Digestion and absorption of carbohydrates in the young bovine

Howard James Larsen
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DIGESTION AND ABSORPTION OF CARBOHYDRATES

IN THE YOUNG BOVINE

by

Howard James Larsen

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Dairy Husbandry

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State College

1953
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INTRODUCTION

The ruminant species occupy an unique and somewhat central position among domestic animals as regards the placement of digestive organs and digestive processes. On one side of the ruminant species realm are monogastric animals having no provision for the utilization of large quantities of cellulose materials, while on the other are monogastric species possessing a highly developed cecum for the purpose of cellulose digestion. The digestive ability of the monogastric animals other than those with highly developed cecum is limited to the utilization of foodstuffs which are concentrated energy sources and are low in cellulose components. Digestion is accomplished principally by digestive secretions of the gastrointestinal tract. The end products of enzymic hydrolysis are principally amino acids, fatty acids, glycerol and the monosaccharide glucose, the latter being the primary energy source of the monogastric animal.

Digestion in the polygastric animal is not restricted to the plant grains but extends to the plant stems and leaves as well. This versatile property is not made possible by the presence of a cellulolytic enzymic secretion of animal origin but rather by the cellulose-splitting microorganisms which inhabit the rumen in large numbers. The end products of cellulose cleavage by the microorganisms have been shown to be the lower fatty acids, principally acetic, which has been shown to be the primary source of energy for the ruminant as opposed to glucose for the monogastric species (27).
In view of the above considerations, it is conceivable that perhaps there may exist between the mono- and polygastric animal striking differences in metabolic pathways. If perchance great differences do exist, great care must be exercised in the application of information gathered in one species of either the mono or polygastric group to species of the opposite group. Indeed this danger has long been recognised, but by all too few investigators and reviewers. It is recorded that Von Furth had warned workers against uncritical introductions of definitions like pepsin and trypsin from vertebrate physiology into comparative physiology (49). Generally speaking, this warning has not been heeded and consequently this unwarranted transfer of unqualified information gathered in one species to the study of comparative physiology and metabolism has perhaps presented an hitherto unrecognized barrier to obtaining answers to problems of a nature specific to the species in question.

In an earlier study at this station (18) ten-month old calves were rendered essentially monogastric by feeding the animals directly into the oesophago-abomasal cavity. Although the ration fed was considered to be adequate nutritionally for the well-being of a monogastric animal, these calves reacted adversely as indicated by emaciation, weakness, diarrhoea and loss of weight. It was observed also that finely ground corn which was present in the feed seemed to be digested incompletely, thus suggesting a possible limitation of the ability of the ruminant to digest starch. Therefore, the present study was initiated (employing the same feeding procedure) to determine indirectly and directly the digestibility by ruminants of glucose, maltose, starch and corn. Indirect measurements
were made by blood glucose absorption curves while direct measurements were made by analysis of cecal ingesta and feces. By approaching the problem from both of these avenues it was hoped to determine whether the ruminant animal is able to digest starch of feed origin without previous ruminal conditioning.
REVIEW OF LITERATURE

No experiments were found which deal with the particular objectives of this experiment so the review will discuss literature relevant to the work.

Starches or Starchy Supplements As Energy Sources

A great deal of research effort has been expended in the quest for a suitable supplement to or substitute for whole milk in calf rearing. Not overlooked has been the possibility for substituting corn starch or similar high starch grain products for a portion of the milk diet ordinarily needed by the young animal for adequate growth and maintenance. Success generally has not been achieved when this type of feed was used as an energy source in calf nutrition. Shaw and co-workers (40), being aware of the rather abundant source of starch and its possible value as a supplement to the calf diet, undertook to ascertain how early in life the calf could utilize starch or starch-containing feeds. The results of the work with two calves revealed the approximate digestibilities for starch at various ages as follows: 4 to 7 days, 20 percent; 12 to 15 days, 40 percent; 21 days, 60 percent; and 26 days, 90 percent. These results strongly suggested that the milk diet of a calf could be supplemented with a starchy feed and that starchy material may be rapidly increased in the diet as
the calf grows older. Also, as a result of this work, the thesis was advanced that quite probably a calf but a few hours old can not digest an appreciable amount of starch because of the absence of an amylolytic enzyme. Moreover, the quality of starch splitting enzymes must increase very rapidly in the first few days of life since at the age of 3 to 4 weeks the calves were able to digest a ration in which nearly 10 percent of the dry matter was starch. Subsequent results of other research workers were less encouraging as regards the use of starchy feeds as a milk supplement.

In the course of some experiments by Norris (25) in rearing dairy calves on cereal gruel instead of whole milk, it became necessary to obtain a clearer concept of gastrointestinal function of animals fed relatively high starch diets. Observations on calves so fed indicated that there frequently existed a condition of slight indigestion and abnormal bacterial activity, sufficiently great to slow down the rate of growth. Because of the relatively large amount of protein in the gruel diet, it was at first thought that such bacterial activity was putrefactive in nature. Experiments by Maynard and Norris (23) with four calves reared on whole milk and six calves reared on a high-starch gruel, consisting largely of less fibrous portions of seeds, showed that the pH of the feces usually was acid when digestive troubles were observed. If these troubles were associated with putrefaction, one would expect the feces to be alkaline due to the production of amines which are strongly basic. Therefore, in the light of this work by Maynard and Norris (23) which indicated that
no more putrefaction was taking place with the cereal diet than with the milk diet, products of putrefaction were not considered the cause of digestive disturbances.

Bacteriological studies by Bull and Rettger (17) on the effect of carbohydrate feeding substantiate the above conclusion. They found that lactose, milk and mixed grains were specific articles of diet which exerted an influence on the intestinal bacteria. Lactose when fed in sufficient quantities (2 to 3 grams daily) brought about a complete transformation of the flora of the white rat within 2 to 3 days. Milk required a longer time and did not bring about a complete change. The raw grains were slowly acted upon by an altered microflora population of the intestines and the grains were broken down into intermediate carbohydrate products which may or may not have been absorbed. These findings along with those of Maynard and Norris (23) led Norris (25) to the belief that the bacterial activity obtained from feeding a high-starch diet was a process of fermentation and the object of his work was to investigate this point further. The results of the latter (25) indicate a much greater production in the feces of volatile fatty acids and alcohols with a cereal grain diet relatively rich in starch than with a whole milk diet. Norris was unable to state definitely that this was caused by fermentation through the activity of bacteria. However, Harden (12) earlier (1901) had shown that Bacillus coli communis, isolated from the feces of both man and animals, will ferment glucose to acetic acid, alcohol and other products.
Also in the work of Norris (25) it was observed that the feces of the calf which received the whole milk were always non-acid to litmus while the feces of the other calves were constantly acid to litmus and, in addition, the former were uniformly medium to light in color, while the latter were always very dark. The feces of two of the calves on the gruel were consistently slimy or stringy and bits of undigested meal were present. This work appears to be in agreement with the work of Shaw and co-workers (40) which gave some indication that calves cannot completely digest rations which are relatively rich in starch. In this latter work there was also noted some correlation between the rise in acid and alcohol production, an increase in the excretion of dry matter, and a decrease in digestibility.

