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XXI. *On the Origin of Buds.* By the Rev. Patrick Keith, F.L.S.

*Read April 7, 1829.*

PHYTOLOGISTS have been at all times much puzzled to account for the origin of buds. Hence the variety of opinions which they have advanced, or advocated, on the subject. Pliny believed them to be formed from the pith, but without giving us any particular account of the ground of his belief\*. Malpighi believed them to be formed from the pith, or from the cellular tissue which he regarded as *viscera* peculiarly destined to the elaboration of the sap and protrusion of future buds†. Du Hamel seems to have entertained different opinions upon this subject at different periods. In the outset of his researches he believed buds to be formed from the wood or pith of the former year. But what are we to say of the first year itself? Afterwards he regarded them as proceeding from pre-organized germs existing in the proper juice, and deposited by it in the course of its descent from the leaves, so as to pervade the whole plant. Where the pre-organized germs were themselves formed, I think we are not told. But his proof of their existence is as follows:—Having taken some cuttings of a willow, he stuck them in the ground, and made them, at the same time, to pass through a barrel filled with earth, so as to have a portion exposed to the air between the ground and the barrel, and another portion projecting above the top of the barrel. The part inserted in the

\* *Nat. Hist.* lib. xvii. cap. 21.

† *Anat. Plant.* 13.

ground



ground produced roots, and the part passing through the earth contained in the barrel produced also roots ; but the other two portions produced branches. It was of little consequence whether the cuttings were inserted in the ground by the upper or under extremity, as relative to their original growth, and they vegetated even when made to pass through the barrel horizontally. Hence Du Hamel concluded that germs both of the root and branch are dispersed throughout the whole extent of the plant, and are developed as the exigency of the case requires\*.

Others have contended that buds are generated only from the *plexus* of the vessels of the inner bark ; because, perhaps, it is from the inner bark that the union of the graft and stock is effected in the well-known operation of grafting.

Mr. Knight seems to have embraced the opinion of Du Hamel with some slight modifications. I do not mean to say that he has adopted the appellation, or even the notion of pre-organized germs. But he contends that buds are generated in the alburnum by means of the agency of the descending proper juice ; and thus dispersed, as we may infer, over the surface of the whole plant. His proof is as follows :—The runners connecting the tubers of a potatoe with the root were intersected and immersed by both portions in a decoction of logwood. The decoction passed along in both directions. But it was in the direction of the tubers that the proof wanted was elicited. For there, the decoction was found to have passed through an elaborate *plexus* of vessels between the bark and alburnum, which was seen to approach the skin at the base of the buds†. Hence it was inferred that buds are formed by the agency of the descending proper juice in its passage through the vessels of the inner bark.

\* *Phys. des Arb.* liv. iv. chap. v.

† *Phil. Trans.* 1803, p. 289.



Also the alburnum, according to Mr. Knight, possesses the power of regenerating buds. A number of plants of the Apple, Pear and Plum, which were raised from seed in the spring of 1802, were again cut down to the collar in the autumn with part of the root exposed. In the beginning of the following spring, protuberances were observed on the bark of the exposed roots, which were found to be processes issuing from the alburnum. They were incipient buds, and were ultimately protruded into shoots. Experiments upon the stem and root of aged trees gave the same result; establishing, as Mr. Knight thinks, the position, that the alburnum, or the proper juice deposited in it, possesses the peculiar property of the organizing of buds; whence it follows, as a corollary, that the origin of any bud is not more deeply seated in the stem than the layer of alburnum from which it is protruded into a shoot.

This common doctrine of Du Hamel and of Knight, and I might add of Mirbel also, is combated by a late writer on the subject of Vegetable Physiology; who contends, in direct opposition to their theory, that all buds protruded from the surface of the plant, *at whatever period of its growth, have been originally formed* at the centre of the stem or branch on which they appear; that is, in the original or annual shoot; and have been pushed outwards horizontally through every additional layer of alburnum while yet in a soft state, though it requires some peculiar excitement to protrude them into shoots, which may not occur till after a period of many years\*. The bud in its progress outwards is represented as leaving behind it a pale streak of parenchyma indicating its path, which is in the direction of the medullary rays, and very perceptible in a transverse section of the Willow taken near the place of the protrusion of a young shoot. This rule can apply only to woody

\* *Library of Useful Knowledge.*



plants which have their diameters augmented by the addition of annual and concentric layers. It may include dicotyledonous perennials; but dicotyledonous annuals, and monocotyledonous plants, as well as plants without cotyledons, it cannot possibly apply to.

