IV. On the Formation of the Bark of Trees. In a Letter from T. A. Knight, Esq. F. R. S. to the Right Honourable Sir Joseph Banks, K. B. P. R. S. &c.

Read February 19, 1807.

My DEAR SIR,

An extraordinary diversity of opinion appears to have prevailed among naturalists, respecting the production and subsequent state of the bark of trees.

According to the theory of Malpighi, the cortical substance, which is annually generated, derives its origin from the older bark; and the interior part of this new substance is annually transmuted into alburnum, or sap wood; whilst the exterior part, becoming dry and lifeless, forms the exterior covering, or cortex.

The opinions of Grew do not appear to differ much from those of Malpighi; but he conceives the interior bark to consist of two distinct substances, one of which becomes alburnum, whilst the other remains in the state of bark: he, however, supposes the insertments in the wood, the "utriculi" of Malpighi, and the "tissu cellulaire" of Du Hamel, to have originally existed in the bark.

HALES on the contrary contends, that the bark derives its existence from the alburnum, and that it does not undergo any subsequent transformation.

The discoveries of Du HAMEL have thrown much light

on the subject; but his experiments do not afford any conclusive result, and some of them may be adduced in support of either of the preceding hypotheses: and a modern writer (Mirbel*) has endeavoured to combine and reconcile, in some degree, the apparently discordant theories of Malpighi and Hales. He contends with Hales, that the alburnum gives existence to the new layer of bark; but that this bark subsequently changes into alburnum, though not precisely in the manner described by Malpighi.

So much difference of opinion, amongst men so capable of observing, sufficiently evinces the difficulty of the subject they endeavoured to investigate: and in a course of experiments, which has occupied more than twenty years, I have scarcely felt myself prepared, till the present time, even to give an opinion respecting the manner, in which the cortical substance is generated in the ordinary course of its growth; or reproduced, when that, which previously existed, has been taken off.

Du Hamel has shewn, that the bark of some species of trees is readily reproduced, when the decorticated surface of the alburnum is secluded from the air; and I have repeated similar experiments on the apple, the sycamore, and other trees, with the same result; I have also often observed a similar reproduction of bark on the surface of the alburnum of the Wych elm (Ulmus montana) in shady situations, when no covering whatever was applied. A glareous fluid, as Du Hamel has stated, exudes from the surface of the alburnum: this fluid appears to change into a pulpous unorganised mass, which subsequently becomes organised and cellular; and the

^{*} Traité d'Anatomie et de Physiologie vegetales

matter, which enters into the composition of this cellular substance, is evidently derived from the alburnum.

These facts are therefore extremely favourable to the theory of HALES; but other facts may be adduced which are scarcely consistent with that theory.

The internal surface of pieces of bark, when detached from contact with the alburnum, provided they remain united to the tree at their upper ends, much more readily generate a new bark, than the alburnum does under similar circumstances: a similar fluid exudes from the surfaces of both, and the same phenomena are observable in both cases. The cellular substance, however, which is thus generated, though it presents every external appearance of a perfect bark, is internally very imperfectly organized; and the vessels which contain the true sap in the bark, are still wanting; and I have found, that these may be made, by appropriate management, to traverse the new cellular substance in almost any direction. When I cut off all communication above, and on one side, between the old bark and that substance, I observed, that the vessels proceeded across it, from the old bark on the other side, taking always in a greater or less degree an inclination downwards; and when the cellular substance remained united to the bark at its upper end only, the vessels descended nearly perpendicularly down it; but they did not readily ascend into it, when it was connected with the bark at its lower extremity only; the result of similar experiments, when made on different species of trees, was, however, subject to some variations.

Pieces of bark of the walnut-tree, which were two inches MDCCCVII.

broad, and four long, having been detached from contact with the alburnum, except at their upper ends, and covered with a plaister composed of bees-wax and turpentine, in some instances, and with clay only in others, readily generated the cellular substance of a new bark; and between that and the old detached bark, very nearly as much alburnum was deposited as in other parts of the tree, where the bark retained its natural position; which, I think, affords very decisive evidence of the descent of the sap through the bark. Similar pieces of bark, under the same mode of treatment, but united to the tree at their lower ends only, did not long remain alive, except at their lower extremities; and there a very little alburnum only was generated. Other pieces of bark of the same dimensions, which were laterally united to the tree, continued alive almost to their extremities; and a considerable portion of alburnum was generated, particularly near their lower edges; the sap appearing in its passage across the bark to have been given a considerable inclination downwards: probably owing to an arrangement in the organization of the bark, that I have noticed in a former memoir,* which renders it better calculated to transmit the sap towards the roots than in any other direction.