In 1937 Shiptaw and co-workers (41) demonstrated that calves will not thrive on a ration consisting principally of soybean flour. Also, Flipse and co-workers (9) observed that the weight gains of calves fed starch were approximately one-half those of animals fed either corn syrup plus lactose or lactose plus starch. It was noted further that following starch ingestion there was no change in blood sugar the first 4 hours and only a moderate increase at the 6th and 8th hours.

More recently Shambye (37) measured the blood glucose rise of the portal blood system of mature ruminants fed hay and crushed oat diet. In all the experiments the concentration of glucose in the portal and arterial blood was practically constant. The differences between the portal and arterial systems varied only slightly but when compared to the normal
arterio-venous levels of sheep the portal blood sugar was slightly above
the ordinary venous concentrations. This suggests that a small amount of
glucose is absorbed from the alimentary tract of sheep, however, this work
demonstrated that there is an absence of any appreciable alimentary hyper-
glycemia in the mature ruminant animal. These findings imply that little
of the grain carbohydrate passes through the rumen undigested by rumen
microorganisms.

In view of the evidence obtained by the above cited investigators,
who found that considerable fermentation took place in the gastrointestinal
tract of animals receiving a high starch diet, it may be possible that the
high digestibilities of starch reported by Shaw (40) were greatly influenced
by a bacterial population in the lower tract of his animals similar to that
described by Hall and Rettger (17), and Maynard and Norris (23).

It may be that the difficulties experienced by Flipse (9) and Shoptaw
(41) in raising calves on high starch diets could be traced in part to
the low apparent digestibility as shown by Norris (25). A possible reason
for low digestibility may be found in the work of Schamsy (37) where he
suggests that the ruminant normally digests very little grain carbohydrate
in the lower tract and, therefore, the facilities for this type of diges-
tion in this area are limited.

Isolated and Intact Visceral Absorption

Some evidence is available which appears to indicate that the gastro-
intestinal tract may behave differently as a unit than it does in segments,
particularly in the case of glucose absorption. There also is equally strong evidence, however, suggesting that the mechanism of glucose absorption is rather stable, confining the rate of absorption to a somewhat limited concentration range. Hole (13) stated that from his observations with rat hexokinase appears to participate directly in sugar absorption and with the phosphatase it functions in a phosphorylation-dephosphorylation cycle. Therefore, the absorption rates of different sugars may be determined by the behaviour of the hexokinase which may in turn be influenced by the amount of adenosinetriphosphate available at the site of absorption. Trumble and Carey (43) in numerous experiments with dogs established the rate of glucose absorption at approximately 1 gram per kilogram of body weight per hour. The concentration of solution, the absolute weight of glucose ingested, the length of absorption period, and the degree of excitement occasioned by experimentation showed no definite relationships to the rate of glucose absorption.

Experiments conducted by Magee and Reid (22) closely paralleled the work of Trumble and Maddock (44) but differed in one respect that the former used isolated loops of the intestine. Glucose solutions were injected into the stomach and intestines of anesthetized cats and rabbits, respectively. A 13.5 percent glucose solution was absorbed into the blood more rapidly than either stronger or weaker solutions. These workers believed therefore that a glucose concentration of 13.5 percent is the optimal solution for absorption in cats and rabbits. The authors also concluded that portal and systemic blood levels are equally reliable as
indexes of the rate of absorption of glucose in the anesthetized animal. It was noted further that with stronger solutions (25 to 50 percent) there was slowing or stasis of blood in the capillaries and copious secretion of mucus.

Trumble and Maddock (44) attempted to ascertain whether the rate of absorption of glucose from the gastrointestinal tract could be increased by introducing the sugar directly into the intestine and continuously maintaining there a supply larger than that available when glucose is administered by mouth. In this series of experiments the observed rate of absorption averaged 0.92 gram per kilogram of body weight per hour which is slightly less than the value observed in other experiments (43) in which the entire gastrointestinal tract functioned as a unit. The concentration of the solutions infused varied from 3 to 32 percent, the dosage per unit of weight varied from 1.0 to 3.9 grams per kilogram, body weight and the duration of the absorption period varied from 0.5 to 3 hours. Varying these factors failed to increase the rate of absorption to a significant extent. From these data it was concluded that introducing glucose directly into the intestine of the dog and continuously maintaining an excess of the sugar at the location does not increase the rate of absorption beyond the maximum obtainable when the intact gastrointestinal tract functions as a unit. Also it was observed that a 13.5 percent glucose solution did not promote absorption from the intestine at a rate significantly in excess of other concentrations either higher or lower than 13.5 percent. This experience is in contrast to the conclu-
sions of other investigators (22) that this concentration (13.5 percent) is the optimal one for the absorption of glucose by the living animal.

Bawlin and co-workers (30) also suspected that where the gastrointestinal tract is used as a physiological unit the mechanism of absorption may be different than when only segments of this unit are used. When the gastrointestinal tract is used as a single unit the information may not be comparable to that drawn in regard to the activity of isolated loops of the tract when subjected to varying concentrations of glucose. By using jejunal loops of the dog Bawlin and co-workers found that the rate of absorption of glucose from these loops was dependent in a large part upon the concentration and volume of the solution used. With increasing concentrations and with increasing volumes of the same concentrations, increasing amounts appeared to be absorbed. When the amount of sugar was plotted against time no linear relationship could be demonstrated. When solutions of glucose varying in concentration from 3.5 to 50 percent were placed in the stomach of the dog the concentrations of the solutions recovered from the jejunum and ileum at the end of one hour were remarkably constant. The authors suggested that the gastrointestinal tract may possess the ability to control the concentration by secretion and absorption of water.

This is further indicated by the data of Bawlin and co-workers (29) which strongly suggest that water is rapidly drawn into the stomach or the small intestine thus diluting the sugar solution which the stomach originally contained. These workers also demonstrated that glucose solutions
varied from 34 percent to more than 400 percent. These experiments lend
strong support to the growing belief that the rumen is a vital organ of
absorption.