It is admitted that buds, though not originating as above, may be produced from any layer of alburnum by artificial means;—what are these means?—but it is contended that Nature never protrudes a branch-bud except in the aforesaid way. At all events, the discovery is not entirely new. It is at least as old as the researches of Mrs. Ibbetson, who saw, as I believe, through the medium of the microscope, the buds in the very act of crossing the concentric layers on their way to the alburnum, and who has advocated and illustrated the fact and the doctrine with the most laudable zeal\*. She thought, indeed, that the bud is originally formed in the root, from whence it ascends by “*the line of life*”—that is, the medullary sheath—till at last some unknown but potent and irresistible cause gives it a horizontal direction, and forces it ultimately to the circumference, in spite of all intervening layers of wood, however numerous and however hard. This was indeed very difficult to believe; and was, as I should suppose, never much believed.

But the subject was not left to be elucidated merely by the labours of Mrs. Ibbetson. It had long occupied the attention of M. Du Petit-Thouars, a French botanist distinguished for his able *Illustrations of the Plants of Madagascar*. In a paper entitled *De la Terminaison des Plantes*, and read at a sitting of the Royal Academy of Sciences on the 7th of October, 1816, he exhibits the result of his observations, and develops his views at some length. The following extracts will show that the doctrine of the central origin and horizontal protrusion of buds

\* *Phil. Mag.* vol. 45. 56.



comes from his hands considerably improved. "A partir de là [the terminal bud], je peux redescendre jusqu'à la base, en suivant une ligne plus ou moins droite, que je regarderai comme l'origine de toutes les branches, c'est l'axe de l'arbre." Again,—“A mesure que l'augmentation en diametre a lieu, ce Bourgeon s'éloigne de plus en plus de son point de depart ; mais à tel point qu'on l'examine, on aperçoit toujours une trace horizontale qui le lie à la moelle centrale. Ainsi, si, comme cela arrive quelquefois, on en trouve un sur un tronc d'un pied d'épaisseur, il est evident qu'il se sera écarté horizontalement de six pouces de son point de depart.”

This view of the subject approaches very near to that of the writer who now advances the doctrine in opposition to the views of Du Hamel and of Knight. Indeed they are both very similar to the view of it that was originally exhibited by Du Hamel himself. Having taken the trunk of a Lime-tree of about four or five inches in diameter, and about the middle of which there was a bud, and having cut it asunder obliquely in the direction of the bud, Du Hamel found that he could trace a ray of a whiter shade than the rest of the wood, extending from the pith to the bud. Hence he concluded that the bud is formed from the pith, and that the ray extending from the one to the other is with propriety denominated a medullary ray\*. This conclusion he afterwards abandoned ; but it is evident that it embraces the doctrine in question, the ground of which I have lately been induced to investigate with some care. I had been looking out, in the course of last summer, for a good subject of inspection, and found rather opportunely the stem of a Willow of about twelve or thirteen years old, which having been felled in the preceding winter or spring, was left lying on the ground, at its full length, and in rather a moist situation, and was in the

\* *Phys. des Arb.* liv. i. chap. iii.



month of August furnished with a number of young shoots protruding from its upper surface. These shoots were evidently formed posterior to the felling of the stem; and if the doctrine was true, they were of course traceable to the centre. Accordingly, having taken a number of transverse sections of the stem of the above Willow, I found that I could, in all cases, trace the path of the progress of the bud by means of the streak of parenchyma, extending from the centre, or nearly so, to the base of the shoot. There were many other streaks terminating, not in shoots, but in an emerging point between the alburnum and bark, which point contained, no doubt, a bud that might have been protruded into a shoot in some future year, if the tree had been allowed to continue growing.

There is a capability afforded no doubt in the annual protrusion of the bud into every additional layer of alburnum, that accounts well for the ready supply and regeneration of buds which almost all perennials furnish when lopped or accidentally mutilated. The fact is evidently hostile, as far as it goes, to the opinions of Du Hamel and of Knight, but it does not amount to a refutation of them: for that which is true of the Willow may not be true of every other tree. There are some trees in which no trace can be observed of the horizontal streak of parenchyma, from the origin of the shoot to the centre of the stem.

