with which the point is armed (see figs. 1 & 7) offers but little resistance to the entrance of the seed, but tends to prevent its withdrawal. The bare sharp point (*p*, figs. 1 & 7) is about ⅓ mm. in length; the hairs which form the plume are graduated, the smallest (¼ mm.) being the nearest to the point, so that they tend to preserve the smallest amounts buried during the wetting process. Moreover the length of the whole plume, measured from the extreme tip of the seed, is only about 4 mm.; and as we have seen that as much as 5 mm. may be buried in one wetting, it is quite conceivable that the seed can resist the uprooting tendency of the drying process. To understand how it can actually be buried deeper, we must examine more closely the act of rotation during drying.

A vertical rod, which is fixed at the upper extremity, will, as it twists on its axis, cause a simple rotation of its lower free extremity. But if the upper or fixed end is not vertically above the lower or revolving end, *i. e.* if the rod is curved, there will, I believe, be a tendency for the rotation to take place about the line joining the upper and lower ends of the rod. The movement imparted to the point will then resemble the circular rocking motion which is employed when a stick is being thrust into the ground. Given pressure from above, a rotating vertical rod will make a cylindrical hole of continually increasing depth; but if this pressure is removed, it will merely continue to rotate in the hole already made. But in the case of a *Stipa*-awn (a *curved* rod twisting on its axis), even when the pressure from above is removed the rocking* tends to continue the burying process. The point of the seed may be compared to a barbed point, like that in the woodcut.



The point P is supposed to be thrust into the ground, *g g′* giving the level of the soil.

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* Whatever may be the explanation of this movement, it certainly occurs.

The free end F is now supposed to rock backwards and forwards, describing arcs alternately in directions *i* & *i i*, in the plane of the paper and about the point P. When F moves in direction *i* the barbs *d d d* will offer little resistance, whereas the barbs *c c c* will in fact act like fulcra, and will enable P to be forced deeper into the ground. On the movement being reversed, this action will be reversed also, *d d d* giving the fulcra, and P being again buried deeper. Although the tendency of a *Stipa*-awn, on drying, is to move (not backwards and forwards in one plane, but) so as to describe a cone, yet I believe the above-described process is essentially what occurs in *Stipa*; for the seed is revolving in soil of densities varying at different points, so that it moves not regularly, but by jerks; moreover the plume is rather more developed on two of the opposite surfaces of the seed than on the intermediate regions, and the point is obliquely set on. In observing the process of drying, I have often seen a distinct rocking movement as the awn attempted to rotate and was continually forced back again. All their aberrations from a structure and from a rotation of mathematical regularity must favour the levering or wriggling movement of which the diagram in the woodcut gives the essential action.

In describing the manner in which the seed of *Erodium* is buried during drying, Hanstein does not enter into any of the above considerations as to a rocking movement &c.; he merely says that " the lower part of the awn begins to contract into narrow spiral coils, causing the cone (*i. e.* seed) to turn on its axis and penetrate the ground; and the erect hairs on it, which point upwards, retain it there like grappling-hooks "*.

It has now been shown by what means the seed of *Stipa* is buried, both as it untwists and also as it returns to a state of torsion. By a combination of these two processes, the awn is thrust into the soil to such a depth as to cover up the seed completely. Thus, in an experiment, in three wettings and three dryings 28 mm. was buried in dry sand: the ordinary length of a seed is 17 mm.; so that this is amply sufficient. In another experiment a seed of 16 mm. length was completely buried in three wettings and three dryings. Another seed, which I entangled in the branches of a low bush, and left out of doors for eight days, had buried itself to a depth of 31 mm., impaling a piece of rotten leaf on its way. Mr. Farrer informs me that the *Stipa*-seeds which blow away from the parent plants succeed in burying themselves in his garden. The question of what advantage it is to the plant to bury its seeds will be discussed in the sequel.

Before passing on to describe the arrangement of structure of which the hygroscopic mechanism consists, I shall give a brief account of the phenomena exhibited by the *Stipa*-awn, considered merely as mechanical actions, and with no reference to the biological conditions in which they occur in Nature.

A simple instrument was made for me by my brother Horace: a piece of *Stipa*-awn, about 5 cm. in length, was employed, taking care to avoid either of the knees (k_1 or k_2). The awn is fixed at one end, and at the other bears a light index, fitted to travel round a clock-face as the awn twists or untwists; the bearing of the awn is so managed that the whole of it can be immersed in different fluids. The *Stipa*-awn is hygroscopically ex-

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* Sachs, p. 841, Eng. Transl. (a perfectly correct abstract of the original).

tremely sensitive *; but as we shall see that it is also very sensitive to changes of temperature, a purely hygroscopic result is not so strikingly demonstrable as one due to a change in temperature and in moisture combined. Thus, breathing on the *Stipa*-hygroscope, held even at arm's length, or bringing the warm and moist hand near the awn, causes distinct movements of the index.

De Luc showed † that water has no *special* virtue in causing the expansion of hygroscopic bodies, and that other fluids can perform the office of filling out the molecular interstices. If the *Stipa*-hygroscope is allowed to dry in the air of an ordinary room, and is then plunged into absolute alcohol, the index shows, by moving in the "dry" direction, that water is being removed from the awn; after a time the alcohol itself is absorbed, and the movement of the index is reversed. On removing the instrument, the index moves in the "wet" direction, in consequence, I suppose, of the absorption of water by the alcohol; ultimately, however, the alcohol evaporates, and the movement of the index is reversed.