Carbohydrate Digestion, Absorption and Metabolism in the Ruminant

In ruminants, feeding is often followed by a slow and variable rise
of blood glucose of only about 5 to 10 mg. percent over several hours.
A partial explanation for this may be the slow passage of feed through the
gastrointestinal tract of the ruminant but it does not explain the observa-
tion that the oral administration of glucose produces little or no aliment-
tary hyperglycemia in sheep, cattle or goats (5). Studies conducted by
Phillipson and McInally (27) demonstrated that glucose, fructose and cane
sugar undergo rapid fermentation in the rumen of the sheep and pass
through the stage of lactic acid to volatile fatty acids. Starch and
cellulose also are fermented but the production of fatty acids is some-
what prolonged. The rapid disappearance of glucose from the ingesta could
not be accounted for by passage to the abomasum. Volatile fatty acids
were found to be stable in the ingesta of the rumen; they do not pass to
the abomasum in large quantity but appear to be absorbed into the portal
blood system by the rumen or omasum.

Reid (31) found the range of blood sugar values in sheep to be quite
wide varying from 25 to 50 mg. percent. This sugar appeared to be pri-
marily glucose as is also the case in other mammalian species. The level
in ruminants is affected to a lesser degree than in non-ruminants by consumption of food, by administration of glucose to the non-fasting animal and by short periods of fasting up to 46 hours duration. Since glucose is not a normal constituent of the diet of the ruminant it is improbable even when present that it ever reaches the small intestine in significant quantities. Reid (32) studied the ability of the tissues to take up acetic acid and glucose. In the initial observations the volatile fatty acid level in the peripheral circulation was consistently higher than that accepted for non-ruminants, and in view of present knowledge of ruminant digestion, some relationship between the low arterial-venous glucose differences and the relatively high volatile fatty acid levels seemed probable. A chromatographic analysis revealed clearly that much of the acetic acid absorbed via the portal system passed through the liver into the peripheral circulation. Moreover, it was shown that the arterial-venous volatile fatty acid difference is due to the efficient uptake of acetic acid by the tissues. This investigator also stated that the small amount of propionic acid in the general circulation as compared to the amount in portal blood indicates that this acid is removed from the portal system by the liver almost as rapidly as it is absorbed from the gastrointestinal tract.

Propionic acid thus may be the principal contributor to the blood glucose unless the rumen-produced bacterial polysaccharides can be shown to be of amounts significant for glucose production in the small intestine.

Reid (32) observed that after insulin injection of sheep the blood glucose level did not fall to the level at which hypoglycemic symptoms are
normally observed in non-ruminants. Five reasons were postulated for this
phenomenon: the blood glucose levels at which symptoms would be observed
in sheep may differ from those at which similar signs are seen in the non-
ruminants, and probably more important, differences may exist between
ruminants and non-ruminants in intermediary metabolism since glucose may
be considerably less important and acetic acid of greater importance in
extrahepatic tissue metabolism. Reid also noted in subsequent work (34)
that sheep possess low glucose tolerance level as compared with mono-
 gastric animals. This may be due in part to an intrinsically low ability
of the extrahepatic tissues to dispose of injected glucose, as compared
with non-ruminants. Glucose tolerance tests were also conducted by Reid
(34) by injecting glucose directly into the abomasum by puncture and by
permanent fistula. In no experiment after the administration of 10 to
100 grams of glucose had the glycemic level returned to normal in five
hours. The rate of increase was also slower than that experienced with
dogs. These observations serve to indicate that ruminant intestinal and
extrahepatic tissues, respectively, absorb and metabolize glucose much
more slowly than those of the dog. This investigator also stated that the
differences noted were probably in the quantitative aspects of glucose
metabolism and probably in its hormonal control which are in turn condi-
tioned by the nature of the dietary carbohydrates and their digestion.

Holmes (14,15) administered glucose to mature ruminants and to young
calves by stomach tube and by mouth, respectively, to gain information on
glucose tolerance levels. In all cases the glucose blood levels of calves
greatly exceeded those of the mature animals. A possible explanation, as stated by Holmes, was that the renal threshold of the young animal is much higher than that of the mature animal. More probably, however, the glucose administered to the mature animal was fermented in the rumen thereby prohibiting direct absorption. Bell and Jones (5), investigating glucose tolerance in the bovine, administered glucose orally, subcutaneously and intravenously. No significant change occurred following oral administration, significant hyperglycemia was obtained with subcutaneous injection and high levels persisted due to slow absorption, and intravenous glucose administration produced a marked hyperglycemia with a return to normal within 2 hours in all cases. Contrary to the findings of Reid (32), Bell and Jones (5) stated that glycogenesis in the ruminant parallels that observed in other species, from which the latter assume that the storage and regulating mechanism in the bovine is similar to that of other animals.

Schaabye (38) investigated the influence of orally-administered glucose on the portal blood of sheep by the use of a specially constructed cannula which would allow sampling of the portal blood. It was concluded that even large amounts of either glucose or other easily fermented carbohydrates such as sucrose or starch will be broken down to a great extent in the rumen to volatile acids, which are absorbed from the rumen, reticulum and omasum. On the basis of these results, Schaabye stated that it is doubtful whether any appreciable quantities of carbohydrate reach the small intestine under normal feeding conditions, except possibly during the first few hours after ingestion of a feed rich in starch or in the form of complex carbohydrates synthesized by bacteria or other microorganisms inhabiting
the rumen. In the latter connection it is pointed out by Van Der Wath (45) that the isodophilic substance synthesized by certain cocci during starch digestion in the rumen is partially metabolized before the bacteria leave this organ. Schambye examined the portal and venous blood of sheep for blood reducing sugar. The portal blood was obtained with the aid of a London cannula and venous blood from the jugular. The changes in the portal blood sugar were found to be small and since the portal and arterial differences were also very small it was concluded that small amounts of glucose were probably absorbed from the alimentary tract of sheep fed hay and concentrate diets. It was suggested that the amounts of volatile acids absorbed are of such a magnitude that these acids must be regarded as essential products of digestion and that their nutritional importance to ruminants is at least as great as that of the glucose actually absorbed.

The significance of glucose in ruminant metabolism appears, from much of the above cited literature, to be shrouded by a great deal of uncertainty. It appears from most of the results of the latest investigations (31, 32, 33, 34, 36, 37, 38) that glucose does not hold an important a position in the ruminant metabolism as in that of the non-cellulose utilizing animals. The lower fatty acids, principally acetic, propionic, and butyric produced in the rumen appear to be the principal source of energy, of fats and of glucose in the cellulose-utilizing animals (27, 35). Numerous studies (16, 26, 36, 37, 38, 43, 47) suggest that in the normal functioning ruminant very little grain carbohydrate in its natural state or as hexose is available for absorption in the lower tract of the ruminant.
EXPERIMENTAL

Experimental Animals and Managemental Practices

Three bull calves, ranging in age initially from 8 to 9 months, were used during the course of the experiment. Two were Milking Shorthorns and one was a Holstein. When animals 3671 and 3688 were approximately 12 weeks of age the rumen fistulæ operations were performed and about 4 weeks later the cecal fistulæ were made. In the case of animal 3701 the cecal and ruminal fistulæ were prepared simultaneously at approximately 12 weeks of age. While the fistulæ were in the process of healing, the animals were housed in the isolation barn at the Iowa State College Dairy Farm in individual pens which were cleaned daily and were kept bedded with a deep layer of straw. The animals were allowed free choice of fresh water and green leafy alfalfa hay and were fed approximately 2½ pounds of the herd concentrate mixture daily per calf. The concentrate mixture was composed of corn, 400 parts; soybean oil meal, 100 parts; linseed meal, 200 parts; oats, 500 parts; wheat bran, 200 parts; steamed bone meal, 26 parts; and iodized salt, 14 parts.

