**The Structure and Functions of the Intestinal Villi**

**As Presented to the University of Edinburgh and the Anatomical Museum**

**Compiled by Michael T. Tracy**

In the early 19th century, significant advancements were made in understanding human physiology through meticulous anatomical observations. Among these contributions, John Goodsir's work on the intestinal villi stands out for its detailed examination of the structures responsible for nutrient absorption in the small intestine. Delivered as a lecture at the Royal College of Surgeons during the summer of 1842 and winter of 1842-43, Goodsir's findings illuminated the intricate processes that underlie digestion and absorption, offering a comprehensive view of the microscopic anatomy and function of the intestinal villi.

Goodsir began his lecture by referencing earlier observations made by Mr. Cruikshank and Dr. William Hunter, who noted the existence of lacteals and their openings in the intestines. Goodsir examined these claims using improved methods and instruments, leading to several key observations. He described the villi as possessing bulbous, opaque extremities filled with vesicles of various sizes. These vesicles, when viewed under different microscopic magnifications, revealed their structure and function in nutrient absorption. Goodsir observed that the villi's extremities were crowded with spherical vesicles, which varied in size and had an opalescent, milky appearance.

Through his experiments, Goodsir noted that the villi, when engorged with chyle, lacked their usual epithelial covering. This led him to investigate further by feeding a dog and examining its intestines post-mortem. He found the lacteals full of milky chyme, with the gut's cavity containing a mix of chyme and a brownish fluid. The villi were turgid and appeared to be in a state of erection, covered by a smooth membrane that connected with the follicles of Lieberkuhn.

Goodsir detailed the structure of the villi, noting the presence of lacteals and blood vessels. He described the vesicles at the villi's extremities as being similar to the spongiole of a plant's root, suggesting an analogous function in absorption. The lacteals within the villi did not directly connect to these vesicles, which instead seemed to absorb and then release their contents into the villi's substance. This process mirrored the secretion and absorption dynamics observed in other cells throughout the body.

Goodsir proposed that the primitive cell, central to both nutrition and secretion, plays a crucial role in absorption. He emphasised that these cells selectively absorb nutrients necessary for building tissues or producing secretions, and this absorption is a specific and directed process. He challenged existing notions by asserting that absorption and secretion are not opposite forces but rather stages of the same process.

During digestion, Goodsir explained, the increased blood flow to the gut causes the villi to shed their protective epithelium, exposing them for absorption. The villi, now coated with a mix of chyme and epithelial cells, begin their function. The vesicles within the villi draw materials from the blood and the gut's contents, growing until they release their absorbed nutrients into the villi's structure. These nutrients are then transported via the lacteals.

Goodsir also compared the villi's function to the processes in plant roots, suggesting that both rely on growth and solution absorption mechanisms. He highlighted that in both plants and animals, cells are the primary agents of absorption, growth, and nutrient assimilation. This insight bridged botanical and zoological physiology, underscoring the universality of cellular functions in nutrient uptake.

The following is the lecture viz.

"The Structure And Functions Of The Intestinal Villi.

Mr. Cruikshank, in treating of the orifices of the Lacteals and Lymphatics,[1] states that he and Dr. William Hunter observed the openings by which the lacteals communicated with the cavity of the gut in portions of the intestine of a woman who died after eating a hearty supper. The two preparations of the intestine on which these anatomists made their observations, came into the possession of the College of Surgeons in Edinburgh, as part of the collection of the late Sir Charles Bell.

I removed one of the villi from Mr. Cruikshank's preparation, and had no difficulty in recognising what had been described and figured by the original owner of the preparation. With a low power the extremity of the villus appeared bulbous and opaque. With a higher power I observed that this opacity was due to the existence, at the extremity of the villus, of a number of vesicles of different sizes. The larger vesicles were pretty uniform in size, and about twenty in number. The smaller were of different sizes, and more numerous, and appeared gradually to pass into the granular texture of the attached extremity of the villus. No blood-vessels could be detected, but along the neck of the villus distinct traces of two or more opaque lacteals were visible. The vesicles and the lacteals, when viewed by transmitted light, were of a light brown colour; but when examined as opaque objects, they stood out of a dead white appearance, contrasting strongly with the semi-transparency of the surrounding texture. Repeated examinations of these preparations satisfied me that Dr. William Hunter and Mr. Cruikshank were quite correct in describing and figuring radiating lacteals within the villi, but that they were led into error in describing those vessels as opening on the free surface of the gut, partly by imperfect instruments and methods of observation, partly by the general prejudice of the period in favour of absorbent orifices. I also satisfied myself of what appeared highly probable from the commencement of the observations, that the villi, when turgid with chyle, were destitute of their ordinary epithelial covering.[2] This circumstance I could not avoid connecting with the fact of the stomach throwing off its epithelia during the process of digestion. I determined, therefore, to investigate the process of absorption of chyle in fresh subjects, as the facts exhibited in Mr. Cruikshank's preparations indicated the probable existence of complicated processes going on in villi during digestion. The analogy of the vesicular bulbous extremity of the villus, to the spongiole of the vegetable, forced itself upon me, and the existence of milky chyle, within closed cells, led me to anticipate an explanation of some of the phenomena of digestion.