The effects of temperature on the awn are extremely curious, and agree with those observed by De Luc ‡: he found that a rise in temperature affects hygroscopic bodies in the same way as increased moisture, whereas a fall in temperature acts like dryness. With a *Stipa*-hygroscope the experiment is a pretty one; it is allowed to remain in warm water until the index comes to rest; if it is then removed, and plunged into cold water, the index gives a quick start through 90° or more in the direction of drying (*i.e.* against the hands of a watch). On replacing it in the warm water a rapid movement in the opposite, or "wet," direction takes place. The experiment may be performed in another way. If the hygroscope is placed in the current of hot air from a lamp, the rise in temperature tends to make the index move in the wet direction; but it also *dries* it, and therefore tends to make it rotate in the opposite direction: the struggle is made obvious by the fluttering motion of the index. The ultimate result is the victory of the "drying" rotation. The coincidence in the effects of heat and moisture accounts for the extreme sensitiveness of the *Stipa*-hygroscope to being breathed on.

The first theory which suggests itself to account for the effects of temperature is, that as an increase in the quantity of water in the molecular interstices makes the awn untwist, an increase in bulk of the water already permeating the tissues acts in the same manner. In support of this view my brother Horace showed that it cannot be due to *air* contained in the tissues; for the index does not move when the receiver of an air-pump under which it is placed is exhausted, or when the air is readmitted. In performing this experiment we immersed the hygroscope in oil or in mercury, to obviate the effects of the change of temperature resulting from the change of air pressure; before this precaution was taken the index moved distinctly as the air was removed or let in, although the thermometer only registered a change of 2° F.§

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* It has been employed as a hygrometer (Watts, Dict. of Chemistry, iii. p. 233).

† Phil. Trans. 1791, p. 11.

‡ *Loc. cit.* p. 16.

§ The sensitiveness to changes in temperature was well exhibited by my brother, who observed that on lifting the *Stipa*-hygroscope out of water it always moved very slightly in the *cold* direction, but that this movement disappeared at the temperature of the dew-point, showing that it was due to evaporation.

My brother then suggested that if it were due to the expansion or contraction of the water contained in the tissues, the results ought to be exactly reversed when water at 4° C. was used as the higher temperature, 0° being the lower one, because water expands instead of contracting in passing from 4° to freezing-point, and therefore the *Stipa*-hygroscope ought to behave as if 0° was a higher temperature than 4°. Preliminary experiments showed that a difference of 4° is clearly indicated by the hygroscope; but, to our surprise, we found that the hygroscope behaves exactly as if water expanded in passing from 0° to 4°. We therefore concluded, like De Luc, that the effects of temperature have nothing to do with the expansion of water. He placed his hygrometer in quicklime, by which means he obtains what he calls "absolute dryness," and found that changes of temperature affected his instrument in "nearly the same" manner as when in water.

The only explanation left appears to be that the woody tissue itself expands with heat. But, from the experiments of Villari *, it appears that the expansion of dry wood with heat is *extremely* small compared with the expansion due to imbibition. I find it impossible to believe that the rapid rotation through a considerable angle is due to this cause. The following curious phenomenon negatives such a view, but must also remain quite unexplained. It will be made clear by detailing an experiment. Two vessels of water were employed, whose temperatures differed by about 63° C. In the cold water the index of the hygroscope stood at 130; on putting it into the hot water the index moved quickly to about 240 (not exactly noted), and returned slowly to 115. That is, it first makes a rapid *untwisting*, or *wet* movement, and then returns to a point on the *dry* side of its original position—that is, a point representing increased torsion of the awn; so that on moving into hot water it untwists rapidly, and then twists slowly up beyond its original degree of torsion. Exactly similar but reverse results ensue on removing the awn from hot to cold water. These experiments have been frequently repeated by my brother and by myself.

The Mechanism of Torsion.—In Sachs's 'Handbook' † the twisted growth of trees is explained by the internal parts not growing as fast as the external tissues, the unequal longitudinal tensions satisfying themselves by producing torsion. To apply this to the torsion of the *Stipa*-awn, we must suppose that, on drying, the internal parts contract more strongly than the external. This action may be imitated, as Sachs remarks, by slipping an elastic tube over a second of smaller calibre; the internal one is then stretched, the external one being left as it is, and the two are bound together in several places. On the release of the internal tube, the external one will not permit any shortening of the internal tube except by the whole system turning into an irregular helix. Hildebrand ‡ offers a similar explanation for the torsion of the awn of the "Springhafer" (*Avena sterilis*). He says that one surface of the awn contracts on drying more strongly than the opposite surface, and the awn twists on itself to satisfy the unequal tension thus produced. Hanstein § explains the torsion of the awns of the Geraniaceæ in a similar way. For a long time I concluded that some explanation of a kindred nature

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* Quoted in Sachs: English Translation, p. 649.

† English Translation, 1874, p. 770.

‡ Pringsheim's Jahrb. für w. Bot. 1873, Bd. ix. "Schleuderfrüchte."

