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RECENT WORK ON ANIMAL FATS

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IN NEW ZEALAND the fat that research workers are most concerned with is butterfat. It is not generally realized that lamb and mutton, as well as cheese, contain 30% or more fat. Fat, in fact, is the main constituent of New Zealand exports, providing about 39% of the total weight.

Animal fats, apart from butter, are of interest to the industrialist as raw materials for the manufacture of soap, detergents, margarine and a host of other products. In fact, in U.S.A. where animal fats are in good supply much attention has been paid to finding new uses. As a result, it is now a common practice to add animal fats to animal and poultry feeds to improve their texture and food value. It has been suggested in U.S.A. that animal fats will eventually take their place alongside coal and petroleum as raw materials for the manufacture of chemicals.

Apart from their industrial uses, animal fats are important in other spheres. The amount, distribution and colour of the fat of an animal affect the quality of the carcass and this is important to the animal breeder. In the bacon pig, where the dietary fat has a profound influence, the firmness of the fat also affects the quality of the carcass.

Animal fats, because of their high caloric value and their contribution to the palatability and growth rate, appear to be valuable constituents in the diet. They cannot, however, be recommended without certain qualifications. There is a body of opinion that the high consumption of animal fats in well nourished countries may be associated with the high incidence of atherosclerosis, which is the number one killer in such countries.

As a basis for industrial utilization, or for the understanding of the biological aspects of animal fats, it is necessary to know the types and proportions of the fatty acids present as well as their manner of combination in the glyceride molecule. Moreover, fats as isolated are not pure substances, but contain dissolved in them unsaponifiable constituents. These are usually present in small amounts (of the order of 1%), but in some organs,

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such as the liver, the amounts are considerably greater, and, furthermore, the fatty acids may be present mainly as phospholipids rather than as triglycerides or true fats.

There is no doubt that chemists have earlier derived satisfaction from the isolation and identification of new fatty constituents. It is felt now, however, that the interest is centred more upon the mechanism of formation of these constituents. This biochemical approach was not possible earlier because of the inadequacy of existing techniques, but with the introduction of isotopic labelling and of elegant analytical procedures, such as gas-liquid chromatography, a new era has emerged. Not merely can the nature of the fatty substances present in animal tissues be understood, but their origin in the body can also be traced. In fact, the changes in outlook in fats research are so revolutionary, that it is not possible to obtain a proper perspective without providing some historical background. The literature on fats has grown enormously. Some of it is found in journals now devoted specifically to this purpose, such as the *Journal of the American Oil Chemists' Society*, but much of it is still scattered in biochemical, chemical, nutritional, dairy science, and other journals.

For the present purpose some of the earlier milestones in fats research will be reiterated before touching on matters relating to present day progress.

The nature of fats as esters of glycerol and fatty acids was first revealed by Chevreul in 1823, who, in addition, isolated several fatty acids from milk and depot fats. In the middle of the last century, Berthelot, another French chemist, synthesized many triglycerides, thereby confirming Chevreul's views on the nature of fats.

The nineteenth century closed with the isolation and characterization of most of the now well-known fatty acids, albeit in impure form. There were, however, no effective methods for the determination of the proportions of the fatty acids, as may be illustrated by the fact that whereas one investigator recorded 2% stearic acid in butterfat, another found 40%.

The occurrence of other fatty substances, such as phospholipids, in which fatty acids are also present, became increasingly evident before the end of the century, though confusion as to their exact nature remained. On the more biochemical aspects, it was still undecided as to whether fat was hydrolysed before absorption or taken through the intestinal wall directly in particulate form. Some even supposed that, despite

the pH conditions (about pH 7) in the intestine, the fat was absorbed as soap. This confused situation remained unresolved until at least twenty years ago, and it would be venturesome to suggest even now that the apparently elementary phenomenon of fat absorption is completely understood.

Carbohydrates are not of much consequence as components of animal tissues, though glycogen is stored in the liver and elsewhere. Proteins, on the other hand, have been widely recognized as important constituents of animal tissues, and much attention has been devoted to elucidating their nature in terms of the amino acids present, and the need for these essential building stones in the diet. The work of Emil Fisher on proteins carried out more than half a century ago has been emphasized in textbooks dealing with chemistry and with biochemistry. By comparison, fats, which in many humans, as well as in livestock animals, are in excess of muscle or protein, and form a substantial part of the total weight, have been consistently neglected. Nevertheless, it must have occurred to some that not all of the fat present in the body has come from the dietary fat. The classical experiment of Lawes and Gilbert, carried out on pigs at Rothamsted in 1866, remained for over 70 years as the only convincing evidence for the formation of fat in the animal from carbohydrates using fat-free protein and carbohydrate diets. Longenecker confirmed in 1939(a) the Rothamsted experiments, demonstrating the endogenous formation of fat. The newer knowledge has merely provided the mechanism for these transformations.