A dog was fed. Three hours afterwards he was killed. The lacteals were turgid, and the gut was found to be full of milky chyme, with an admixture of thin brownish fluid of a bilious appearance. The milky matter was situated principally towards the mucous membrane; the brown fluid occupied the cavity of the gut.

The white matter consisted of a transparent fluid, with a few oil-globules and numerous epithelia.

Some of the epithelia I recognised as those which cover the villi. They were pointed at their attached extremities, flat at the other. Many of them were single, others were united in bundles, adhering principally by their flat or free extremities, as if a fine membrane passed over and connected the edges of their extreme surfaces. Occasionally these epithelia presented a distinct nucleus; but generally, and whether single or in bundles, they exhibited in their interior a group or mass of oil-like globules, which, when viewed as opaque objects, had a peculiar semi-opaque or opalescent appearance.[3] Others of the epithelia, contained in the chyme, were prismatic, single, or in columns. They were the lining epithelia of the follicles of Lieberkuhn, and presented the usual nuclei.

The mucous membrane displayed the villi turgid, as if in a state of erection, and as I had anticipated, naked or destitute of epithelia, except at their bases, where a few still adhered. Each villus was covered by a very fine smooth membrane, which, from its free bulbous extremity, passed on to its sides, and became continuous with the germinal membrane of the follicles of Lieberkuhn. These villi, when removed from the mucous membrane, and examined with a low power, were semi-transparent, except at their free or bulbous extremities, which appeared both by direct or transmitted light white and opaque. Under higher powers the summit of the villus, somewhat flattened, was observed to be crowded, immediately under the membrane before mentioned, with a number of perfectly spherical vesicles. These vesicles varied in size from 1000 to less than 2000 of an inch. The matter in their interior had an opalescent milky appearance. Towards the body of the villus, on the edges of the vesicular mass, minute granular or oily particles were situated in great numbers, and gradually passed into the granular texture of the substance of the villus.

The trunks of two lacteals could be easily traced up the centre of the villus, and as they approached the vesicular mass they subdivided and looped. In no instance could one of these lacteals be traced to any of the spherical vesicles, nor could any direct communication between the structures be detected.[4] The blood-vessels and capillaries, with their columns of tawny blood disks, could be seen passing in radiating lines and in loops across the villus, immediately under the fine membrane already mentioned. This membrane, perceptible on the body and neck of the villus only by the smooth surface it presented, was most distinctly traced at the free extremity of the villus, as it passed from the surface of one vesicle on to that of another.[5] The vesicles, pushing the membrane forward, and grouped together in masses on its attached surface, gave the extremity of the villus the appearance of a mulberry. When viewed on a dark ground as an opaque object, the point directed to the light, a villus in this condition is remarkably beautiful, the play of the light on the surface of the highly-refractive semi-opaque and opalescent vesicles giving them the appearance of a group of pearls.

In villi turgid with chyle, which have been kept for some time in spirits, the contents of the vesicles are opaque, the albumen having become coagulated.

To understand the part which the vesicles of the villus play in digestion, it is necessary to be aware of certain of the functions of the cell, with which physiologists are yet unacquainted. Not only are these bodies the germs of all the tissues, as determined by the labours of Schleiden and Schwann, but are also the immediate agents of secretion. A primitive cell absorbs from the blood in the capillaries the matters necessary to enable it to form, in one set of instances, nerve, muscle, bone, if nutrition be its function; milk, bile, urine, in another set of instances, if secretion be the duty assigned to it. The only difference between the two functions being, that in the first, the cell dissolves and disappears among the textures, after having performed its part; in the other, it dissolves, disappears, and throws out its contents on a free surface. Now, it will be perceived, that before a cell can perform its functions as a nutritive cell, or as a secreting cell, it must have acted as an absorbing cell. This absorption, too, must necessarily be of a peculiar and specific nature. It is in virtue of it that the nutritive cell selects and absorbs from the liquor sanguinis those parts of the latter necessary for building up the peculiar texture of which the cell is the germ. It is in virtue of this peculiar force that the secreting cell not only selects and absorbs, but also in some instances elaborates, from the same common material, the particular secretion of which it is the immediate organ. And it is by the same force that the cell becomes the immediate agent of absorption in certain morbid processes.