§ *Loc. cit.*

must hold good for *Stipa*. I assumed that if there existed unequal longitudinal tensions along opposite surfaces of the awn, there would be inequality of contraction or expansion in a radial direction, and that the sectional outline would alter in shape on drying. I could observe no such alteration, and found, in fact, that on swelling in water the awn increased in diameter very nearly equally in all directions. I concluded, therefore, that the inequality of expansion must be between the internal and external tissues, and not between two longitudinal halves. I saw no way of confirming or destroying this hypothesis; but I always felt a difficulty in the fact that the *Stipa*-awn is *always* twisted in one direction, whereas the above-mentioned unequal distribution of tensions would give a tendency to twist in either direction. Ultimately all theories of unequal contraction of the awn as a whole were overturned by observing that longitudinal sections and mere strips torn from the awn were capable of twisting up into precisely the same right-handed screw as the whole awn. This proved that torsion-power may reside in a combination of a few cells. The fact that a transverse section of the twisted awn of *Anemone montana* shows only broken-down tissue in the centre, convinced me that torsion is possible where the twisting-organ has *no* strongly contracting tissue in the centre. These two observations suggested that the power of torsion must reside in the individual cells composing the awn. I therefore boiled a piece of *Stipa*-awn in dilute nitric acid and chlorate of potassium; by subsequent teasing in a drop of water, the cells were isolated with great ease. The slip of glass was then held over a spirit-lamp, and a light teasing action continued, to prevent the cells adhering to the glass on drying. On examining the object under the microscope the torsion of the individual cells was beautifully seen; besides individual cells, numerous little ropes of two or three cells are seen, *all* twisted in the direction of torsion of the awn, *i. e.* that of a right-handed screw (see fig. 14).

To this observation it may be objected that the treatment with hot acid may have conferred the power of torsion on the cells. To this it may be answered, (1) that small portions, separated by *mechanical* means, exhibit torsion when dried; (2) that pieces of awn treated with boiling nitric acid and chlorate of potassium (if they are not teased into their constituent cells) undergo torsion on drying, proving that the cause of the torsion, whatever it be, is not affected by the treatment with acid.

I believe that both the internal and the external cells of the awn are capable of independent torsion; but whether this be so or not, it is certain that the small external cells exhibit the power in a far higher degree. This cleared up what had always seemed a great difficulty, viz. the instantaneous movements of the *Stipa*-hygroscope; for it removes the seat of hygroscopic action from the internal tissues to a more accessible part near the surface. In accordance with the present theory, it is found that the individual cells possess the same delicacy of action as the whole awn. I have actually seen a single cell under the microscope untwisting and twisting up again as my hand approached and was withdrawn from its neighbourhood.

Supposing it then to be granted that the cells composing the awn are capable of independent torsion, we have yet to show that the twisting of the awn as a whole will be the result. The cells are of an elongated form, and are of course closely attached to one another, so that unless they are isolated they cannot twist on their own axis, since this would require a sliding movement between each cell and its neighbours. The following experiment demonstrates the way in which each cell satisfies its tendency to twist on its own axis.

A number of *Stipa*-awns (exclusive of feather and knees) are soaked in water, and when thoroughly untwisted are firmly tied into a cylindrical bundle or faggot. Here we have represented the state of things in an awn: each constituent awn in the bundle represents one of the cells of an awn, and, like them, tends to twist on its own axis on drying. It is found that, on drying, the bundle of awns is converted into a *rope*, its constituents passing helically round like the strands. And just in the same way the cells which make up an awn (of which the bundle of awns is a *schema*) satisfy their tendency to twist by forming a rope of cells twisted in the same direction as themselves.

If, then, we have a number of cells so connected together that they are incapable of independent torsion (and this is the case in the awn of *Stipa*), and if, further, each cell has a tendency to twist on its own axis (as we know to be the case with *Stipa*), then it cannot be doubted that the torsion of the mass of cells as a whole will be the result. That this is actually the mechanism by which the awn twists is conclusively shown by the fact that the constituent cells of the feathery non-twisting portion have *no* such power of independent torsion when isolated and dried in the manner already described.

The Bending of the Awn at the Knees (k_1 & k_2).—If we compare a section of the feather-bearing portion of the awn with a section of the twisting part, we find that the difference between them lies in this: in the twisting part the cells are all thick-walled (excepting the central ones, *c*, and two small masses, *m* & *m*, fig. 11); but in the feather all the cells are hollow, and it looks as if the central mass of thin-walled cells had increased so as to fill up the whole interior of the section. And since this thin-walled tissue is not hygroscopic in the feathery portion, we may assume that it is not so in the twisting part. Comparing a section taken low down in the awn (fig. 11) with one taken at the upper knee (fig. 13)*, we find a marked difference in the distribution of the non-hygroscopic tissue. At the upper knee the cells are passing into the hollow condition found in the feather; but this change does not attack all parts simultaneously: the small masses of non-hygroscopic tissue, *m* & *m*, have enlarged and coalesced with the central mass (*c*); and it is the cells surrounding the coalesced masses which exhibit the commencement of the loss of thickening in their walls. We may divide the section by a line *x y*, on one side of which there are many hollow cells, on the other all thick-walled cells. The twisting-power, which is already weak in the portion of the awn between the two knees, must be disappearing at k_2, since in the feather it is quite gone. When drying commences, the mass of thick-walled cells contract longitudinally; and the mass of hollow cells not being able to contract to the same extent, the awn will bend with the non-