Precautions were taken to keep the animals free from infection and sources of contamination by liberal use of spray and "Smear 62" fly repellent, the latter being applied freely and directly to the operational incisions. Considerable time was required to prepare the fistulæ for the
actual experimental feeding phase; therefore, it was necessary to keep the animals in the isolation barn for about three months. They were then moved to individual pens in the experimental calf barn where they were bedded with shavings. Free choice of water was allowed and all other feeds were withheld with the exception of the experimental diets.

Operative Procedure for Ruminal and Cecal Fistulae

To permit feeding directly into the omaso-abomasal cavity each experimental animal was fitted with a permanent rumen fistula, and each animal also was fitted with a cecal fistula to permit sampling of the digested material prior to passage through the large intestine. The operational procedure was preceded by close clipping of the hair and thorough disinfection of the area of the paralumbar fossa. In the preparation of rumen fistulae in calves 3671 and 3688, a vertical incision of approximately 3 inches in length was made in the left paralumbar fossa whereas the incision in calf 3701 was circular and approximately 3 inches in diameter. The incision in both operational procedures carried through the skin, muscle, and peritoneum to the rumen wall. The skin then was sutured directly to the rumen wall, taking care not to puncture the latter as the presence of rumen liquid at the point of incision would have prolonged the healing process. In this manner the rumen wall was brought in close contact with the edges of the incision of the skin and in a few days a solid skin to rumen wall apposition was attained. Fifteen ml. of a 6 percent solution
of nembutal per 100 pounds of body weight was used as a general anesthetic in the case of calves 3671 and 3688. A local anesthetic only was used with apparent success when performing the operations on calf 3701.

The rumen wall was allowed to remain exposed to the atmosphere for five or six days during which time necrosis occurred and the exposed area of the circular incision (calf 3701) was cut out about one-half inch from the original skin to rumen apposition leaving a circular fistular opening to the rumen. In the case of calves 3671 and 3688 a slit was made in the exposed rumen wall and shortly thereafter the necrotic edges sloughed off back to the skin to rumen apposition. The circular rumen opening of calf 3701 was approximately 3 inches in diameter while the openings of calves 3671 and 3688 were slits about 2½ inches long. Fitted wooden plugs were installed in the fistulae when healing had progressed sufficiently to allow closure of the opening. Periodic increasing of the size of the wooden plug caused a stretching of the skin and rumen wall and the opening eventually became large enough for entry of the hand and arm for the purpose of feeding directly into the omaso-abomasal cavity.

In the preparation of the ocusal fistulae (through the skin, musculature and peritoneum) a vertical incision 1½ inches long was made in the right paralumbar fossa of all calves, immediately following the ruminal operation in calf 3701 and about 3 weeks following the ruminal operation in calves 3671 and 3688. The oesum, which normally does not lie directly against the abdominal wall, was brought out to the incision and sutured to the exposed edges of the skin. Since the incision was only about 1½
inches long, necrosis did not occur in the cecal operation as was the case with the rumen fistulae. The cecum of calf 3701 was allowed to remain intact (no incision into the cecal cavity) until about 3 months after the operation. During this time a thin layer of tissue grew over the wound. The opening into the cecum of calves 3671 and 3688 was made about 1 week after healing of the skin to the cecal wall was certain. Cecal fistulae were kept closed with wooden plugs similar to those used in the rumen fistulae, except that the latter were much larger.

Fistular Maintenance

Considerable difficulty was encountered in keeping the plugs in the cecal fistular openings and without plugs there was considerable danger of the cecum prolapsing through the fistular opening. This occurred several times with calves 3671 and 3688 in which the opening into the cecum was prepared shortly after the initial incision through the skin musculature and peritoneum. This difficulty was minimized in 3701 where the fistula was not opened until needed. To counteract the danger of cecal prolapse a rubber belt was constructed to encircle the animal, covering the plug in the cecal opening. With the use of such precautions this danger of prolapse, which always caused considerable hemorrhage and sometimes endangered the life of the calf, was reduced.
Description of Diets

Four diets were fed in this experiment. Five to 5½ pounds of experimental ration were calculated to be sufficient for maintenance plus approximately one pound gain in weight daily. They were balanced rations fortified with vitamins and minerals. Composition of the diets is shown in Tables 1 and 2.

Table 1. Basic Ingredients of the Experimental Diets

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<td>Starch</td>
<td>21.6</td>
<td></td>
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<tr>
<td>Dried malt syrup</td>
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<td></td>
<td>28.1</td>
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<tr>
<td>Dextrose</td>
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<td></td>
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</tr>
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<td>Total</td>
<td>39.0</td>
<td>34.8</td>
<td>39.6</td>
<td>34.8</td>
</tr>
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</table>

*Amounts listed were adequate for entire experiment.*

As shown in Table 1, diets 2, 3 and 4 were basically the same as diet 1 except that the N.F.P. of the corn was replaced with powdered corn starch, maltose of dried malt syrup and dextrose, respectively.
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**Table 2:** Measurement and Direction Correspondence of the Experimental Plane
The starch of diet 2 was a commercial grade of corn starch. Chromatographic analysis of the starch diet showed essentially no sugar or dextrins to be present. The dried malt syrup was composed of maltose, 76 to 78 percent; dextrins, 11 to 15 percent; protein, 4 to 5 percent; and ash, 1.5 percent. The starch was chosen to replace the N.F.E. of diet 1 because it was felt that a powdered form of corn starch would be nearly devoid of all natural starch granular structure, which in its original form may contribute some difficulty to digestion in the gastrointestinal tract. In diets 3 and 4 maltose and glucose respectively, were chosen to substitute for the N.F.E. of diet 1 since maltose is the disaccharide naturally formed by starch hydrolysis and glucose is the normally formed end-product of starch digestion in the gastrointestinal tract. Employing the dried malt syrup to supply the maltose of diet 3 increased the N.F.E. of this diet over diet 1. Since maltose was the constituent of interest in diet 3 it was thought best to replace exclusively the N.F.E. of diet 1 with this disaccharide.