Long before the end of the nineteenth century, many investigators had fed oils and fats to different animals, and it became established in textbooks that dietary fats were taken up into the depot fats. However, such a picture is an over-simplification, and the writer feels that to some extent help in further clarifying our knowledge has been given by a textbook error. Without giving the original source, Armstrong and Allen, in a Leverhulme Lecture delivered in 1924, stated that horses fed pasture laid down fats similar to those of sheep and oxen. This statement is repeated in 1947 in Hilditch's well-known textbook on fats, and if it had not been for the writer's opportunity to inspect horse oil subsequently, and to compare it with sheep fat from animals grazing on similar pasture, he would no doubt have continued to believe the textbook. The facts are, however, that horse oil, like the pasture oil, is rich in the liquid unsaturated linolenic acid, while the hard mutton tallow contains little or none of this component.

What is it that has caused these two species, living on the same pasture, to lay down such different kinds of fat? As will be explained later, the difference is to be attributed to the presence of a rumen in the sheep with its populations of active micro-organisms. Those specializing in ruminant metabolism, who rightly regard the rumen as highly significant for the breakdown of dietary cellulose and protein, have overlooked its effect on dietary fat or even emphasized that such an effect does not exist.

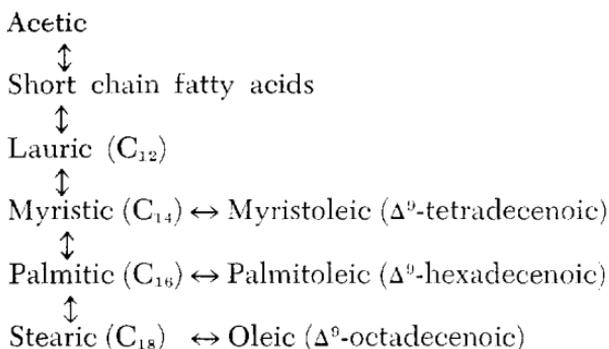
Now that the trend of events in the development of our knowledge of animal fats has been outlined, it is proposed to consider in more detail the recent work, but here it must be emphasized that only certain aspects can be touched on by way of example. For this purpose fat formation and the role of fat in nutrition have been selected. The former covers a wide field in which great progress has been made, while the latter is of current interest as it is indicative of the growing belief that fats have a role in the diet other than merely providing calories.

Fat Formation

The subject of fat formation can be subdivided into two parts, as it is now well recognized that the fat in an animal comes from two sources: (a) Endogenous by synthesis from non-fatty dietary constituents within the animal, and (b) Exogenous, or from the dietary fat.

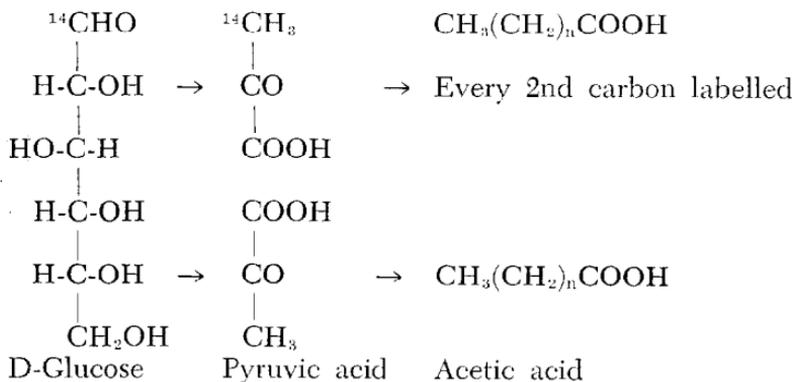
Although, as already stated, the formation of fat from carbohydrate was long established, the mechanism for this process remained unknown until the development of the isotopic labelling technique.

Although β -oxidation, whereby fatty acids were degraded by the animal two carbons at a time, has been amongst the most firmly established principles in biochemistry since its discovery by Knoop in 1905, the converse or the condensation of C_2 units to form higher fatty acids was without proof until 1944. Using acetate labelled with ^{13}C in the carboxyl group and with D in the methyl group, Rittenberg and Bloch (1944, 1945) established that this substance was converted into fat by mice and rats. Moreover, the degradation of the fatty acid molecules both in this experiment as well as in the later investigations of other workers was consistent with the head to tail condensation of acetic acid. The extension of this work has since demonstrated the following interrelationships in the synthesis and degradation of fatty acids in animal depot fats.



