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THE ANIMAL AS A CONVERTER OF MATTER AND ENERGY

A Study of the Rôle of Live Stock in Food Production

BY

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American Chemical Society
Monograph Series

BOOK DEPARTMENT

The CHEMICAL CATALOG COMPANY, *Inc.*
19 EAST 24TH STREET, NEW YORK, U. S. A.
1925

Printed in the United States of America by
J. J. LITTLE AND IVES COMPANY, NEW YORK

GENERAL INTRODUCTION

American Chemical Society Series of Scientific and Technologic Monographs

By arrangement with the Interallied Conference of Pure and Applied Chemistry, which met in London and Brussels in July, 1919, the American Chemical Society was to undertake the production and publication of Scientific and Technologic Monographs on chemical subjects. At the same time it was agreed that the National Research Council, in coöperation with the American Chemical Society and the American Physical Society, should undertake the production and publication of Critical Tables of Chemical and Physical Constants. The American Chemical Society and the National Research Council mutually agreed to care for these two fields of chemical development. The American Chemical Society named as Trustees, to make the necessary arrangements for the publication of the monographs, Charles L. Parsons, Secretary of the American Chemical Society, Washington, D. C.; John E. Teeple, Treasurer of the American Chemical Society, New York City; and Professor Gellert Alleman of Swarthmore College. The Trustees have arranged for the publication of the American Chemical Society series of (a) Scientific and (b) Technologic Monographs by the Chemical Catalog Company of New York City.

The Council, acting through the Committee on National Policy of the American Chemical Society, appointed the editors, named at the close of this introduction, to have charge of securing authors, and of considering critically the manuscripts prepared. The editors of each series will endeavor to select topics which are of current interest and authors who are recognized as authorities in their respective fields. The list of monographs thus far secured appears in the publisher's own announcement elsewhere in this volume.

The development of knowledge in all branches of science, and especially in chemistry, has been so rapid during the last fifty years and the fields covered by this development have been so varied that it is difficult for any individual to keep in touch with the progress in branches of science outside his own specialty. In spite of the facilities for the examination of the literature given by Chemical Abstracts and such compendia as Beilstein's Handbuch der Organischen Chemie, Richter's Lexikon, Ostwald's Lehrbuch der Allgemeinen Chemie, Abegg's and Gmelin-Kraut's Handbuch der Anorganischen Chemie and the English and French Dictionaries of Chemistry, it often takes a great deal of time to coördinate the knowledge available upon a single topic. Consequently when men who have spent years in the study of important subjects are willing to coördinate their knowledge and present it in concise, readable form, they perform a service of the highest value to their fellow chemists.

It was with a clear recognition of the usefulness of reviews of this character that a Committee of the American Chemical Society recommended the publication of the two series of monographs under the auspices of the Society.

Two rather distinct purposes are to be served by these monographs. The first purpose, whose fulfilment will probably render to chemists in general the most important service, is to present the knowledge available upon the chosen topic in a readable form, intelligible to those whose activities may be along a wholly different line. Many chemists fail to realize how closely their investigations may be connected with other work which on the surface appears far afield from their own. These monographs will enable such men to form closer contact with the work of chemists in other lines of research. The second purpose is to promote research in the branch of science covered by the monograph, by furnishing a well digested survey of the progress already made in that field and by pointing out directions in which investigation needs to be extended. To facilitate the attainment of this purpose, it is intended to include extended references to the literature, which will enable anyone interested to follow up the subject in more detail. If the literature is so voluminous that a complete bibliography is impracticable, a critical selection will be made of those papers which are most important.

The publication of these books marks a distinct departure in the policy of the American Chemical Society inasmuch as it is a serious attempt to found an American chemical literature without primary regard to commercial considerations. The success of the venture will depend in large part upon the measure of coöperation which can be secured in the preparation of books dealing adequately with topics of general interest; it is earnestly hoped, therefore, that every member of the various organizations in the chemical and allied industries will recognize the importance of the enterprise and take sufficient interest to justify it.