The minerals and vitamins listed in Table 2 constitute the quantitative and qualitative requirements per 150 pounds of the final diet. To insure homogeneity of the minerals and vitamins in each diet a premix of all constituents listed in Table 2 was made, with soybean oil meal being employed as the dispersing medium. This premix was divided into four

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a Produced by A. E. Staley Manufacturing Company, Decatur, Illinois.
b Produced by Fleischman Distilling Corporation, New York, N. Y.
equal lots and one portion was added and mixed thoroughly with each of the four diets respectively. This soybean oil meal constituted part of that indicated in Table 1.

For digestibility measurements, chromium oxide was added to the rations at a level of approximately 1 percent. To facilitate uniform mixing of the indicator a premix of chromium oxide and soybean oil meal was made and divided into four equal portions. One portion was added, with thorough mixing, to each of the four diets. The soybean oil meal was a portion of that indicated for each ration of Table 1.

Prior to the final mixing of the diets, all constituents not in a finely ground or powdered form were ground to pass a 0.04 inch screen. Grinding to this fineness was necessary to prevent clogging of the pump, (which was used to feed the animals omace-abomasally), to maintain homogeneity and to increase the surface exposed to enzymatic action. Thorough mixing of all diets and premixes was accomplished in a Hobart mixer. No noticeable lack of homogeneity was noticed after extended periods of standing.

**Digestion and Absorption Trials**

Prior to the actual experimental feeding trial all animals were functional ruminants, and in order to eliminate possible interference from rumen ingesta which would pass down the tract if the rumen were allowed to function normally it was necessary to stop rumen activity.
Therefore, three days prior to the beginning of experimental feeding the animals were placed on a whole milk diet and solids were evacuated from the rumen to insure a gastrointestinal tract relatively free of ingesta at the time experimental feeding was initiated. From previous experience (13) it was thought best to feed each animal an experimental diet for only a two-day interval since a longer period would result in adverse physiological conditions such as extreme weakness, emaciation and weight loss. Between each two-day feeding period whole milk (15 pounds daily) was fed for two-day intervals by nipple bucket. No spillage into the rumen was noted during milk feeding, indicating efficient functioning of the oesophageal groove. The feeding regime for each animal is shown in Table 3.

Table 3. Dietary Regime

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Experimental diets were fed twice daily, approximately 2½ pounds of dry mixture per feeding, in the form of a slurry (1 part dry mixture: 1 part warm water) mixed thoroughly and pumped directly from a bucket into the oesophageal cavity through a hose placed in the reticulooesophageal
erifice. No difficulty was encountered in this operation and very rarely was any of the feed regurgitated from omasum to reticulum. In previous experiments (18) with this type of feeding it was found that feed placed in the omaso-abomasal cavity would traverse the remainder of the gastro-intestinal tract in 8 to 10 hours. Therefore, in the present investigation two omaso-abomasal feedings (a 24-hour period) were allowed to elapse before ceal or fecal samples were collected for digestibility analysis. By following this procedure it was thought that any "carry over" effects from the previous treatment or from the milk diet could be minimized.

During the course of all treatments and during all intervening periods the rumen was kept empty, except that water was allowed free choice.

During each trial blood samples were collected from the jugular vein of each animal daily at 0, 1, 2, 4, 6, 8 and 10 hours after the morning feeding. An anticoagulant and a preservative, potassium oxalate and sodium fluoride, respectively, were added to each sample. The blood samples were stored under refrigeration during the 10-hour collection period. Subsequently they were deproteinized with barium hydroxide and zinc sulphate and the filtrate was stored under refrigeration until the samples of the second day of the respective treatment were collected and deproteinized. All samples from each animal then were analyzed for reducing sugars by the method of Somogyi (42).

Ceal samples were collected with a specially adapted automobile sump pump at 8 and 10 hours after the morning feeding of the second day of each trial and each sample was stored in a separate container. The fecal
samples were collected by stimulation of defecation at approximately the
same time, but the two samples (8th and 10th hours) were composited. All
cecal and fecal samples were autoclaved at 15 pounds pressure for 10 min-
utes immediately after collection to inactivate organisms and enzymes
which might digest any carbohydrate present. Immediately after auto-
claving, the samples were quick frozen and held in a frozen state until carbo-
hydrate and chromium analyses could be carried out.

**Exteriorized Visceral Trials**

This phase of the experimental work was conducted with two of the
animals (3666 and 3671) used in the digestion trials. The animals were
allowed to revert to normal functioning ruminants. Hay and concentrates
were fed free choice until recovery apparently was complete. The animals
were subjected to the exteriorized visceral studies at two separate times,
calf 3671, the older of the two Milking Shorthorns, being sacrificed first.

With calf 3671 the rumen was flushed with warm water to remove all
ingesta; then nembutal was injected (15 ml. per 100 pounds body weight of
a 6 percent solution), which was the general anesthetic used. After anes-
thetization a midline incision was made from the point of the sternum
posterior for a distance of about 15 inches. The ventral lobe of the
rumen, the small intestine and the cecum were brought to the exterior for
easy accessibility. The rumen lobe was held in such a position as to
localize the 200 ml. of 50 percent glucose injected into the rumen. Two
10-inch sections of the small intestine and the cecal diverticulum were ligated prior to injection of 50 ml. of 50 percent glucose solution into each. The blood supply of all sections studied was intact. Samples of venous blood from the various sections were taken prior to glucose injection and at approximately 20 minute intervals thereafter for 30 minutes, during which time dehydration of the viscera was prevented by periodically wetting with warm water. Great difficulty was encountered frequently in obtaining cecal blood samples and occasionally in obtaining blood samples from other sections. After the animal was sacrificed the gastrointestinal tract was removed from the animal and the ligated sections were identified as follows: the posterior ventral sac of the rumen, the anterior portion of the ileum, the posterior portion of the ileum and the posterior portion of the cecal diverticulum.

The second study, with calf 3688, was similar in most respects to the experiment with the previous animal, but, in addition, it seemed desirable to determine the effect of Nembutal upon the blood reducing sugar levels. Therefore a blood sample was taken from the jugular vein prior to nembutal injection and at 20 minute intervals thereafter throughout the experiment. Blood samples from the veins of the rumen and ligated sections of the jejunum, ileum and cecum were taken as described in the previous study. Two hundred ml. of a 50 percent glucose solution was injected into the rumen lobe and 50 ml. in each of the other sections as in the previous study. The cecum was inaccessible for injection of sugar solution and for blood sampling; consequently the animal had to be moved to facilitate
access to the cecum. Because of this situation cecal absorption was
checked for 30 minutes subsequent to the initial 30 minutes at which time
it was necessary to discontinue the observations since the animal appeared
near death.