One of the difficulties in accepting acetate as the precursor in the production of endogenous fat has been the apparent absence of acids below C_{10} in animal fats. Now, however, more sensitive methods have revealed their presence (Hansen and McInnes, 1954). Moreover, the British workers Popjak (1952) and Folley (1952) have now demonstrated the extraordinary activity of the mammary gland in connection with fat synthesis. Here the products of synthesis are stabilized by their rapid removal from the milk ducts, giving the full range of even-numbered carbon fatty acids from C_2 to C_{16} . In ruminants, the products of digestion in the rumen consist largely of acetate, which is transported in the blood stream to the udder so that it is particularly easy to visualize the sequence of events in fat formation. Following the intravenous injection of labelled acetate into a lactating goat, a relationship was found between specific activity, chain length and the biochemical mechanism of fatty acid synthesis by the successive addition of acetic acid molecules to the carboxyl end.

It has become clear that the conversion of proteins and carbohydrates to fats involves their prior degradation to acetate. This may be illustrated in the case of glucose as follows:



What has been described shows that acetate is the building stone of fat. Acetate *per se* is not active, however, and it was not until 1951 that Lynen and Reichert showed that the active unit was in fact the thioester formed from coenzyme A and acetic acid.

The attachment of the sulphhydryl group of coenzyme A to the acetyl group confers on it the properties of an acid as well as labilizing the methyl hydrogen. With such head and tail activations of the acetyl molecule it is possible to visualize the chemical mechanisms of the biological synthesis in terms of Lynen's fatty acid cycle (Fig. 1).

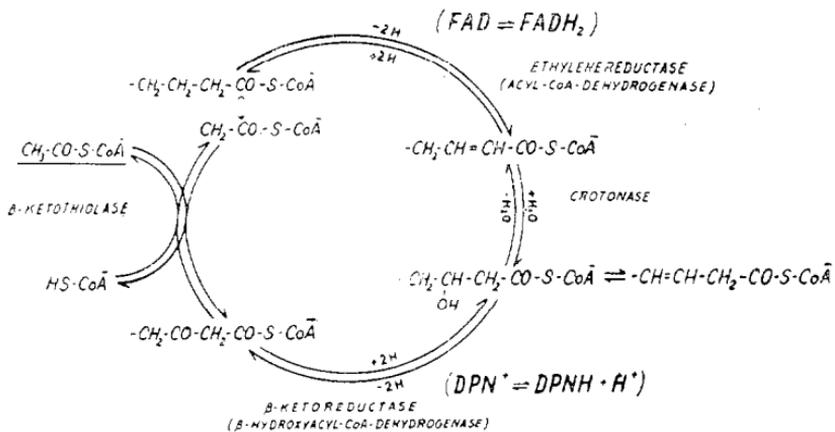


Fig. 1: Fatty acid cycle (according to Lynen, 1954).

The synthesis of fatty acids is achieved by a repetition of four consecutive steps catalysed by enzymes as follows:

- (1) One molecule of acetyl coenzyme A condenses with another giving acetoacetyl-coenzyme A.
- (2) Acetoacetyl coenzyme A is reduced to β -hydroxybutyryl coenzyme A in the presence of reduced diphosphopyridine nucleotide.
- (3) β -hydroxybutyryl-coenzyme A undergoes degradation to crotonyl-coenzyme A.
- (4) Crotonyl-coenzyme A is reduced to butyryl-coenzyme A in the presence of reduced flavine.

In these four steps the carbon chain of the original acetyl coenzyme A is extended by two carbon atoms. An additional acetyl coenzyme A and four additional hydrogen atoms are required. The repetition of the cycle eight times in a spiral-wise manner will produce stearyl-coenzyme A.

When fatty acids are oxidized, the reaction shown in the Lynen fatty acid cycle above are reversed, giving acetyl-coenzyme A which in turn combines with oxaloacetate to pass into the citric acid cycle to be oxidized into carbon dioxide and water. The level of fatty acid oxidation is therefore determined by the rate at which oxaloacetate becomes available. If this rate falls off through depression of carbohydrate metabolism as in diabetes, then acetyl coenzyme A cannot be metabolized completely. Acetoacetyl-coenzyme A accumulates and gives rise to the 'ketone bodies' of the blood by being hydrolysed by a deacylase, found only in liver, to give free acetoacetate.