I have in very few instances been able to make the walnuttree reproduce its bark from the alburnum, though under the same management I rarely failed to succeed with the sycamore and apple-tree. Pieces of the bark of the apple-tree will also live, and generate a small portion of alburnum, though only attached to the tree at their lower extremities;

Philosophical Transactions of 1804.

probably owing to a small part of the true sap being carried upwards by capillary attraction, when the proper action of the cortical vessels is necessarily suspended.

The preceding experiments, and the authority of Du HAMEL, having perfectly satisfied me, that both the alburnum and bark of trees are capable of generating a new bark, or at least of transmitting a fluid capable of generating a cellular substance, to which the bark in its more perfectly organized state owes its existence, my attention was directed to discover the sources from which this fluid is derived. Both the bark and the alburnum of trees are composed principally of two substances; one of which consists of long tubes, and the other is cellular; and the cellular substance of the bark is in contact with the similar substance in the alburnum, and through these I have long suspected the true sap to pass from the vessels of the bark to those of the alburnum.* The intricate mixture of the cellular and vascular substances long baffled my endeavours to discover from which of them, in the preceding cases, the sap, and consequently the new bark, proceeded; but I was ultimately successful.

The cellular substance, both in the alburnum and bark of old pollard oaks, often exists in masses of near a line in width, and this organization was peculiarly favourable to my purpose. I therefore repeated on the trunks of trees of this kind, experiments similar to those above-mentioned which were made on the walnut-tree.

Apparently owing to the small quantity of sap, which the old pollard trees contained, their bark was very imperfectly reproduced; but I observed a fluid to ouze from the cellular

[•] Phil. Trans. 1805, page 14.

substance, both of the bark and alburnum; and on the surface of these substances alone, in many instances, the new bark was reproduced in small detached pieces.

I have endeavoured to prove in former communications,* that the true sap of trees acquires those properties which distinguish it from the fluid recently absorbed, by circulating through the leaf; and that it descends down the bark, where part of it is employed in generating the new substances annually added to the tree; and that the remainder, not thus expended, passes into the alburnum, and there joins the ascending current of sap. The cellular substance, both of the bark and alburnum, has been proved, in the preceding experiments, to be capable of affording the sap a passage through it; and therefore it appears not very improbable, that it executes an office similar to that of the anastomosing vessels of the animal economy, when the cellular surfaces of the bark and alburnum are in contact with each other; and, when detached, it may be inferred, that the passing fluid will exude from both surfaces: because almost all the vessels of trees appear to be capable of an inverted action in giving motion to the fluids which they carry.

As the power of generating a new bark appeared in the preceding cases to exist alike in the sap of the bark and of the alburnum, I was anxious to discover how far the fluid, which ascends through the central vessels of the succulent annual shoot, is endued with similar powers. Having therefore made two circular incisions through the bark, round the stems of several annual shoots of the vine, as early in the summer as the alburnum within them had acquired sufficient

^{*} Phil, Trans. 1801, 1805, and 1806.

maturity to perform its office of carrying up the sap, I took off the bark between these incisions; and I abraded the surface of the alburnum to prevent a reproduction of it. The alburnum in the decorticated spaces soon became externally dry and lifeless; and several incisions were then made longitudinally through it. The incisions commenced a little above, and extended below the decorticated spaces, so that, if the sap of the central vessels generated a cellular substance (as I concluded it would), that substance might come into contact and form a union with the substance of the same kind emitted by the bark above and below.

The experiment succeeded perfectly, and the cellular substances generated by the central vessels, and the bark, soon united, and a perfect vascular bark was subsequently formed beneath the alburnum, and appeared perfectly to execute the office of that which had been taken off; the medulla appeared to be wholly inactive.

I have already observed, that the vessels, which were generated in the cellular substance on the surface of the alburnum of the sycamore and the apple-tree, traversed that substance in almost every direction; and the same thing appears to occur beneath the old bark, when united to the alburnum. For having attentively examined through every part of the spring and summer, the formation of the internal bark, and alburnous layer beneath it, round the bases of regenerated buds, which I had made to spring from smooth spaces on the roots and stems of trees, I found every appearance perfectly consistent with the preceding observations. A single shoot only was suffered to spring from each root and stem, and from the base of this, in every instance the cortical vessels

dispersed themselves in different directions. Some descended perpendicularly downwards, whilst others diverged on each side, round the alburnum, with more or less inclination downwards, and met on the opposite side of it. The same pulpous and cellular substance appeared to cover the surfaces of the bark and alburnum, when in contact with each other, as when detached; and through this substance the ramifications of the vessels of the new bark extended themselves, appearing to receive their direction from the fluid sap which descended from the bark of the young shoots, and not to be, in any degree, influenced in their course by the direction taken by the cortical and alburnous vessels of the preceding year.