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* In the drawings of the sections, figs. 11, 12, & 13, the stratification of the cell-walls is not represented; nor are the pit-channels given, which are especially numerous in the large internal cells, and which seem to communicate with the vascular bundle in the centre.

hygroscopic half on the convex surface, and the strongly contracting cells on the concave aspect. To prove that the internal cells do contract longitudinally, it is only necessary to split an awn longitudinally; on drying, the split-off pieces bend with the internal surface concave. There can be no inherent tendency in the separate cells at k_2 to bend in the direction assumed by the awn; for a small portion severed by a longitudinal section (such as is shown by the upper dotted line, fig. 13) bends with the internal surface concave, which is in the opposite direction to that in which the whole awn bends.

The bending at the lower knee is more difficult to explain. The hollowing-out of the cells near *m* & *m* has begun even at this part of the awn: two hollow cells are shown in fig. 12; and in other sections I have found more of them occurring. In this section, again, we might draw a line which would divide the awn into a more and a less contractile half. In fact we have at the lower knee a bending-mechanism similar to that which exists at the upper knee, but with an important difference: at k_2 the torsion-power of the awn is exhausted, whereas at the lower knee this is not the case; and since the unequal longitudinal tension just described can satisfy itself by assisting the *torsion*, it does not seem evident how the *bending* of the awn is to be effected. To explain this a hitherto neglected point in the structure must be noticed. If we compare once more a section of the awn close to the seed with one taken at either of the two knees, we find that in the lower section (fig. 11) the ribs *r r*, are separated from one another by approximately equal portions of the circumference; but at the lower knee (fig. 12) the arc on the side *m m* has diminished, while the other has increased. In a wet or untwisted awn, the fact that the ribs approach one another as they pass from below upwards, gives the appearance of a very slight and elongated left-handed screw. And I believe that the approach of the ribs to one another is directly connected with the unequal arrangement of the more and less hygroscopic tissue at the knees. At the lower knee there is, moreover, a single sudden and short turn of a left-handed screw. This I call the "reverse twist," since it is in the opposite direction to that in which the awn twists in drying. The reverse twist is perfectly distinct from the ordinary hygroscopic torsion of the awn; for it is not obliterated by wetting, and is the result of the growth of the tissue into that shape. It is like a single turn of a fluted spiral column made of india-rubber, which could obviously be twisted in either direction independently of its shape. Now since the awn twists in the opposite direction to the reverse twist, the latter will be obliterated as torsion proceeds; and this is, in fact, the case: the awn is twisted both above and below the knee; but at the actual bending-place there is no torsion. When the reverse twist is obliterated, the unequal longitudinal tensions at the point k_1 are employed in producing the bend, instead of satisfying themselves in assisting the torsion. To summarize this imperfect explanation, the torsion-power satisfies itself in obliterating the reverse twist; and then the unequal tension, being brought into a longitudinal direction, satisfies itself by producing the bend.

I suspect it was the reverse twist which deceived Max Wichura*, and led him to describe the awn of *Stipa* as twisted to the right below the knee, and to the left above it.

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* "On the winding of Leaves," Taylor's 'Scientific Memoirs,' May and Aug. 1853, p. 280; the original in 'Flora,' 1852, Jan. and Feb.

I have discussed the mechanism of the bend at some length, because of its extreme importance in the burying-process; for if the awn did not terminate above in a non-twisting horizontal portion, the rotation would not be transmitted to the point of the seed, neither could there be any increase of vertical pressure resulting from the straightening of the awn.

Torsion.—An explanation will now be attempted of the power of torsion which the cells possess.

It is a general property of hygroscopic tissue that the cells composing it are thick-walled. I have already pointed out the difference in this respect which exists between the hygroscopic and the non-hygroscopic tissue of the *Stipa*-awn. Hildebrand ("Schleuderfrüchte") mentions the thick-walled cells composing the awn of *Avena*. We should expect therefore that the power of torsion would depend on the manner in which the cell-walls are thickened.

Before discussing my view, it will be well, first of all, to exclude any cause resembling the unequal internal and external tensions which are supposed to account for the torsion of trees; for this only shifts the difficulty one step further off, and does not account for the constancy of *direction* of torsion. We may now examine the structure of the cells which make up the hygroscopic tissue. A body which swells on imbibing water will expand equally in all directions, if the molecular interstices in which the water lies are symmetrically arranged in all directions. And a cell will have no tendency to twist if its cell-wall expands equally in all directions. Therefore, if we are to account for the torsion of a cell by the expansion or contraction of its cell-wall, we must examine the molecular structure of the wall with special reference to the distribution of the capacity for absorbing water. The well-known researches of Nägeli* are directed to this very point.