Analytical Procedures

Blood glucose and chromium oxide

Blood glucose was measured by the method of Somogyi (42). The chrome
oxide in feeds, cecal ingesta and feces was determined by the method of
Schürch and co-workers (39) except that a few minor modifications were
made which were as follows: (1) All samples were ashed in about 20 gram
aliquots, were thoroughly pulverized and prior to chromic oxide determina-
tion the ash was dried at 100° C. and an aliquot of this was taken for
analysis. (2) The ash aliquot used for fusion in the nickel crucible with
sodium peroxide was equivalent to approximately one-half the sample weight
suggested by the authors of this method. By using the smaller sample it
was possible to obtain from the resulting filtrate, made up to 250 ml.
rather than 500 ml., a relative density in the same range as that sug-
gested in the original procedure. A calibration curve for the purpose of
determining concentrations in the feeds, cecal ingesta and feces samples
was obtained by carrying known quantities of pure chromium oxide through
the entire procedure.
Carbohydrate in foods, casual insects and feeds

The method of Dimler and co-workers (7) for determination of D-glucose and its oligosaccharides by paper chromatography was employed. Prior to chromatographic development the sample was prepared in the following manner: The frozen sample was rapidly thawed with warm water and an aliquot sample of about 5 grams was mixed thoroughly with distilled water in a Waring blender for 1 minute. The resulting mixture was filtered through a Buchner funnel and then was made up to 250 ml. A 25 ml. aliquot of this solution was preserved with phenylmercuric acetate (1 ppm) and was refrigerated until analyzed. From this point on the procedure suggested by Dimler (7) was followed except that the carbohydrate solution was added to the starting line in 5 microliter aliquots instead of the 1 microliter aliquots suggested. Chromatograms were developed with 1-butanol, pyridine, water solvent combination (3:3:1:5) and the test strips were developed with dinitrosalicylic spray reagent. In test runs with solutions of sugars of known quantities very good and consistent recoveries in the range of 97 to 100 percent were obtained.

Starch determination was made by combining the acid hydrolysis method described by the A.O.A.C. (2) and the anthrone sugar determination as described by Dimler and co-workers (7). The procedure was as follows: An aliquot of approximately 5 grams of sample to be analyzed was subjected to acid hydrolysis by the procedure described by the A.O.A.C. The resulting solution was filtered hot and made up to 250 ml. A 25 microliter aliquot portion of the filtered solution was diluted accurately to 10 ml or
more to adjust the carbohydrate content to the range of 3 to 30 micrograms per ml. A 3 ml aliquot of the final solution was placed in a list-free pyrex test tube and the anthrone carbohydrate determination was carried out as described by Dinler and co-workers (?).
Η ύπαρξη της θέσης μιας αυτόνομης καταθέσεως και η δημιουργία μιας αυτόνομης οικονομίας είναι κοινή κοινωνική σκέψη καθώς και η δημιουργία μιας αυτόνομης οικονομίας είναι ένας από τους κύριους στόχους της πολιτικής που έχει προωθηθεί στην περιοχή της Μεσογείου.

Δημιουργία ενός αυτόνομου κοινωνικού συστήματος

Το ακόλουθο στοιχείο δείχνει τη σημασία της δημιουργίας ενός αυτόνομου κοινωνικού συστήματος.

Σύμφωνα με την πολιτική που έχει προωθηθεί στην περιοχή της Μεσογείου, η δημιουργία ενός αυτόνομου κοινωνικού συστήματος θα επηρεάσει την κατάσταση της περιοχής και θα βελτιώσει την ποιότητα της ζωής των κατοίκων.

Δημιουργία ενός αυτόνομου οικονομικού συστήματος

Το ακόλουθο στοιχείο δείχνει τη σημασία της δημιουργίας ενός αυτόνομου οικονομικού συστήματος.

Σύμφωνα με την πολιτική που έχει προωθηθεί στην περιοχή της Μεσογείου, η δημιουργία ενός αυτόνομου οικονομικού συστήματος θα επηρεάσει την κατάσταση της περιοχής και θα βελτιώσει την ποιότητα της ζωής των κατοίκων.

Συνέπεια

Οι δύο στοιχεία που διατυπώθηκαν στην προηγούμενη σημείωση στην περιοχή της Μεσογείου, συμβάλλουν στη δημιουργία ενός αυτόνομου κοινωνικού και οικονομικού συστήματος, που θα βελτιώσει την ποιότητα της ζωής των κατοίκων της περιοχής.

μηχανή
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\(^a^\)Time after feeding.
Figure 1. Effect of Dietary Carbohydrate on Mean Blood Reducing Sugar Levels.
The mean blood reducing sugar levels (Figure 1) following maltose feeding returned to initial values earlier than those following glucose feeding.

Carbohydrate Digestion

The results of the digestibility studies with corn and starch are tabulated in Table 5. No values are presented here for the digestibility of the glucose and maltose diets, since, when these diets were fed, reducing sugar analysis (determined by paper chromatography) of fecal ingesta and fecal excreta showed only traces of sugars. From this evidence it was concluded that glucose was readily absorbed and maltose either was readily hydrolyzed and absorbed or was absorbed as the disaccharide unit.

The percent dry matter, the percent ash and carbohydrate in the dry matter, the percent chromium oxide, and percent chromium oxide of the ash show wide variations between diets, among samples of fecal ingesta and fecal excreta, and among calves. The digestibility studies with the glucose and maltose diets were limited to carbohydrates, thus, for these diets, the other comparisons shown in Table 5 could not be made.

It can be noted that the carbohydrate percent of dry matter is consistently higher in the fecal ingesta and fecal excreta than in the diets. The carbohydrate digestibility values listed in Table 5 show great variation, but the reason for this high variability is not clear. However, diarrhea, of varying intensity, usually occurred on all four diets and this may have been responsible, at least in part, for the great variation
Table 5. Digestibility Studies with Corn and Starch Diets

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<td>10.4</td>
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<td>1.78</td>
<td>17.1</td>
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<td>Fluid</td>
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<td>16.03</td>
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<td>22.9</td>
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<td>Fecal C</td>
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<td>64.7</td>
<td>1.48</td>
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<tr>
<td>C5</td>
<td>16.1</td>
<td>7.4</td>
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<td>87.7</td>
<td>1.56</td>
<td>22.4</td>
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<td>1.26</td>
<td>24.1</td>
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<td>4.9</td>
<td>56.6</td>
<td>1.28</td>
<td>28.0</td>
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observed in digestibility. No data are shown for 3701 on the corn diet at the cecal level since no material appeared to be in the cecum at the time of collection.

Since the carbohydrate digestibility figures as presented in Table 5 showed no consistent trends they were assembled as shown in Table 6. In this manner the "net change" in apparent digestibility between the cecum and the point of excretion could be assessed. The digestibility figures for the 8th and 10th hours at the cecal level were compared individually to the compositcd fecal sample (8th and 10th hours) for each ration and each calf. In this comparison it is conceivable that an error could be introduced into the calculated net change of digestibility since individual cecal values are compared to a composite fecal value. It will be noted, however, that in these calculations the net change for the corn diet is consistently negative and that for starch is consistently positive. The reason for the high negative digestibilities at the cecal level for the starch diet is not clear but some of the possible factors involved will be discussed later.