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Preface.

The production of this monograph was begun by the late Dr. H. P. Armsby during the last months of his life. The completion of the work was turned over to the junior author after Dr. Armsby's untimely death. Such a change of pilots is sure to have some effect upon the course pursued but it is hoped that a long acquaintance with both the man and his work has rendered this change less disturbing than it would otherwise have been. The use of footnote references has seemed to fill the needs of this monograph better than a bibliography. It is hoped that it will be useful to the reader.

Acknowledgment is hereby made of the helpful criticism and assistance rendered by Dr. E. B. Forbes, Dr. Armsby's successor as Director of the Institute of Animal Nutrition, and by Dr. F. G. Benedict of the Nutrition Laboratory of the Carnegie Institution. Without this help and criticism the production of this monograph would have been more difficult.

C. Robert Moulton.

Chicago, Illinois.
September, 1924.

Introduction.

The place of animal foods in the human dietary may well be shown to depend upon their supplying adequately and efficiently some or all of the constituents of an adequate diet. Human dietaries must supply energy in available forms and not accompanied by too much indigestible matter. Part of this energy must be supplied by proteins in order to furnish building material and to make good the losses of protein catabolism. It is generally considered that part of this energy must be supplied in the form of fats, partly to improve the flavor of the dietary, to decrease its bulk, and perhaps also for physiological reasons. The greater part of this energy should be in the form of carbohydrates which furnish cheap and easily available energy. The sugars also impart flavor to the dietary.

Besides the supplying of matter and energy in the above forms the human dietary must supply a variety and quantity of mineral matter or salts. Especially to be mentioned are calcium and phosphorus. Together they make up a very large part of the total ash of an animal. These salts are necessary as building materials for tissues, bones, and secretions, and they function in all processes of the living organism.

In addition a third class or type of substance is needed. The vitamins, of which at least three types are recognized, are essential to the life and well being of animals. Apparently they contribute no energy or mineral matter to the organism but are more comparable to the electric spark which fires an internal combustion engine.

Food for man may be divided into two classes, primary and secondary. The ultimate sources of food elements are the air, the earth, and water. Any food which is produced, for example, by the plant, from these with the aid of the sun can be called a primary food. When the food substances thus produced are used for the production of other food substances through the intervention, or by means of, another organism such as the hog, the resulting product, pork, may be called a secondary food. In this sense all the animal food consumed by man is secondary food. Man and food animals may then be considered as competitors for primary foods. This competition may be more fancied than real, for man is not so constituted physiologically as to be able to turn all of the primary foods to his use. To illustrate, man cannot make use of the entire wheat plant. He can use the grain or at least most of the grain. The remainder of the plant is of no use as a food for man but may be made to contribute to his food supply through the agency of an animal such as the hog, the beef steer, or the dairy cow. The herbivorous animal is of especial value here.

Fish are really in the class of secondary foods. They are sustained by plant or other animal life found in their environment. In a sense they are not competitors of man for food. In another sense the food they eat is grown from nutrients in the water they inhabit, which nutrients had their origin in the land. These nutrients might have been used for the direct production of human food, but as present they cannot be so used. Therefore, fish contribute to man's available food supply without using foodstuffs which man himself would use.

Foods of animal origin include, substantially, meat, milk, and eggs. Fish, of course, are in the same class. They are not cultivated or fed by man but are simply had for the taking. The others must be produced in the present state of society by man by feeding primary foods to the animal that produces them. These animal foods are of value as related to the foregoing functions or attributes of food for the following reasons:

1. They contain little indigestible matter, while the adipose tissue of meat, as well as butter, full cream cheese and milk powder, have high energy values.

2. Animal proteins have, as a rule, higher biological values than do vegetable proteins. A certain proportion of them is desirable in the diet of man and is especially necessary in the diet of growing children. They effectively supplement the vegetable proteins.