He there shows that the cell-wall is composed of parallel lamellæ of alternate degrees of density and refractive indices. The first series of lamellæ are seen in transverse sections of elongated woody cells, as concentric shells, alternately light and dark, and fitting inside each other. This appearance is well known as stratification or "*Schichtung.*" The other systems are essentially of the same nature, but are not so well marked. They give rise to the appearances known as "*Streifung*" or striation; these are series of parallel lines, alternately light and dark, traversing the surface of the cell, and are in reality the edges of parallel lamellæ of alternate densities. There are usually two systems of parallel lamellæ; and they may be inclined to the axis of the cell at almost any angle. Very frequently the two systems wind spirally round the axis in opposite directions. Now according to Hofmeister†, when the tissue of the cell-wall expands during imbibition, it is chiefly due to the swelling of the less-dense striæ; and we have seen that these striæ are spirally arranged; therefore we are led to expect that the imbibition of water will result in some kind of spiral tension: and spiral tension will result in torsion—just as when a string is fastened to one end of a rod, and is coiled spirally round it, and the free end is pulled, the rod will tend to rotate on its axis. And since there are two systems of spiral striation, the tension due to one system must be stronger than that

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* Münchener Sitzungsb. 1864, May & July.

† Lehre v. d. Pflanzenzelle, (1867) p. 197.

due to the other, if any tendency of the cell to twist in one direction more than in the other is to result. Nägeli has shown[*] that imbibition does lead to the torsion of a cell on its axis when one system of striation is more pronounced than the opposite. Fig. 10 is copied from his paper already quoted[†]: *a* shows a cotton-wool fibre in extremely dilute sulphuric acid; *b* is the same fibre in somewhat more concentrated acid. The first treatment merely brings out the striæ more clearly; the stronger acid causes the fibre to swell and to twist on its axis. The importance of these figures is this: in *a* it may be seen that the direction of the striation changes in the lower half of the fibre; and in *b* it is seen that the direction of the torsion changes precisely where the direction of the striation does; not only do cotton-wool fibres twist on the intense imbibition caused by acid, but, as I find, on the intense *abstraction* of water caused by strong drying. From these facts we must conclude that the striation of the cells is the cause of the torsion of fibres of cotton wool.

The elongated cells of the *Stipa*-awn present a close analogy with cotton-wool fibres; not only do they twist on drying, but also, as a result of the great swelling caused by maceration in strong Schultz's solution, they undergo torsion in the opposite direction.

From all these considerations, I cannot resist the conclusion that the torsion of the cells in the *Stipa*-awn is a direct consequence of unequal contraction of the cell-wall due to the striation of the membrane. I have found the investigation of the molecular structure of the cells in the *Stipa*-awn too difficult a task to be included in the present research; I believe, however, I may say that the cells are obliquely and spirally striated, and that one system is more strongly developed than the opposite.

Both Nägeli and Hofmeister give explanations of the ultimate mechanism of the torsion of cells; but in my present need of clear anatomical details it would be useless to apply their explanations to *Stipa*-cells.

I now pass on to describe the remaining seeds or fruits observed by me.

AVENA ELATIOR.

Professor Hildebrand has described the hygroscopic awn of *Avena sterilis*, both as to the mechanism of the twist and the adaptation of the hygroscopic torsion as a means of distribution[‡].

Fig. 4 shows the awn of *Avena elatior* (the empty glumes having been removed). It will be seen that, supposing the fruit to be held vertically, we have, just as in *Stipa*, a vertical twisted part of the awn, and a more or less horizontal part which is not twisted. In *Avena sterilis*, according to Hildebrand[§], the spikelet contains two fertile flowers, and therefore two bent awns. He describes how, in drying, the pressure of the rotating part of the awn against the ground causes the fruit to be projected into the air ("ein Stück fortgeschleudert wird")[‖].

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[*] Münchener Sitzungsb. 1864, July, p. 124.

[†] Tab. i. figs. 8 & 9.

[‡] Pringsheim's Jahrb. *loc. cit.*; and "Verbreitungsmittel der Gramineen-Früchte," Bot. Zeitung, no. 49, 1872.

[§] Schleuderfrüchte, Separatabd. p. 14.

[‖] This curious property has gained for it in Germany the popular name of "Springhafer" (*Hildebrand*). I have met with a curious mention of the wild oat in the 'The Young Man's Companion, or Arithmetic made easy,' 1727:—

He also describes a method of progression by turning over and over, and a kind of creeping movement caused by the extension and flexion of the awns. Prof. Hildebrand suggests that possibly the more important function of the twisted and bent awns of *Avena* and other grasses may be similar to that of *Erodium*, *i. e.* to bury the seeds in the ground. From analogy with *Stipa*, and from other considerations, there can be little doubt that this surmise is correct.

The fruit of *Avena elatior*, 6 times magnified, is given in fig. 4. The vertical part of the awn (attached to the outer palea or flowering glume) is about 5 mm. in length, and is strongly twisted into a right-handed screw of about 4 turns. It follows that, just as in *Stipa*, the horizontal portion (6 mm. long) revolves in the direction of the hands of a watch when the awn is wetted. It is more sensitive hygroscopically than *Stipa*, and untwists very quickly (one turn in from 15″ to 30″) when placed in water, as compared with the *Stipa*-hygroscope, which makes one revolution in 2 or 3 minutes.

