are of considerable potential importance in certain industrial applications of ion exchange. One exhibit showed a chelating resin being used for reducing the copper content of tap water from 1 p.p.m. to less than 0·05 p.p.m. Other ion-exchange materials shown included a range of resins containing ion-exchange groups at the surface only.

## RUMINANT DIGESTION

A DISCUSSION on "Ruminant Digestion" took place on September 8 at a joint session of Section I (Physiology) and Section M (Agriculture) of the British Association, during its meeting in Liverpool.

The opening speaker, Mr. A. G. Singleton (University of Liverpool), discussed the significance of the rate of passage of food through the ruminant stomach, and some of the factors controlling it. The efficiency of the ruminant as a cellulose digester depends mainly on the delaying power of the rumen, which determines the time available for cellulose digestion to occur. If the contents of the four stomach compartments are examined in an animal killed soon after feeding, the rumen and reticulum are found to contain pieces of hay or other food of a relatively large size, the omasum always contains very finely divided particles in a relatively dry state, and the abomasum contains particles of about the same size suspended in a more fluid medium. It seems either that particles do not leave the rumen and reticulum until they have attained a certain smallness of size, or that the omasum reduces their size by a grinding action. Rumination and bacterial action tend to reduce particle size in the rumen. There is little evidence of any triturating activity of the omasum; the dryness of its contents could be due to a squeezing action, but it seems more likely that it is produced by water absorption. There is some evidence that the reticulo-omasal orifice has a valve-like action, and the omasum may control the flow of contents from the reticulum to the abomasum.

The feeding of hay or of straw which has been chopped or ground reduces its digestibility, a fact which was assumed to be due to an increase in the rate of passage of the feed. Balch (1950)[1], however, found that when ground hay was fed with normal hay it passed through the rumen more rapidly; but when the whole ration was ground, it remained in the rumen for an abnormally long period, and fibre was less completely digested. The reason for this is unknown, but the shorter time spent in ruminating, which is known to occur when the ration is ground, may be a contributing factor. This would reduce the amount of salivation, and it is known that an increase in the dry-matter/water ratio reduces the rate of cellulose breakdown.

It has been shown that the composition of duodenal contents influences the motility of rumen, reticulum and abomasum. Acid, protein and fat introduced into the duodenum inhibit the movements of these three compartments. Distension of the duodenum and abomasum also inhibits the movements of other compartments. It appears that chemical and physical factors may exert an important influence on the emptying of the stomach, in addition to the factor of particle size.

Mr. Singleton then described an electromagnetic method which is being used for continuously recording flow through the duodenum, and with which the factors affecting the emptying of the stomach are being investigated.

Dr. R. S. Comline (University of Cambridge) spoke on the nervous control of the ruminant stomachs. A strip of reticulum, attached to its blood and nerve supply, contracts in response to stimulation of vagus, right splanchnic nerve (with the right adrenal removed), left thoracic sympathetic chain, and the intravenous injection of adrenaline. The vagal effects are stronger than the sympathetic and are abolished by atropine. The sympathetic effects are unaffected by atropine, but are prevented by sympatholytic drugs, such as 933 *F.*, and by vagal stimulation. In chronic experiments, ruminants are unable to survive double vagotomy, which abolishes the normal propulsive motility, whereas the sectioning of both splanchnic nerves is without obvious effect.

In decerebrate calves and lambs, the œsophageal groove closes in response to water flowing over the pharynx, or to stimulation of the cut superior laryngeal nerve, which could also produce reflex swallowing. The reflexes of groove-closure and swallowing are closely integrated, but the two responses are affected differently by different stimuli. Reflex groove contractions can be inhibited by stimulation of the abomasal branch of the vagus. In decerebrate adult animals, reflex contractions of the reticulum could be invoked by stimulating the central ends of the abomasal, reticulo-omasal and reticular branches of the ventral vagus. Stimulation of the hypothalamus can produce movements in the alimentary canal, and even rumination.

Dr. Comline then criticized the tendency to call a particular part of the ruminant stomach a pacemaker. The stomach movements are not myogenic, as are those of the heart; they disappear when all extrinsic nerves are cut. A more profitable analogy, he said, is with the control of respiration, where a central rhythm is modified by afferent stimuli.