By the nature of the synthesis endogenous fat will contain fatty acids with an even number of carbon atoms and the preponderance of C_{16} and C_{18} acids is determined by the specificity of the enzymes concerned.

Such fatty acids are known to be desaturated by the animal but only in the Δ^9 position. No reason is known for this limitation to the production of such mono-unsaturated acids, but in the absence of dietary fat the depot fat consists essentially of palmitic, stearic and oleic acids.

To obtain a picture of the depot fats of animal fats the exogenous or dietary fat must also be taken into account. The dietary fat is, of course, considerably modified before deposition in the animal. Though fats are usually 95% or more digestible, higher fatty acids of high melting point are selectively excreted, as are certain unsaturated acids of which the best known example is erucic acid present in rape seed oil. The fats are hydrolysed in the intestinal lumen giving free fatty acids, as well as mono- and diglycerides, but in the course of their passage through the cells of the intestinal wall they are resynthesized into triglycerides or neutral fat, newly formed glycerol being used for this purpose to a considerable extent. They are carried by the lymph into the blood stream where, during the passage through various organs and tissues, an exchange occurs between the fatty acids in the glycerides and the phospholipids which results in an enrichment of the phospholipids in respect to stearic, C_{20-22} unsaturated acids and C_{18} dienoic acid.

The general picture of events in fat formation is given in Fig. 2.

Ruminants appear to modify their ingested fats more than do non-ruminants, so that in contrast to non-ruminants the feeding of unsaturated oils is without obvious effect. However, the experiments carried out in connection with bloat by the

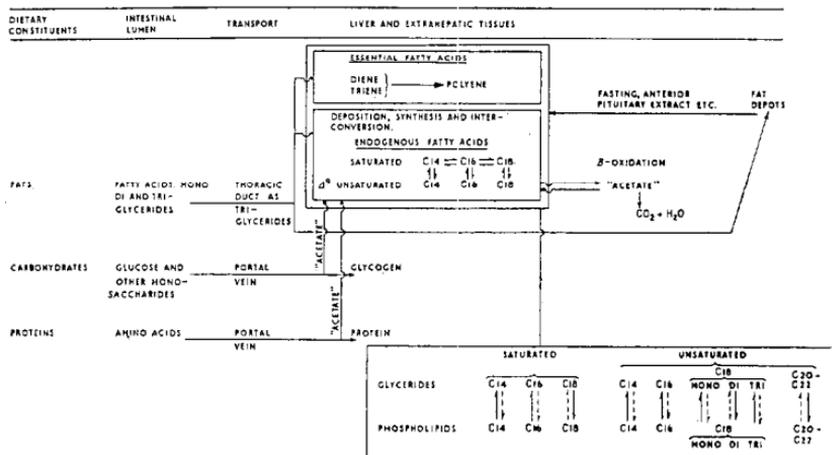


Fig. 2: Generalized pattern of fat formation (Shorland, 1955).

Dairy Research Institute and Plant Chemistry Laboratory have shown that drenching of cows with whale oil has raised the iodine value of the butterfat (McDowall, *et al.*, 1957). Nevertheless, the butter does not appear to contain the original whale oil fatty acids, but only their hydrogenated isomers. (Weenink and Shorland, 1958, unpublished data.). Perhaps the first observation of the effect of the rumen on dietary fat was that of Reiser in 1951. He reported that linolenic acid present in linseed oil was converted by rumen micro-organisms to linoleic acid. This observation appears to have remained unnoticed for some time. However, the work in the Fats Research Laboratory revealed many peculiarities of ruminant fats, including particularly a high content of *trans* unsaturated acids, in contrast to the *cis* acids normally found in plant and animal tissue fats (Hartman, Shorland and McDonald, 1955). In collaboration with the Plant Chemistry Laboratory and the Dominion Laboratory, it was shown that the rumen micro-organisms hydrogenate unsaturated fatty acids more extensively than was supposed by Reiser (*cf.*, Shorland *et al.*, 1955), linoleic acid, the main fatty constituent of pasture, being converted mainly to stearic acid. In addition, from the results of industrial hydrogenation, it was inferred, and established experimentally, that the unsaturated acids of ruminant fats contain appreciable amounts of *trans* and positional isomers of oleic and linoleic acid. Such a situation, as shown in Table 1, was not previously recognized, let alone explained.