It will be seen that the point is blunt, and that it is covered with a plume of hairs pointing backwards as in *Stipa*; but these hairs seem to me too weak to be of much service. The horizontal portion of the awn is not feathered, but armed (as is also the twisting part) with minute reflexed barbs. I have not succeeded in observing the process of burial in *Avena*; nor has Hildebrand seen it. But I found that the seeds of a patch of wild oats growing in a ploughed field had succeeded in burying themselves. I believe that the mechanism of burial is not quite the same in *Avena* as in *Stipa*; the seed is too heavy to be held vertically, and the awn does not seem fitted for so supporting it. Moreover the specimens which I found buried were not in a situation where low herbage could have entangled their awns, but among bare lumps of clay. I presume that the point is pushed laterally against inequalities in the ground, other projections being made use of as *points d'appui*.

In explaining the mechanism of torsion in *Avena*, I am compelled, unfortunately, to differ entirely from Prof. Hildebrand. His view has been already mentioned. Against it I bring forward the arguments:—

(i.) That it does not account for the direction of torsion being constantly the same.

(ii.) That the surface which he believes to be the most contractile is on the *convex* side at the bending-point.

(iii.) The strong argument that the cells, when isolated by nitric acid and chlorate of potassium, exhibit precisely the same power of independent torsion as those of the *Stipa*-awn.

The mechanism of the knee is, I believe, the same in *Avena* as in *Stipa*. Professor Hildebrand figures a section of this awn (which is morphologically identical with that of *Stipa*) as having two cavities answering to the hollow ribs of *Stipa*, and, like them, filled with cells containing chlorophyl in the young state. In this condition the ribs make an

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"The following trick is made use of when any thing in a family is lost, to make the person suspected confess the fault and restore what is lost. Take a beard of wild oat while 'tis greenish, and twist it in the shape of a little cross, giving it to the person suspected, and whose guilt they are pretty well assured of. Give also to the rest of the family little crosses, but made of different stalks, as hay and wheat; put all these in a cut apple, and the little wild oat will grow sensible of the moisture, untwisting itself and turning, to the great amazement of all the spectators."

elongated turn in the direction opposed to the hygroscopic torsion of the awn; and this elongated "reverse twist" is seen in the mature awn when untwisted by wetting. This reverse twist is the consequence of the approach of the ribs to each other as they pass from the lower part of the awn to the point of bending; and I think that, as in *Stipa*, this alteration in form is connected with the longitudinal partition of the awn into a more and a less contractile half.

HETEROPOGON MELANOCARPUS.

The general appearance of the awn of this species is shown in fig. 2. In an ordinary room in winter it has but one knee, as shown in the figure; but I have since found that by drying it at a higher temperature a lower knee appears; in the wet state a "reverse twist" can be made out. The seed has a sharp oblique point, and a well-developed plume of hairs; the awn, like that of *Stipa, Avena*, and *Anemone*, is twisted into a right-handed screw. There are no feathery hairs on the non-twisted part of the awn; but it is covered throughout its entire length with minute reflexed barbs. I find it capable of burying itself on becoming wet; but whether it does so on becoming dry I am not sure.

HETEROPOGON CONTORTUS

has a doubly bent twisted awn, of which the vertical part is roughly 13 mm., the part between the knees 10 mm., and the non-twisted part 4 cm. in length. It twists in the same direction as *Stipa* &c.; and, when wetted, I have found it able to thrust itself into sand.

ANDROSCEPIA ARUNDINACEA.

The strongly bent and twisted awn is shown in fig. 3. I do not possess the complete fruit of this species, and could not make any trial of its burying-powers.

ANTHESTERIA CILIATA

somewhat resembles *Heteropogon melanocarpus*, with a bent and twisted awn, and a fine plume of hairs.

Lagurus ovatus has a bent and twisted hygroscopic awn. And I find the following kinds of grasses mentioned as having bent and twisted awns—*Aira, Arrhenatherum, Holcus**, *Streblochæta nutans, Danthonia, Chetobromus Dregeanus, Macrochloa arenaria*†. I think it is probable that these have the power of burying themselves.

RANUNCULACEÆ.

ANEMONE MONTANA.

Fig. 6 gives the general appearance and proportions of the achene of this plant. The slight hairiness of the awn probably aids in the distribution of the seed. It is exceedingly remarkable that the general features of the above-mentioned burying-seeds, all members of the order of Grasses, should be repeated in a Ranunculaceous plant.

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* 'British Flora,' Hooker.

† Max Wichura, translated in Taylor's Scientific Memoirs, May and Aug. 1853.

We have :—(1) seed more or less pointed, with a plume of hairs directed backwards (see fig. 8); (2) vertical awn twisting, when dried, into a right-handed screw; (3) horizontal, non-twisting portion rotating, when wet, in the direction of the hands of a watch, and coming into the same straight line with the lower part of the awn when the untwisting is complete; (4) cells of the twisting part capable of independent torsion.

With some difficulty I succeeded in observing the seed of *Anemone montana* bury itself almost completely during the process of becoming wet. I do not know whether it is capable of being buried deeper as it dries. Le Maout and Decaisne * figure the achene of *Anemone pulsatilla* as bent and twisted. Max Wichura † describes *Clematis azurea* as having the appendages to the carpels twisted.

GERANIACEÆ.

I merely mention this family to point out the general resemblance presented by the coccus and awn in some of its members to the burying-mechanisms already described. Fig. 5 (a dry *Pelargonium*-coccus) shows the flat, ribbon-like awn twisted into a right-handed screw, the knee, the horizontal non-twisted portion, the pointed fruit, and the plume of grappling-hairs.