'Absorption,'[6] says Professor Muller, 'seems to depend on an attraction, the nature of which is at present unknown, but of which the very counterpart, as it were, takes place in secretion; the fluids altered by the secreting action being impelled towards the free surface only of the secreting membranes, and then pressed onwards by the successive portions of fluid secreted. In many organs, for instance in those invested with mucous membranes absorption by the lymphatics and secretion by the secreting organs, are going on at the same time on the same surface.' It appears, however, from what is stated in the present chapter, and in the *Trans. Roy. Soc. Edin*.[7] that Professor Muller, and indeed all the physiologists hitherto, have been in error in supposing the forces of secretion and absorption as of different and opposite tendencies the one attractive, the other repulsive. They are both attractive, absorption being but the first stage in the process of secretion. Secretion, in fact, differs from absorption, not physiologically, but morphologically.

What has been stated in the present paper explains also how, in the mucous membranes, 'absorption by lymphatics and secretion by secreting organs are going on at the same time on the same surface.' There is no physiological mystery in this. It depends on a morphological circumstance. The absorbing chyle-cells are on the attached surface of the germinal membrane the secreting epithelia are on its free surface; the former are interstitial cells the latter peripheral; the former cast their contents into the substance of the organism the latter into the surrounding medium.

The primitive cell, then, is primarily an organ of specific absorption, and secondarily of nutrition, growth, and secretion.

As the chyme begins to pass along the small intestine, an increased quantity of blood circulates in the capillaries of the gut. In consequence of this increased flow of blood, or from some other cause with which I am not yet acquainted, the internal surface of the gut throws off its epithelium, which is intermixed with the chyme in the cavity of the gut. The cast-off epithelium is of two kinds that which covers the villi, and which, from the duty it performs, may be named protective epithelium, and that which lines the follicles, and is endowed with secreting functions. The same action, then, which, in removing the protective epithelia from the villi, prepares the latter for their peculiar function of absorption, throws out the secreting epithelia from the follicles, and thus conduces towards the performance of the function of these follicles.

The villi, being now turgid with blood, erected, and naked, are covered or coated by the whitish-grey matter already described. This matter consists of chyme, of cast-off epithelia of the villi, and of the secreting epithelia of the follicles. The function of the villi now commences. The minute vesicles which are interspersed among the terminal loops of the lacteals of the villus, increase in size by drawing materials from the blood through the coats of the capillary vessels, which ramify at this spot in great abundance. While this increase in their capacity is in progress, the growing vesicles are continually exerting their absorbing function, and draw into their cavities that portion of the chyme in the gut necessary to supply materials for the chyle. When the vesicles respectively attain in succession their specific size, they burst or dissolve, their contents being cast into the texture of the villus, as in the case of any other species of interstitial cell.

The debris, and the contents of the dissolved chyle-cells, as well as the other matters which have already subserved the nutrition of the villus, pass into the looped network of lacteals, which, like other lymphatics, are continually employed in this peculiar function. As long as the cavity of the gut contains chyme, the vesicles of the terminal extremity of the villi continue to develope, to absorb chyle, and to burst, and their remains and contents to be removed along the lacteals.

When the gut contains no more chyme, the flow of blood to the mucous membrane diminishes, the development of new vesicles ceases, the lacteals empty themselves, and the villi become flaccid.

The function of the villi now ceases till they are again roused into action by another flow of chyme along the gut.

During the intervals of absorption, it becomes necessary to protect the delicate villi from the matters contained in the bowel. They had thrown off their protective epithelium when required to perform their functions, just as the stomach had done to afford gastric juice, and the intestinal follicles to supply their peculiar secretions. In the intervals of digestion the epithelium is rapidly reproduced.

The germinal membrane, which, as I have stated, not only forms the outer membrane of the follicles, under the epithelia, but also the underlying membrane of the villi, contains in its substance germinal centres of an oval form, situated at pretty regular distances. From these the epithelium appears to be reproduced during the intervals of absorption, as stated in the first chapter.

During this process of development, the primary membrane appears to split into two laminae, the epithelia passing out from its nuclei between these. This would account for the epithelia, particularly the prismatic and conical, adhering by their free extremities.