At the same time, the opinions of Du Hamel and of Knight, though strongly sanctioned, are not altogether indisputably established by the facts which they adduce in support of them. For it may be said that the result of their experiments would have been the same, whether we suppose buds to originate at the centre, or at the circumference. The buds had, indeed, gained the circumference; but whence they came, or by what route, there is no positive evidence to show. Yet this question  
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might have been decided by experiments made by the above or by other phytologists many years ago, if the experimenters had but instituted them with that particular view. Dr. Hope's experiment, for example, might have decided it. If any bud issued from the wood that was formed within the displaced and hollow bark of the Willow on which his experiment was made; then buds are, to say the least, occasionally generated and protruded into shoots without having been formed originally at the centre, and without having come horizontally to the circumference. So also in the experiments of Du Hamel and of Knight,—if any shoot issued from the new layers that were superinduced by vegetation over a decorticated portion of alburnum that had been left exposed to the action of the atmosphere, so long as to destroy its vitality, then were buds generated and brought to the circumference through a route different from that of the horizontal channel. Yet as no fact of this sort has hitherto been observed or recorded, as far as my reading or recollection goes, and as wounds by decortication or by excision are continually happening and again healing up, I began to think of looking out for examples, which, if they existed, it could not be very difficult to find.

On the 20th of September last I observed a shoot actually issuing from the lip formed over the section of a lopped branch of a Lime-tree. The tree grew in the garden of the Vicar of Ashford in Kent. In what did the bud originate? In the lip, or in the truncated branch? On the 25th I caused a portion of the trunk to be sawed off, so as to expose the origin of the bud as much as possible. The inspection of it was not decisive, as the lip was the growth of one year only, and the bud seemed rather to have come from the interior of the wood.

On the 30th of the same month, I observed in my walks an Elm-tree of about eight or nine inches in diameter, and twenty feet



feet in height, the stem of which had been wounded some years ago, by a portion of its bark having been stripped off to the extent of about ten inches in length by five or six in breadth, and at about a foot and a half from the ground. On the edges of this wound was formed a lip of new bark and wood, narrowing its extent, and forming a margin of between two and three inches in breadth. The surface of the lip was marked with ridges and furrows indicating a growth of at least three years ; and from the last and innermost ridge there had issued two shoots of several inches in length in the course of the preceding summer. Now it was to be inferred, that these shoots could not have originated in, nor proceeded from, the pith or central layers of wood, because the vitality of the outer layer had been destroyed by means of its exposure to the atmosphere, in consequence of the decortication of part of the trunk ; so that it could no longer afford a passage for a centrifugal bud. Nor could these shoots have made their way to the place of their protrusion, from any given point in the sound part of the layer that was partially decorticated ; because in that case the buds would have had to travel across the divergent layers, which there is no proof of their being able to do, or example of their having ever done.

On the 13th of October I caused a horizontal section, penetrating to a sufficient depth, to be made both above and below the shoots, and the portion between the sections to be extracted. The inspection of the extracted portion corroborated my inferences in every particular. The buds had no radiant nor radical connexion with the centre of the stem, as was evident from the intervening layer of dead wood, to which the bark and wood of the lip were indeed vegetably agglutinated, but not connected by a continuity of living growth. Beyond that layer the medullary rays began anew, and took a totally different direction. Hence it follows irresistibly, that the shoots in question originated merely  
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in the lip, and sprung from buds, which, if not formed by, were yet conveyed to, and deposited in, the alburnum through the medium or agency of the proper juice, without having ever been connected with the pith or central layers of the incipient stem, and without having been annually protruded towards the circumference through each successive layer of wood.

Thus the doctrine of Du Hamel and of Knight is established indisputably, at least to a certain degree, and corroborated by a new and irrefragable proof; whilst the deductions of the writer who combats it have been shown to possess less of the character of universality than we find to be claimed for them, and to rest upon an induction of particulars rather too limited in its extent. Particularly it has been shown by the above facts, that "an adventitious bud, or bud appearing on an old stem or branch," does not always "originate in a germ generated at the development of the stem or branch on which it appears," and that a plant may contain latent germs besides those which are annually carried outwards in a horizontal direction.

If it be said that the central origin of the bud, together with its horizontal protrusion, is the rule, the position will readily be admitted, at least with regard to the subjects already examined, and perhaps with regard to others also. Yet it is quite as important to know the exception, as to know the rule itself; because exceptions are the means which Nature has recourse to in extraordinary cases. It may be but seldom that buds are protruded in the way I have now stated, or that the shoots issuing from them are augmented into branches of any great importance. But the same thing may be said of buds issuing from the surface of a large trunk, even after having finished their horizontal course. They seldom attain to any great size, unless the stem is truncated, when the others would doubtless do the same; and it is those shoots only that are protruded in the first year



year of the stem's growth, before it has acquired anything of horizontal extent, that constitute the leading branches.