It is undeniably true, as Hanstein points out, that the external surface contracts more strongly than the internal one in drying; but this does not account for the direction of torsion; I find that, as in the above-described awns, the cells are capable of independent torsion.

I have made no experiments on the burying-powers of the Geraniaceæ, as these have been already described by Hanstein, Roux, and Asa Gray.

When we find among organisms belonging to widely different groups a curious structural mechanism, repeating itself and performing in each case the same function, we conclude that this function is an important one in the economy of the plant. Thus, for instance, the importance of the distribution of seeds is pointed out by the existence of burs in widely different orders, such as the Compositæ (Burdock), Rosaceæ (*Geum*), and Rubiaceæ (*Galium aparine*)—of plumes to enable the seed to fly on the wind in many Compositæ, Apocynaceæ, Onagraceæ, &c.

Now in the burying seeds which we have been considering we have a similar case, a given function performed by essentially similar mechanism in plants belonging to widely different orders; and we accordingly conclude that the power of thrusting themselves into the ground is of special service to the seeds under consideration. Two theories suggest themselves.

(i.) My father has observed that certain seeds are almost incapable of germinating in the light, whereas they do so readily in the dark. This fact suggested that the power of self-burial has been developed to remedy the injury which the incapacity of the seeds to germinate in the light must cause to the species. I therefore made a comparative trial to determine this point. A number of *Stipa*-seeds were placed in a vessel half filled with

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* English Translation, p. 175.

† Taylor's Scientific Memoirs, Aug. 1853, p. 302.

damp sand, and covered with a glass plate; half of the seeds were thrust into the sand*; the rest were allowed to remain on the surface. Contrary to my expectation, the seeds exposed to the light began to germinate first. I regret that I did not make a second trial with another lot of seeds; I think, however, that the above result is sufficient to overturn the theory in question, at least as far as *Stipa* is concerned †.

(ii.) The only other hypothesis which I have been able to form is, that by burying themselves in the ground the seeds are enabled to escape being eaten by birds. The fact that many of them are Gramineæ, and therefore likely to be sought after as food, favours this view ‡.

The developmental stages through which any structural mechanism has passed is always a most interesting question. Unfortunately I am as yet unable to enter into this question with respect to the burying seeds. We have seen that the mainspring of the mechanism is hygroscopic torsion; now many cells become twisted on drying, such as cotton-wool and bast fibres, the tubes of *Erineum* §, and curiously enough the beautifully striated cells which support the glands in *Byblis gigantea*.

Again, hygroscopic torsion depends on the spiral striation of the walls of the twisting cells. Now lamination or differentiation into more or less watery layers is probably a universal condition of the formation of cell-walls; so that the materials, as it were, for the development of hygroscopic torsion are certainly existent. The variability in the torsion of the cotton-wool cell shows that a want of unanimity in the direction of torsion would be one of the difficulties to be overcome in the process of development. Through what steps the hygroscopic sensitiveness has passed in development I am at a loss to say.

Finally, I venture to hope that my explanation of the torsion of awns may ultimately throw some light on other forms of torsion; and to this point I hope soon to direct my attention.

* For whatever reason the seed is buried, it would seem desirable that it should remain undisturbed. The joint by which the awn is attached to the seed seems adapted for this purpose; for after remaining a few days in damp soil the awn can be detached by the slightest touch. Roux points out the same thing in *Erodium*.

† G. Roux, *loc. cit.* states that *Erodium*-seeds germinate better when buried to the "normal" depth than when more or less deeply covered by soil. The details are not given in a manner to carry conviction.

‡ The seed of *Anemone montana* (one of the burying seeds) contains a large quantity of endosperm; the seed of this species is moreover, as far as I can make out, destitute of the acrid principle so common in the Ranunculaceæ, and which is found at least in some representatives of the neighbouring genus *Clematis*. Is it possible that the acrid principle may serve to prevent animals or birds eating the seeds of the Ranunculaceæ? as we know to be the case with the Bitter Almond ('Variation of Animals and Plants,' 2nd edit. vol. ii. p. 218). If so, the deficiency in the seed of *Anemone montana* of an acrid principle may be connected with the development of the burying-mechanism.

§ Sachs, 'Physiologie Végétale,' (translation: Geneva, 1868) p. 453, quoted from Nägeli and Cramer, 'Pflanzenphys. Untersuch.'

DESCRIPTION OF PLATE XXIII.

Fig. 1. Fruit and awn of *Stipa pennata* (natural size). *p*, the sharp point; *v*, the vertical twisted part of the awn; k_1 and k_2, the lower and upper knees; *f*, the non-twisted and more or less horizontal part of the awn.

2. Fruit and awn of *Heteropogon melanocarpus*. Letters corresponding to fig. 1.

3. Awn of *Androscepia arundinacea*. Letters as above.

4. Fruit and awn of *Avena elatior*. × 6.

5. Carpel and beak of *Pelargonium*. Letters as above. × 3½.

6. Achene and tail of *Anemone montana*. Letters as above: natural size.

7. Lower part of the fruit of *Stipa pennata*. × 6½.

8. Achene of *Anemone montana*. × 5 (about).

9. Upper part of *v* in fig. 1. × 7 (about). *r* and *r* are spirally running ribs, seen in section at *r* and *r* in figs. 11, 12, 13.