TABLE 1: COMPARISON BETWEEN TYPICAL NATURALLY OCCURRING C₁₈ UNSATURATED FATTY ACIDS AND THOSE FOUND IN RUMINANT FATS.

Typical plant and animal fats	Ruminant fats
Monoene—CH=CH— Δ ⁹ <i>cis</i>	—CH=CH— Δ ⁸ , Δ ⁹ , Δ ¹⁰ , Δ ¹¹ <i>cis</i> and <i>trans</i>
Diene —CH=CH.CH ₂ .CH=CH— Δ ⁹ <i>cis</i> , Δ ¹² <i>cis</i> .	—CH=CH.CH ₂ .CH=CH— non-conjugated Δ ⁹ <i>cis</i> or <i>trans</i> Δ ¹² <i>cis</i> or <i>trans</i> also probably other positions of double bonds. —CH=CH.CH=CH— conjugated e.g., Δ ⁹ <i>cis</i> or <i>trans</i> Δ ¹¹ <i>cis</i> or <i>trans</i> —CH=CH.CH ₂ .CH=CH— Double bonds separated by two or more methylenic groups.

In addition to acetate, the breakdown of carbohydrates by the rumen bacteria also furnishes propionic acid. By the isotopic labelling techniques, James *et al.* (1956) have shown that propionate is the precursor of the *n*-odd numbered acids which have been shown to be normal constituents of ruminant fats. It seems probable that the branched-chain acids belonging to the *iso* and *anteiso* series, which have been found in ruminant fats also originate from the lower branched fatty acids homologues formed in the rumen from the breakdown of protein as shown in Fig. 3.

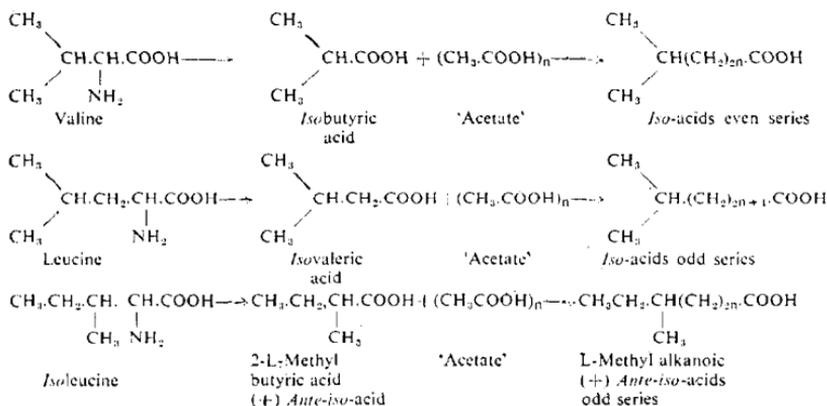


Fig. 3: Transformation of amino acids to branched-chain fatty acids (Shorland, 1956).

Despite the fact that the branched-chain and *n*-odd numbered acids amount collectively to perhaps 4% of the total fat of ruminants, their presence was discovered prior to 1951. Formerly the inclination was to accept differences in fatty acid composition between species as inherent in the species themselves, but now the explanation can be sought in a study of the biochemical processes involved in fat formation.

Hilditch and Lovern, in the evolution of natural fats published in 1936, drew attention to the simplification of fatty acid composition in proceeding from the less developed to the more highly developed forms. In particular, fishes, as compared with mammals, contained high proportions of C₂₀₋₂₂ unsaturated acids in their depot fats.

It is now more appropriate to look at the data from the point of view of biochemical processes. For example, fish, apparently, are unable to synthesize fat from non-fatty sources. The fats laid down are therefore essentially those present in the diet.

Amphibia have access to aquatic fat, but in addition, they can synthesize fat from non-fatty sources. Their fats are the result of a mixture of exogenous and endogenous fat. Finally, in ruminants, owing to hydrogenation, the unsaturated fats of the diet are largely converted to saturated. Their fat has the appearance of being entirely of endogenous origin when examined by ester fractionation techniques, but when studied by infra-red spectroscopy, the presence of *trans* acids characteristic of ruminant fats and derived by hydrogenation of dietary fat in the rumen is revealed.