Dr. A. T. Philipson (Rowett Research Institute) contributed a paper on absorption from the rumen of the sheep. The rumen, reticulum and omasum are lined by stratified squamous epithelium, but the layer of keratinized cells is much thinner than in skin. The finding that the concentration of short-chain fatty acids is about 7–10 times greater in the rumen than in the abomasum suggests that absorption takes place, and this has been proved by showing the presence of fatty acids in significant concentrations in the blood leaving the rumen. Many investigations have been made on the rates of absorption of short-chain fatty acids, and it is agreed that absorption is more rapid when the $p$H is acidic than when it is neutral or just over $p$H 7, and that an acidic $p$H has a greater effect with propionic than acetic acid, and with $n$-butyric than propionic acid.

A comparison of the fatty acids in the rumen with those in blood leaving the rumen does not agree with these findings. It is found that the proportions of fatty acids in blood and rumen are similar, except that less butyric acid is present in blood. This led to an investigation of the metabolism of these acids by the rumen wall, which showed that considerable losses of butyrate occur, while losses of acetate are small. Metabolism of propionate is increased by the presence of carbon dioxide. The discrepancy is explained by the fact that about half the butyrate absorbed enters the blood stream, the rest being metabolized, while a little less than one-third of the propionate disappears. The acetate losses are likely to be less than 5 per cent of the total. It is probable that the rates of absorption of these acids are related to their metabolism by the epithelium, but the evidence is meagre. Fluoroacetate inhibits their absorption, but not differentially; monoiodoacetate has no effect on the rates of absorption. Phosphorylating mechanisms, therefore, do not seem to be concerned.

With acetate it is possible to study absorption from very weak solutions, as it is not metabolized to any great extent. It is found that absorption is proportionally more efficient for lower than for higher concentrations. A possible explanation is that a mechanism exists for transporting acetate across the epithelium, but as the concentration in rumen rises the mechanism becomes saturated and any further transport is by the slower process of physical diffusion.

Pennington has shown that rumen epithelium *in vitro* can form ketone bodies from butyrate. The oxygen consumption of the epithelium is considerable, even when no fatty acids are present in the medium. Glucose and butyrate increase oxygen consumption, but acetate does not. Propionate increases oxygen consumption only when carbon dioxide is present. Fixation of carbon dioxide occurs during the metabolism of propionate, and at least part of the propionate disappears via the tricarboxylic cycle, for succinate, an intermediary, increases when the cycle is arrested by the presence of malonate. The epithelium shares the unusual ability to form ketone bodies with liver and kidney. Another product of microbial activity is ammonia, and this is absorbed in substantial quantities, 0·3–0·4 gm. ammonia–nitrogen/hr. from concentrations of 50 mgm. ammonia–nitrogen/100 ml.

The removal of end-products is necessary if a reasonably constant environment is to be maintained for the bacteria, and in this respect hydrogen-ion concentration is important. Saliva provides a buffer; but the permeability of the rumen to ions in solution is also important. Any solution in the rumen tends to change to a *p*H of 7·2–7·4, whether acid or alkaline originally, and this is due to a differential passage of ions across the epithelium in both directions. When fatty-acid anions are absorbed, a proportionate amount of bicarbonate enters the rumen. In the rumen liquor of normal sheep potassium and inorganic phosphorus are in a much higher concentration than in plasma; magnesium and calcium are also in excess, while sodium and chloride are lower, so that concentration gradients are not the only factors involved.

Phosphorus apparently penetrates the epithelium only in minute quantities, while potassium is readily absorbed from rumen liquor or aqueous solutions. Sodium and chloride can traverse the epithelium in both directions, even against a concentration gradient. Water can pass across the epithelium in quantity: hypotonic solutions placed in the empty rumen lose water, and hypertonic solutions gain water. The quantities absorbed do not increase directly with an increase in molarity, which suggests that there is a maximum rate of water flow under these conditions. The omasum is permeable to water, and it is known to concentrate phosphorus, magnesium, calcium and chloride, either by water absorption or the passage of ions across its epithelium.