10. Cotton-wool cells. *a*, in dilute, *b*, in stronger sulphuric acid (from Nägeli). × 200.

11. Section of awn of *Stipa pennata* close to seed. *r* and *r* hollow spiral ribs (see fig. 9); *c*, central vascular bundle; *m* and *m* smaller masses of the same tissue; *c*, *m*, and *m* are non-hygroscopic. × 80.

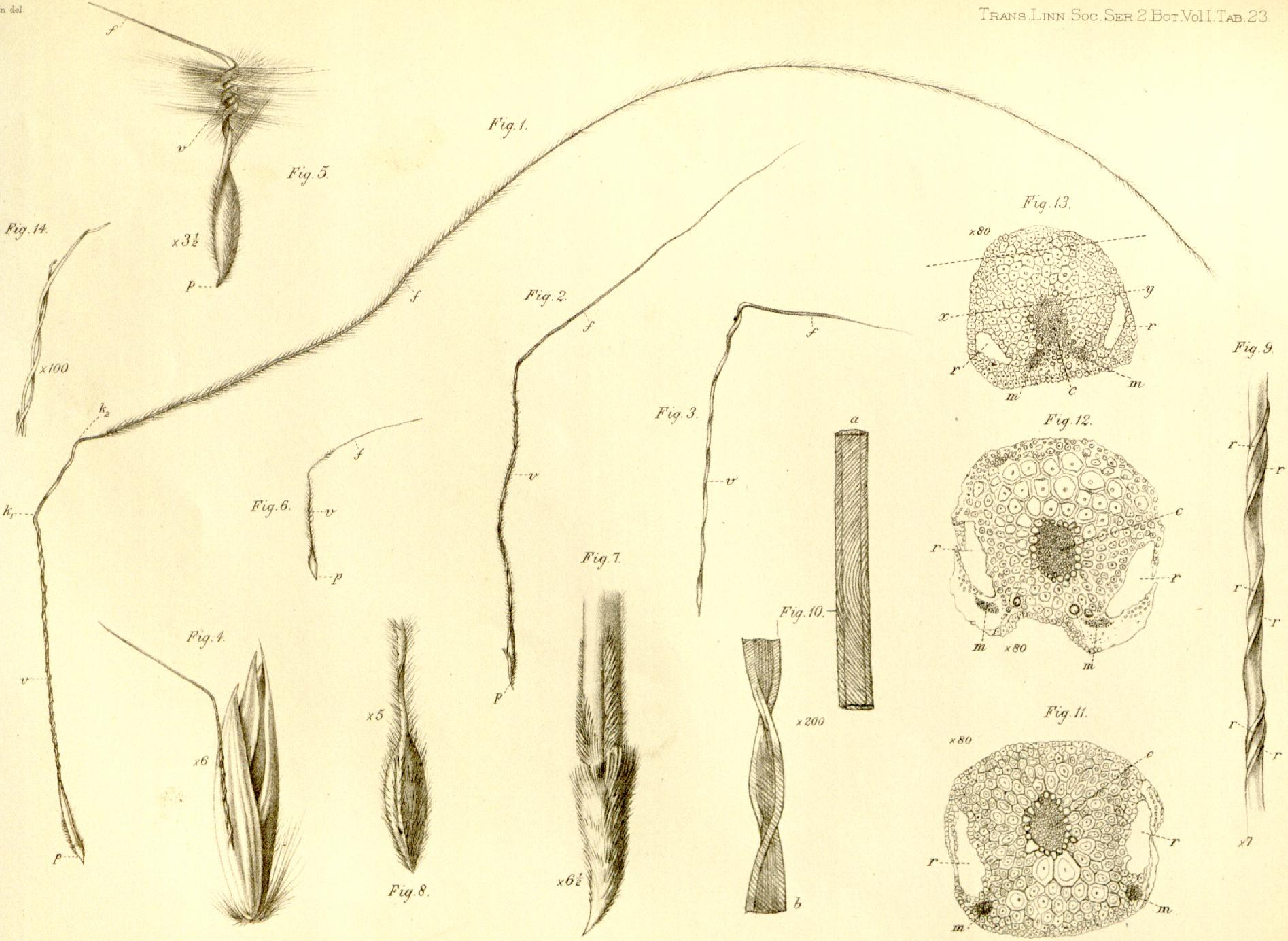
12. Section of awn of *Stipa pennata* at k_1, fig. 1. Letters as in fig. 11. × 80.

13. Section of awn of *Stipa pennata* at k_2, fig. 1. Letters as in figs. 11 and 12. *x y*, line dividing awn into a more and a less hygroscopic part. On the other dotted line see text, p. 160. × 80.

14. External cells from the awn of *Stipa pennata*, isolated with nitric acid and chlorate of potash and then dried, to show the power of independent torsion residing in the cells of the awn. × about 100.

A.R.Darwin del.

Trans. Linn. Soc. Ser. 2 Bot. Vol. I. Tab. 23.



C.Berjeau lith.

TORSION SEEDS, AWNS & SECTIONS OF GRASSES, &c.

M&N.Hanhart imp.