When the mean of the 8th and 10th hour cecal samples for each calf is used to determine the net change, some variation is eliminated and the net changes for corn and starch remain negative and positive, respectively. When the mean digestibility for all animals on each diet is obtained as shown in Table 6 and the net change is calculated from the means, the net change for corn is approximately minus 11 percent and that for starch is approximately plus 53 percent. Calculation of the digestibility of corn
### Table 6. Calculated Net Changes between Cecal and Fecal Digestibility Values

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<tr>
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<th>Starch</th>
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<td>Fecal</td>
<td>Net change</td>
<td>Cecal</td>
<td>Fecal</td>
<td>Net change</td>
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<td>-13.36</td>
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</tr>
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<td>59.66</td>
<td>56.78</td>
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<tr>
<td>Mean²</td>
<td>-3.93</td>
<td>-12.30</td>
<td>-8.37</td>
<td>8.60</td>
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<td>Calf 8 hr.</td>
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<td>-48.10</td>
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| All Mean calves | 0.69 | -10.18b | -10.87 | -31.46 | 21.84 | 33.30 |

Mean digestibility all values

| Mean of corn and fecal values | 0.99c |       | 0.07c | 21.84 |

---

²Net change between mean of the cecal values and the fecal values.

bObtained from calves 3671 and 3688.

cObtained by averaging cecal and fecal means for corn and starch, respectively.
and starch of the respective diets from overall mean values at the cecal and fecal levels shows plus 0.39 percent for corn and minus 4.31 percent for starch.

Absorption by Isolated Visceral Sections

Changes in blood reducing sugar levels following injection of glucose into ligated sections of exteriorized viscera of the bovine are presented in Table 7 and are shown graphically in Figure 2. Blood samples were taken from efferent blood vessels of the respective visceral sections. Values for venous blood from the jejunum and for jugular blood are available only for calf 3638.

Following injection of glucose into the jejunum a rapid and relatively constant rise in blood reducing sugar levels was noted, indicating considerable absorption from this area. A relatively constant rise also was noted following glucose injection into the ileum but the rate of increase was considerably less than that observed for the jejunum. The cecum and rumen values show a definite rise in blood glucose at 20 minutes after glucose injection into the respective viscera but subsequently a decline was noted. Samples of blood from the jugular vein of calf 3638 were obtained at time intervals similar to those employed in sampling blood from the isolated visceral sections. Blood reducing sugar levels in the jugular blood were relatively constant during the period of observation, suggesting that Nembutal injection and glucose administration into the isolated
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*Table 7. Blood Hemoglobin Percent Levels vs Age*
Figure 2. Blood Reducing Sugar Absorption from Isolated Portions of the Exteriorized Tract.
sections had no appreciable effect on these values. The glucose values of Table 7 cannot be quantitatively compared since the blood volume of each section studied was unknown. However, it seems apparent that all of the isolated sections of the gastrointestinal tract absorbed glucose, although perhaps with variable efficiency, when glucose was introduced into these sections.
DISCUSSION

Digestion and Absorption in the Intact Animal

It may be well to review briefly the relevant aspects of carbohydrate metabolism in the ruminant before discussing the results of the present investigation. Not until recently has the metabolism of the ruminant species been considered to be different from that of the non-ruminant. The change of thinking in regard to ruminant animals was encouraged chiefly by the discovery that the volatile fatty acids produced in the rumen are not metabolites having no apparent value to the animal but in reality are substances which contribute immeasurably to the pool of useful products of digestion (27). The lower fatty acid production in the ruminant paunch was not readily accepted as a vital step in the breakdown of cellulose. Woodman (47), in a review as late as 1930, stated that all evidence indicated that the primary end product of cellulose digestion was glucose and that the glucose passed into the lower tract to be absorbed for subsequent conversion to fat and energy, as was evidenced in the carbohydrate digestion of other species. Comparison is made in this review (47) to species outside the realm of cellulose-utilizing mammals, which have a somewhat different type of metabolism and cannot use appreciable amounts of acetic acid in the diet.

Woodman and Evans (48) continuing the work on the mechanism of
cellulose digestion in the ruminant organism reported in 1938 that the
normal end-products of fermentation of pulped paper at 65° C. were organic
acids and gaseous compounds. However, when an antiseptic such as toluene
was shaken into the medium at the "head" stage of the reaction and the
incubation was continued at 37° C., the production of glucose could be
demonstrated without difficulty. This finding was interpreted as showing
that glucose is an intermediate product in the breakdown of cellulose by
bacteria, and that the glucose thus produced is absorbed in appreciable
quantities and is utilized in the metabolic processes of the ruminant.
Without taking into consideration the possible nutritional value of the
fatty acids, Woodman and Evans were unable to reconcile their results
with the 1905 findings of Kleiber which showed that digested cellulose
and starch have almost equal fat forming powers in the ruminant animal.
A reason for the difficulty in reconciliation of these findings lies in
the fact that (on the basis of investigations with rats) Woodman and Evans
discounted the value of fatty acids. In their investigations rats had
shown poor use of these "metabolites". Thus the application of informa-
tion obtained from one species of animals to rather distantly related
species proved hazardous and misleading. It has been shown by a number
of investigators (16, 36, 37, 38) that glucose is not a normal end product
of digestion in the pouch of the ruminant since this monosaccharide is
readily attacked by the microorganisms present.

Eldeen and Phillipson (8) have contributed greatly to the knowledge
of the significance of volatile fatty acids in the metabolism of the
ruminant. These workers stated, ten years after the report of Woodman
and Evans (49), that there is no reason to suppose that the volatile fatty
acids are waste products of digestion since the large heat increment which
follows feeding in the ruminant may well be in part the result of the
rapid metabolism of acetic acid. Furthermore, propionic acid is known to
be converted to carbohydrate while butyric acid behaves as long chain
fatty acids.

Owen (26) emphasized that the production of fatty acids by rumen bacte-
ria has far-reaching effects and renders the metabolism of the ruminant
very much different from that of other mammals. To give substance to this
statement Owen cites the work of Popjak and associates in London5 in which
these investigators, using radioactive carbon, found acetic acid to be of
great importance in mammary gland metabolism. The work of McClymont6
was cited in this same regard. In addition, calculations were made by Owen
from the work of Barcroft7 which showed that the metabolizable energy of
volatile acids absorbed from the rumen is equivalent to about 40 percent
of the basal metabolism of the sheep. The above biochemical and physio-
logical observations show that the ruminant possesses enzyme systems with
the ability to utilize the acetic, propionic and butyric acid which results
in large quantities from the metabolism of its alimentary symbionts.