The last speaker was Mr. R. J. Garner (University of Bristol), who discussed the intermediary metabolism of ruminants. Most of the carbohydrate digested is absorbed as short-chain fatty acids, all available evidence indicating that very little glucose is absorbed from any part of the alimentary tract. Of these fatty acids, propionic is the only one known to be glycogenic; it is rapidly converted into glucose in the liver, and very little enters the peripheral circulation. Acetic acid is oxidized by many tissues in both ruminants and non-ruminants, and it is also utilized for fat synthesis. The high arterio-venous differences in acetic acid concentration in the sheep's head and the cow's mammary gland indicate that it is metabolized extremely rapidly by ruminant tissues. Butyric acid is usually considered to be ketogenic, yet intravenous injection of sodium butyrate has been stated to relieve hypoglycæmic symptoms in lambs and rabbits. However, it is known that butyric acid is selectively metabolized by rumen wall, largely to ketone bodies, so that only a small proportion of the butyrate produced enters the blood.

The adult ruminant depends on short-chain fatty acids for most of its energy, and shows striking changes in its behaviour towards glucose. One of the most remarkable features of the adult ruminant is its ability to tolerate extremely low blood-glucose levels. The erythrocyte of the ruminant is relatively impermeable to glucose, so that the level of glucose in whole blood approximates to plasma levels. Even when this fact is considered, the ruminant is in a permanent state of hypoglycæmia as compared with most other species. This low blood-sugar level is accompanied by a reduced ability of ruminant tissues to utilize glucose. When injected intravenously it is removed from the blood at a much lower rate than from the blood of man or dog. In this respect the ruminant resembles a diabetic man.

Young ruminants on a milk diet have a blood-sugar level and glucose tolerance similar to non-ruminants: the appearance of adult conditions coincides with the development of rumen function. It has been suggested that it is the onset of ruminal digestion which initiates the change in behaviour towards glucose, and there is some evidence that this change can be postponed by prolonged milk feeding, withholding roughage, or including antibiotics in the diet.

The rise in blood fatty acid which follows the onset of ruminal digestion coincides with a pronounced fall in blood-sugar level, which suggests that the increased intake of these acids may be a factor. However, horses and rabbits also absorb considerable quantities of fatty acids from the cæcum, and yet remain normal in blood-sugar level and glucose tolerance. Fermentation in the rumen also leads to a fall in the amount of carbohydrate absorbed. In the non-ruminant, a high-fat, low-carbohydrate diet causes a reduction in blood-sugar level, a reduced glucose tolerance and a reduced rate of absorption of glucose from the intestine (due to a lowered hexokinase activity), a change approximating to the normal state of affairs in the ruminant.

The effect of diet on intermediary metabolism is not understood. It has been suggested that certain products of metabolism, including acetate, act as cellular regulators, shifting the emphasis in metabolism from carbohydrate to fatty acid according to nutritional conditions. Rumenal fermentation may cause the change in carbohydrate metabolism simply by altering the proportions of carbohydrate and fatty acid available to the cell. Attempts to alter these proportions absorbed by the adult ruminant have led to no observable changes in carbohydrate metabolism. The low normal blood-sugar level of adult ruminants may be a result of a change in balance between the pancreatic, anterior pituitary and adrenal hormones which regulate it. Dietary factors can affect the functional activity of the anterior pituitary and possibly of the adrenal cortex, and can also alter the sensitivity to insulin.

The foregoing evidence suggests that nutritional conditions are chiefly concerned in bringing about the observed peculiarities in intermediary metabolism and hormonal balance in ruminants. In conclusion, Mr. Garner suggested that the low blood-sugar level may be an adaptation of physiological importance in conserving carbohydrate for essential purposes.

A. G. Singleton

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# OBITUARIES

## Mr. R. Burne, F.R.S.

By the death of Richard Burne, British zoology has lost far more than the maker of minutely perfect dissections and the writer of accurate and beautifully illustrated descriptions of animal structures, whose working life was spent among John Hunter's specimens in the Royal College of Surgeons. Burne was a shy, quiet man, who avoided publicity and, probably owing to a slight stammer, rarely read papers before scientific societies or delivered lectures to students. Few really knew him well, and still fewer were in a position to appreciate his outstanding abilities as a comparative anatomist. It was not until he was in his sixtieth year that he was elected a Fellow of the Royal Society.