Whenever the vessels of the bark, which proceeded from different points, met each other, an interwoven texture was produced, and the alburnum beneath acquired a similar organisation: and the same thing occurs, and is productive of very important effects, in the ordinary course of the growth of trees. The bark of the principal stem, and of every lateral branch, contains very numerous vessels, which are charged with the descending true sap; and at the juncture of the lateral branch with the stem, these vessels meet each other. A kind of pedestal of alburnum, the texture of which is much interwoven, is in consequence formed round the base of the lateral branch; which thus becomes firmly united to the tree. This pedestal, though apparently a part of the branch, derives a large portion of the matter, annually added to it, from the cortical vessels of the principal stem; and thence, in the event of the death of the lateral branch, it always continues to live. But it not unfrequently happens, that a lateral branch forms a very acute angle with the principal stem, and, in this case, the bark between them becomes compressed and inactive; no pedestal is in consequence formed, and the attachment of such a branch to the stem becomes extremely feeble and insecure.* Instead of the reproduced buds of the preceding experiment, buds were inserted in the foregoing summer, or attached by grafting in the spring; and, when these succeeded, though they were in many instances taken from trees of different species, and even of different genera, no sensible difference existed in the vessels, which appeared to diverge into the bark of the stock, from these buds and from those reproduced in the preceding experiments.

It appears, therefore, probable, that a pulpous organisable mass first derives its matter either from the bark, or the alburnum; and that this matter subsequently forms the new layer of bark; for, if the vessels had proceeded, as radicles,† from the inserted buds, or grafts, such vessels would have been, in some degree, different from the natural vessels of the bark of the stocks; and it does not appear probable, even without referring to the preceding facts, that vessels should be extended, in a few days, by parts successively added to their

[•] The advantages, which may be obtained by pruning timber trees judiciously, appear to be very little known. I have endeavoured to ascertain the practicability of giving to trees such forms as will render their timber more advantageously convertible to naval or other purposes. The success of the experiments, on small trees has been complete, and the results perfectly consistent, in every case, with the theory I have endeavoured to support in former memoirs; and I am confident, that by appropriate management, the trunks and branches of growing trees may be moulded into the various forms best adapted to the use of the ship-builder; and that the growth of the trees may at the same time be rendered considerably more rapid, without any expense or temporary loss to the proprietor.

[†] Darwin's Phytologia.

extremities, from the leaves to the extremities of the roots; which are, in many instances, more than two hundred feet distant from each other. I am, therefore, inclined to believe, that, as the preceding facts seem to indicate, the matter, which composes the new bark, acquires an organisation calculated to transmit the true sap towards the roots, as that fluid progressively descends from the leaves in the spring; but whether the matter, which enters into the composition of the new bark, be derived from the bark or the alburnum, in the ordinary course of the growth of the tree, it will be extremely difficult to ascertain.

It is, however, no difficult task to prove, that the bark does not, in all cases, spring from the alburnum; for many cases may be adduced in which it is always generated previously to the existence of the alburnum beneath it: but none, I believe, in which the external surface of the alburnum exists previously to the bark in contact with it, except when the cortical substance has been taken off, as in the preceding experiments. In the radicle of germinating seeds, the cortical vessels elongate, and new portions of bark are successively added to their points, many days before any alburnous substance is generated in them; and in the succulent annual shoot the formation of the bark long precedes that of the alburnum. In the radicle the sap appears also evidently to descend* through the cortical vessels,† and in the succulent annual shoot it as evidently passes up through the central

^{*} Phil. Trans. 1805 and 1806.

[†] I wish it to be understood, that I exclude in these remarks, and in those contained in my former Memoirs, all trees of the palm kind, with the organisation of which I am almost wholly unacquainted.

vessels,* which surround the medulla. In both cases a cellular substance, similar to that which was generated in the preceding experiments, is first formed, and this cellular substance in the same manner subsequently becomes vascular; whence it appears, that the true sap, or blood of the plant, produces similar effects, and passes through similar stages of organisation, when it flows from different sources, and that the power of generating a new bark, properly speaking, belongs neither to the bark nor alburnum, but to a fluid, which pervades alike the vessels of both.

I shall, therefore, not attempt to decide on the merits of the theory of Malpighi, or of Hales, respecting the reproduction of the interior bark; but I cannot by any means admit the hypothesis of Malpighi and other naturalists, relative to the transmutation of bark into alburnum; and I propose to state my reasons for rejecting that hypothesis, in the next communication I have the honour to address to you.

I am, my dear Sir,

Your much obliged obedient Servant,

T. A. KNIGHT.

Elton, Dec. 18, 1806.

^{*} Phil. Trans. 1805. MIRBEL has called the tubes, which I call the central vessels, the "tissu tubulaire" of the medulla.