Animal Fats in Nutrition

Animal fats and plant fats are sometimes thought of as necessarily possessing different properties. However, if non-ruminants are considered it is found that their depot fats tend to resemble those of the diet. It is possible, for example, by feeding large amount of corn oil (Longenecker 1939b) to rats to produce depot fats the composition of which is indistinguishable from corn oil. Ruminant fats on the other hand, because they have been subjected to hydrogenation, differ from plant fats in their relative absence of linoleic acid or vitamin F, which is essential to growth of rats and other animals. However, so far as humans are concerned, the conditions for producing a vitamin F deficiency are apparently so stringent that they have never been attained. The question of efficiency of the linoleic isomers present in ruminant fats has also been

raised, but again there is no evidence that this has any practical significance. A possible harmful effect of hydrogenated fat is suggested from experiments in which rats were fed 28% hydrogenated arachis oil as a source of fat (Aaes-Jorgensen, *et al.*, 1957). The animals developed sterility, curable by the addition of linoleic acid. The results are interesting but their human implications are unknown.

There remains much scope for testing individually the constituents of animal fats. Towards this end the Fats Research Laboratory has collaborated with the Nutrition Research Department in Dunedin. As an example of the type of work in progress, rats have been fed 0.1 g of (+)14-methyl hexadecanoic acid, a branched-chain acid present in ruminants. It appears that this acid is stored and degraded in much the same way as the normal saturated fatty acids (Livingston, *et al.*, 1957).

As mentioned earlier, the nutritive value of animal fat lies in its high caloric value of 9 as compared with 4 or 5 for carbohydrates and proteins. In addition, the calories from carbohydrates and proteins are more effectively utilized when fat forms a substantial part of the diet. Such a diet improves the capacity for work as compared with a fat-poor diet. Using isocaloric diets it has been found that animals grow better when the proportion of fat is increased up to perhaps an optimum level of 30%.

Against this background of enthusiasm for animal fats must be weighed the hypothesis fostered, particularly by Ancel Keys (1957), that there is a relationship between fat intake and the incidence of atherosclerosis. Atherosclerosis, or the formation of mushy deposits in blood vessels, is a primary cause of death in adults in well-nourished countries where the fat intake is also high. These deposits are rich in cholesterol and other lipids. It cannot be stated, however, whether such deposits are the cause or the result of the disease. If they are the cause, then it would seem reasonable that to control the disease cholesterol formation should also be controlled. Most of the cholesterol is formed endogenously from acetate. Experimentally, it has been found that, whereas animal fats raise the cholesterol content in blood, unsaturated fats such as corn oil or fish oil lower the level, as does also starvation.

The hypothesis that fats are concerned with atherosclerosis is an interesting one, and some authorities would advocate that for treatment it is perhaps worth while restricting the intake of animal fat and even substituting corn oil. However, few as

yet have advocated any radical change in diet for the majority. The hypothesis that fat, particularly animal fat, is the primary cause of atherosclerosis is not proven, but it is to be regarded for the moment as an incentive to carrying out further work in the hope that it will contribute towards an understanding of one of the major problems of our time.

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DISCUSSION

Q : : *The question of the importance of fat depots in animals in relation to heat tolerance has recently been raised in Australia; the latent heat of fusion of such fat has been suggested to confer an advantage as regards heat toleration. Could Dr. Shorland comment on this idea?*

A : : I am unaware of the latent heat of fusion of the fat depots as a factor in the heat toleration of animals. Fatty depots are usually thought of as being liquid at the body temperature.

Q : : *Could Dr. Shorland comment on the possible relationship of fatty acids in plants and the destruction of vitamin E in plant material either living or in the process of digestion?*

A : : In the living plant it is probable that vitamin E and the fatty acids are separated so they cannot interact. It is only when the plant tissues

are macerated as in chewing that an interaction is likely to occur. It is generally believed that vitamin E deficiency diseases require the presence in the diet of highly unsaturated fatty acids. In this regard linolenic acid (the main fatty constituent of the pasture) should be highly effective.

Q: : *I am unable to line up Dr. Shorland's reply with the information which he gave earlier regarding the hydrogenation of linolenic acid in the rumen. Could the factor be one of the other unsaturated acids which is not so dehydrogenated?*

A: : Your point in regard to the hydrogenation of linolenic acid by the ruminant is relevant in as much as the greater part of this acid appears to be converted in the rumen to the saturated stearic acid. Nevertheless some conjugated dienoic acid is formed and this is taken into the fatty depots. Feeding experiments using linseed oil show that the amount of conjugated dienoic acid in milk fat increases with increasing intake of this oil. Moreover dienoic acids appear to be converted into highly unsaturated C₂₀-C₂₂ acids. The unsaturated acids of the diet, while being largely converted to saturated forms, nevertheless make some contribution to the amounts of unsaturated fatty acids in the depots and hence presumably contribute to the probability of vitamin E deficiency.