Burne carried the art of self-effacement to almost extreme lengths. He was always ready to credit to others the work that, as a matter of fact, he had himself accomplished. He worked in Lincoln's Inn Fields just as William Clift, more than a century before him, had done : a man whose whole purpose was the perpetuation of John Hunter's ideals as they were exemplified in his Museum. Like Clift, he had no care as to who was given the credit so long as the work was done. Burne also found a likeness to Clift in that he was at heart a Londoner who loved to seek out odd corners and old associations around Lincoln's Inn Fields and the Inns of Court. Probably some of his happiest times were spent when, in the genial company of his fellow comparative anatomist, Frederick Gymer Parsons, he wandered about the Inns of Court when the day's work was done and all was quiet in the deserted streets around the precincts of the Temple. An eminent zoologist he most certainly was ; but beyond that, all those who knew him best will always remember that he was a gentle and a generous man in whom no thought of self-interest ever intruded in the work to which he devoted his life.

Richard Higgins Burne, the son of a solicitor, was born in London on April 5, 1868. He was educated at Winchester and proceeded to Oriel College, Oxford, where he graduated in natural science in 1889. For two years after leaving Oxford he worked at the Royal College of Science in South Kensington and here came under the influence of that gifted teacher Thomas George Bond Howes, who was then assistant professor of zoology and succeeded Huxley in the professorship in 1895. In 1892, Burne was appointed as anatomical assistant at the Royal College of Surgeons and started his long and faithful service to the Museum that only terminated with his retirement in 1934. Charles Stewart was conservator when Burne joined the staff, and after his death in 1907 there began the long and happy association with Sir Arthur Keith that lasted for the next twenty-three years. In 1908, Burne's office was changed to that of assistant curator and in 1912 to physiological curator.

It is impossible to over-estimate the value of Burne's work in the service of the Hunterian Museum, and had it not been for his carefully compiled descriptive catalogues of the specimens, it would have been impossible to face the task of reconstruction after the terrible losses by enemy action in 1941. The Gold Medal of the College was awarded to him in 1925 and never was it better bestowed.

Among Burne's most important published works are probably those dealing with the minute ramifications of the vascular system of certain fishes. Moreover, these papers are the most characteristic, since they are founded on the minutely perfect dissections in the preparation of which he developed such extraordinary skill. A handbook of his dissections of the Cetacea, edited by Dr. F. C. Fraser, was issued by the British Museum last year. But Burne's real life-work is embodied in the catalogues of the Hunterian Museum and in the collection of unpublished notes and drawings preserved in the College. In 1937, he was appointed a Hunterian Trustee, and until his death his advice and his vast knowledge of the contents of the Museum were invaluable during the critical years of the Second World War and after the disaster that swept away so much of his life's work.

F. Wood Jones

## Prof. L. Prandtl, For.Mem.R.S.

The death of Ludwig Prandtl on August 15 at Göttingen has taken from the aeronautical world one of its greatest pioneers, perhaps the greatest of them all in the field of theoretical aerodynamics. He was seventy-seven years of age, having been born in 1875. He was educated as an engineer. He occupied several teaching posts before going to Göttingen in 1907, where he spent the rest of his life and inaugurated a school of aerodynamics and hydrodynamics which soon became famous throughout the world. While he will be remembered chiefly for his theoretical work, he was also a brilliant experimentalist, and he set up at Göttingen a comprehensive aeronautical laboratory which contained the first really successful return-flow wind tunnel. Prandtl had appreciated the two essential features for steady flow in such a tunnel, namely, a fine-mesh honeycomb and a rapid contraction just ahead of the working section. In this tunnel he experimented with airship models at a time when the Germans believed that the heavier-than-air type of aircraft would have a great commercial future. He also studied the drag of spheres and cylinders and was apparently the first investigator to realize the importance of stream turbulence in connexion with the critical Reynolds number of such bodies.

In the theoretical field, Prandtl's original thinking illuminated almost all the fundamental problems of aerodynamics and opened new paths to the many scientists at Göttingen and elsewhere who were able to appreciate his ideas and to follow them up. Among his earlier investigations was the study of the behaviour of an aerofoil of finite span, in which he gave mathematical precision to the ideas outlined years before in Britain by F. W. Lanchester, and