Still it may be said that the origin of the bud is not yet fully accounted for, as it is its path that has been traced and rendered visible rather than its source. If we are to trace buds to their earliest indications of existence, it will be necessary to go back to the seed. In many seeds the rudiments of buds may be discovered in the protuberance that is usually formed at the collar of the embryo plant\*, at first a simple vesicle; afterwards, as germination advances, an enlarged globule; at last, in the matured shoot, a distinctly visible body; one or more buds crowning the shoot, some protruding from its surface, and many, as it appears, imbedded in the alburnum. How have they been generated? and how dispersed or distributed through the plant? Either we must suppose that the embryo plant contains already in miniature all the buds to which it can ever possibly give development, arranged, as we must also suppose, in a determinate order, and waiting only the occurrence of such conditions as shall afford the nutriment necessary to vegetable growth, and give dispersion or distribution to the buds by the general expansion of the whole. Or we must suppose that the bud or buds already existing in the embryo plant have the power of generating new buds, which the plant has the power of propelling to their appointed stations.

The first hypothesis, which is that of Leibnitz, is encumbered with many difficulties, as embracing the doctrine of the involution of all future generations in the first individual of the species;—thus, baffling the powers of the most acute imagination, and explaining nothing after all. It is indeed so thoroughly enigmatical as to stand but very little chance of being ever generally adopted. Yet if we embrace, without modification, the

\* Keith's *Phys. Bot.* ii. 389.



doctrine of the writer, who discards the hypothesis of Du Hamel and of Knight, I cannot see how we are to do without it ; as he seems to acknowledge no movement of any individual bud beyond that which must arise from the general expansion of the whole shoot, excepting a horizontal movement. But if it has been shown that buds do occasionally issue from points on the surface of the stem, to which they could not possibly have come by any horizontal channel, then we shall be compelled to account for their appearance in some other way.

The second hypothesis is not without its difficulties, any more than the first ; but it accounts much better for the anomaly in question. The impenetrable veil which overhangs the subject of generation, whether animal or vegetable, whether seminal or by a bud, conceals for ever from the observation of man the commencement of those recondite and mysterious processes by which the operation is effected, and leaves us no resource beyond that of watching its future results, and forming our opinions by inference. Hence the hypotheses of Du Hamel and of Knight, by both of which we have the means of conveying buds to every new layer of wood in all imaginable cases, not excepting even the case that I have now presented to the notice of this Society ; and yet we need not confine ourselves to the precise terms or principle of either the one or the other. Du Hamel gives to the plant a profusion of what he calls pre-organized germs, but I do not recollect that he specifies their origin. Mr. Knight gives to the proper juice an unlimited capacity of forming and of dispersing buds,—which may be thought to be rather too gratuitous, particularly as his experiments do not so much prove that buds are formed by the proper juice, as that they are nourished by it. But if it is admitted that one bud has the capacity of generating others like itself, the difficulty is surmounted. Say that this process is effected by the bud or



buds lodged in the embryo plant, or protruding from the surface of the shoot, and the new formed bud, or rudiment of a bud, a minute, and insulated, and imperceptible globule or filament; there is nothing incredible in the supposition of its being carried upwards with the current of the ascending sap in its passage through the alburnum; or, of its entering even the plexus of the vessels of the inner bark, being again carried downwards with the current of the descending and proper juice, as well as ultimately deposited in a situation favourable to its future evolution. The necessity of accounting for the appearance of the bud and shoot that originated in the lip of the closing wound of the Elm-tree,—that is, in a new layer of alburnum that was spreading over the surface of an old and dead layer,—renders the adoption of this or of some such hypothesis indispensable. Not that the horizontal progression of the bud as a general rule is to be denied. The fact is established beyond a doubt. But that the exception to the rule must be accounted for also; and even upon the principle of the rule itself, I am not sure that the longitudinal progression of the bud may not be occasionally wanted, if it were but to bring buds up to the point of their horizontal protrusion.

If we admit the above process in the shoot of the first year, we shall have no difficulty in extending it to the shoots of future and succeeding years. The buds crowning the primary shoot or distributed over its surface, will evolve and develop their parts in the manner of the bud of the embryo plant; and the buds of future shoots, in the manner of those of the primary shoot; so that the growth of the primary shoot is an epitome of the growth of the whole plant; and that which illustrates the one will illustrate also the other. There may be error in our inferences: but if the microscopic observations, to which I have already alluded, are good for anything, we must believe that buds do actually ascend



ascend the stem either through the tubes of the medullary sheath, or through the tubes of the alburnum, or through both; and although botanists have hitherto had their doubts with regard to the accuracy of the observations in question, yet, after the novel and extraordinary views of Nature which have been opened up to us of late by a microscopical observer of undoubted ability and veracity, we must not be surprised at the wonders seen by others, nor discard their alleged facts without due examination.





Keith, Patrick. 1830. "On the Origin of Buds." *Transactions of the Linnean Society of London* 16, 421–433.

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