Such are the processes which would appear to take place in the villi of the intestinal tube during digestion and absorption. When considered in relation to the functions of digestion and absorption of chyle, these processes are highly interesting.

The labours of the chemist have now so far simplified the theory of digestion, as to deprive the stomach of the vitalising or organising powers so long ascribed to it.

Every step in this chemico-physiological inquiry leads to the conclusion, that the changes which the food undergoes while in the cavity of the gut are entirely of a chemical nature.

If we continue, then, to apply the term digestion to that series of processes by which the aliment is assimilated to the matter of which the body is composed, we must divide the series into two groups. The first group will include all those changes which take place within the digestive tube, but exterior to the organism. The second will include those which present themselves after the alimentary matter is taken up into the animal body, and becomes buried in its substance. The first group of processes are mechanical and chemical in their nature. They may be considered in a great measure as peculiar to the animal, although even vegetables throw out from their roots matter which, acting on some of the materials of the surrounding soil, prepares these for absorption.

The second group of processes is common to animals and vegetables. In these, for the first time, are alimentary substances taken into the tissues of the organism. In animals, as in plants, as I have already pointed out, these alimentary substances are drawn by a peculiar force into the interior of the cells, after escaping from which they pass on by the absorbent system. The chemist has not yet informed us of the change which the matter has undergone during its passage from the cavity of the gut, or from the soil, into the afferent lacteals and the sap-vessels; but if in vegetables, as in animals, this matter passes into the cavities of the cells of the spongiole before it passes on to the sap-vessels, then it is highly probable that the organising and vitalising part of the function of digestion commences in the cells of the spongiole and of the extremity of the villus.

The extremity of the fibril of the root of a plant elongates by the cells added to its tissue by the germinating spongiole. The spongiole is, therefore, an active organ of growth as well as of absorption. It is to the fibril of the root, what I have denominated in the animal tissues the nutritive centre. I conceive it to be probable, therefore, although as to this I have made no observations, that absorption by, and elongation of, the fibril of the root, vary inversely as one another. This supposition is founded on the assumption that the cells of the spongiole do not absorb by transmission, but by growth and solution.

In the villi of the intestines of animals, my own observations lead me to believe that absorption by growth and solution is the process which actually takes place.

The vesicular extremity, like the spongiole of the root-fibril, is the primitive nutritive centre of the villus. The villus originates in a cell. During the development of the villus, this spot or cell was employed only in procuring materials for the growth of the organ. In the perfect animal the formative function of the spot ceases; its action becomes periodical, active during digestion, at rest during the intervals of that process. The same function is performed, the same force is in action, and the same organ, the cell, is provided for absorption of alimentary matters in the embryo and in the adult, in the plant and in the animal. The spongioles of the root, the vesicles of the villus, the last layer of cells on the internal membrane of the included yelk, or the cells which cover the vasa lutea of the dependent yelk, and the cells which cover the tufts of the placenta, are the parts of the organism in which the alimentary matters first form a part of that organism, and undergo the first steps of the organising process."[8]

John Goodsir's lecture on the intestinal villi provided groundbreaking insights into the microscopic anatomy and physiology of nutrient absorption.  His detailed observations and comparisons with plant structures offered a new understanding of how the body assimilates nutrients, challenging and refining existing theories.  Goodsir's work not only advanced the field of digestive physiology but also emphasised the critical role of cells in the processes of absorption and secretion.  His contributions laid a foundation for future research in both human and comparative physiology, highlighting the interconnectedness of life processes across different organisms.

[1] William Cruikshank, *The Anatomy of the Absorbing Vessels of the Human Body*, 2d ed. 1790, page 56.

[2] This opinion was subsequently abandoned by the author. (Eds.)

[3] Is this appearance due to a partial absorption of chyle by these protective epithelia?

[4] See Gulliver's translation of Gerber's *General Anatomy*, pp. 272 and 273.

[5] Mr. Bowman, in the article "Mucous Membrane," *Cyclopaedia of Anatomy*, does not admit this portion of the membrane. It certainly cannot be detached as a separate membrane.

[6] Muller's *Physiology*, page 30 Baly's Translation.

[7] *Trans. Royal Society, Edin*. 1842, "On the Secreting Structure, and Laws of its Function." See also No. XXV. of this volume.

[8] Turner, William (ed.) and Lonsdale, Henry (contrib.). *The Anatomical Memoirs Of John Goodsir F.R.S. Late Professor Of Anatomy In The University Of Edinburgh, Volume II* (Edinburgh: Adam and Charles Black, 1868): 393-402.