5National Institute for Medical Research, London.
6Veterinary Research Station, Glenfield, N.S.W.
7Cambridge University, Cambridge, England.
There are two cases of the lemma, the Greek and the Hebrew. For example, in the case where the noun is masculine, the article is 

οὗτος

(he) and in the case where it is feminine, the article is

ὕστατος

(she).
hydrolyzed for the most part by alpha- and beta-amylase, respectively. As far as is known (46) the amylases of vertebrates are primarily the alpha-amylases and, therefore, these animals may be unable to hydrolyze beta starch which is the primary component of starch in grains (46). If this be the case, specificity exerts a strong influence on the digestive abilities of our domestic animals.

In the carbohydrate digestibility studies of the present investigation the marked differences between the glucose and maltose diets and the starch and corn diets may be attributed to the specificity of, or to the lack of, intestinal and pancreatic enzymes. The inadequacy of the amylolytic enzymes in the bovine is exemplified by the large amounts of starch present in the feces and in the cecal material. The calculated digestibilities of carbohydrate of the diets show a considerable variation but clearly indicate that the ability of the lower part of the bovine digestive tract to utilize starch is limited. A factor contributing to the negative digestibility values may have been the variable chromium oxide percentage of the dry matter (Table 5).

Baker (3, 4) and Van Der Math (45) entertained the hypothesis that the major portion of the carbohydrate ultimately utilized by the ruminant is available via the isophilic microorganisms as bacterial polysaccharides or as "paraglycogen" after ingestion of the isophilic by protozoa. Under such a set of conditions amylase must of necessity be present. In almost direct contrast to the hypothesis of Van Der Math and Baker, other workers (5, 16, 27, 36, 37, 38) suggest that very little carbohydrate, including
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On the basis of the investigations cited above little can definitely be stated concerning the quantitative aspects of intestinal amylase in the ruminant; however, it has been demonstrated that a strong alpha-amylase is produced by rumen microflora (34,45). The relative strength of pancreatic amylase of various species was investigated by Vonk (46) and that of ruminants was found to be quite weak. This researcher believed the low pancreatic amylase activity to be related to the efficient mastication of feed by ruminants and to the decomposition of carbohydrates which occurs chiefly through the activity of symbiotic bacteria of the rumen.

Since considerable uncertainty exists as to the activity, and actual quantitative production, of amylase in the small intestine, it may be possible that the extremely low digestibility of the corn and starch rations fed to the animals in the present experiment was due to inadequate production of intestinal and pancreatic amylase. In addition, it is possible that the amylase which hydrolyzes the bacterial polysaccharides may be rather specific and may be unable to attack either corn starch in a finely powdered state or the starch of corn, finely ground, in its natural state.

The net digestibility changes between cecum and rectum (Table 6) in all cases for all animals are negative for corn and positive for starch. This is true whether calculating net change with either single or composite fecal values or employing the average of all fecal or fecal values. The consistent negative net change values for the corn diet seem to imply that the carbohydrate content of the ingesta increased between the cecum and point of excretion. Such a change seems unlikely since there is no con-
maltose appeared to be readily hydrolyzed and absorbed. This is substantiated by the observation that virtually no reducing sugars appeared in either the fecal material or fecal excreta. It is conceivable, however, that some of the maltose could have been absorbed as the disaccharide fragment since it was introduced into the tract quite rapidly and in rather high concentrations. The observations made in the present study serve to support the concept that the ruminant is somehow handicapped in its ability to derive energy from the starch fraction of the natural grain without the assistance of a normally functioning rumen.

Absorption by Isolated Visceral Sections

The visceral absorption studies were conducted to investigate the ability of various sections of the ruminant gastrointestinal tract to absorb glucose. At the outset, it was recognized that the absorptive capacity of an animal under general anesthesia, with the abdomen open along the midline and the viscera exposed, might be abnormal. Nevertheless, it was thought that an investigation of this nature would yield some valuable and applicable information.

The portions of the tract showing marked absorption of glucose were the jejunum and the ileum which are the sections commonly believed to have the greatest absorptive capacity. The high concentration (50 per cent) of glucose injected into the lumen of the isolated portions possibly could have altered the permeability of the cellular membrane of the
blood reducing sugar level were noted when halbutal was used as a general anesthetic (Figure 2).

A number of investigators (8, 16, 27, 26, 37, 38) are of the opinion that the ruminant is rarely, if ever, called upon to obtain a very great portion of its energy supply from glucose absorbed from the gastrointestinal tract. The energy appears to come rather from the lower volatile fatty acids produced by microorganisms in the rumen. If this be the case, consideration must be given to the source of glucose in the blood of the bovine. This is answered to the partial satisfaction of some investigators (8, 32, 35) by the observation that propionic acid, one of the important lower fatty acids produced in the rumen has been shown to be a precursor of glucose in the ruminant. From the results of the absorption trials discussed herein it appears that the ruminant may be capable of absorbing glucose in varying degrees from sections of the gastrointestinal tract where glucose may be produced, namely, rumen, small intestine and cecum.

The present investigation has raised a number of questions concerning the digestion and absorption of carbohydrate in the ruminating bovine. Apparent low digestibility of grain carbohydrate and starch suggest that the appropriate amylolytic enzymes are not produced in abundance in the gastrointestinal tract of the bovine. The high incidence of diarrhea during ensame-abomasal feeding suggests that factors (mechanical or chemical) inherent in the natural feed may possibly provoke diarrhea. Significance also may be attached to the observation that starch appeared to undergo additional digestion in the large intestine. If such were the
of food consumption

consumption and the role of the large numbers of
hydrogenation in production and consumption
 phenomenon of food by the process which may affect normal
manner. The food in some countries, have been characterized
and in some others, production methods and consumption patterns
would also contribute to the consumption of food here are a variety of factors

possibility emerging that interest in food from the work which

consideration concerning a normal diet

that we have or that we expect, which is not even

case, the way in which the factors that shape the (or shapes)
Δύσκολη η ημέρα στον Στράτο, δεν είναι υπόλοιπο δραματικά έργα της τάξης μας. 

Poetry unreadable due to distorted characters.

Συνεπειά
In the absorption studies with isolated visceral sections, it was found that glucose was absorbed rapidly from the jejunum. The ileum appeared to be less efficient and the rumen and cecum were least efficient, but all sections absorbed glucose.
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ACKNOWLEDGEMENTS

The author wishes to express his appreciation to Dr. N. L. Jacobson for his assistance and guidance in the direction of this work and for his constructive criticism in the preparation of this manuscript. He is also grateful to Dr. E. N. Stoddard for his assistance in this investigation.

The writer also desires to express his sincere appreciation to Dr. L. G. Payne for performing the fistular operations on the experimental subjects and to Dr. R. S. Allen for his aid and instruction in the laboratory analyses necessary for this study.