3. Aside from the vitamins associated with certain of them, animal fats are probably not superior to vegetable fats. The dietary habits of northern races, however, call for a supply of animal fats, although the manufacture of the so-called nut margarines, vegetable shortenings and vegetable oils tends to a greater utilization of vegetable fats.

4. Most animal foods contain minimum amounts of carbohydrates and are of little significance as a source of these substances, with the exception of the lactose of milk.

5. Animal products provide a good supply of most of the mineral elements needed. Milk stands pre-eminent in supplying all but iron. Flesh is especially important for the iron and phosphorus content but is lacking in calcium and perhaps sodium and chlorine. Edible glands supply most of the mineral elements but here again calcium is lacking.

6. As sources of vitamins A and B milk and dairy products are important. Fresh milk probably supplies adequate amounts of vitamin C for the infant. Eggs supply vitamins A and B also. Meat supplies all three vitamins, which supply seems to be adequate when meat forms the sole or chief

source of food. The edible organs, however, are rich in vitamins A and B.

The above discussion has dealt with the adequate quality of animal foods. Quantitatively the animal is of importance as a mechanism for utilizing inedible plant products or an economic surplus of edible ones. It converts poor vegetable proteins into better animal proteins and changes more or less unavailable carbohydrates—pentosans, cellulose, etc.—into easily available energy. This monograph will deal largely with the efficiency of the animal in converting plant matter into energy for human consumption.

The subject divides itself into two parts:

I. The chemical processes by which the qualitative changes indicated above are effected and by which inedible materials are rendered more or less available.

II. The quantitative efficiency of the animal as a converter of protein and especially of energy. The more important methods of investigation will be described here.

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PART I.

THE CHEMICAL PROCESSES OF CONVERSION.

Chapter I.

The Raw Materials, Feeding Stuffs.

Origin. The crops grown upon the farm and range, inclusive of pasturage, together with a variety of by-products of the preparation of certain of them for use as human food or for other purposes, constitute the raw materials out of which are manufactured the animal foods consumed by man, with the exception of fish and molluscs (oysters, clams, etc.) which, at least in the United States, constitute but a very small fraction of the total dietary.[1] They will be designated here as feeds, or feeding stuffs, reserving the term, foods, for materials eaten by man.

Classes of Feeding Stuffs. Feeding stuffs are conveniently divided into three major classes, namely: concentrates, or concentrated feeds; coarse fodders, or roughage; and roots and tubers.

By concentrates is meant feeding stuffs containing much nutriment in a small bulk. They include the grains and other seeds as well as a large number of by-product materials derived both from vegetable and animal sources. Chemically they are characterized by a relatively low percentage of crude fiber, ranging from practically 0 to perhaps 10 or 12 per cent.

Coarse fodders consist substantially of the vegetative organs of plants and include hay, straw, and other forms of forage either fresh, ensiled, or dried. Chemically they contain a relatively large percentage of crude fiber and are bulky feeds, containing a large proportion of difficultly soluble ingredients.

Roots and tubers resemble fresh or ensiled coarse fodders in containing a large percentage of water, while on the other hand they resemble the concentrates in containing relatively little woody fiber and in being highly digestible.

Components. That plants contain a great variety of chemical individuals differing quantitatively and qualitatively from species to species and from stage to stage of growth needs no more than mention. As related to nutrition, however, they may be regarded as sources of five classes of compounds, viz.: proteins, non-proteins, carbohydrates, fats, and ash, it being always remembered that feeding stuffs *contain* these groups

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[1] In 1921 the value of fish products in this country amounted to only 3.5 per cent of the value of meat products.

but are not *composed* of them exclusively. For the purposes of this work it will suffice to characterize very briefly the members of these five classes.[2]

Vegetable Proteins. Few vegetable proteins other than those of seeds have been studied to any extent. The relatively small quantities in which proteins occur in other parts of the plant and the difficulty in separating them from each other has prevented any extended study of them. Osborne[3] names 24 simple proteins as the principal ones which have been isolated from various seeds and whose composition and properties have been studied. These include 4 albumins, 15 globulins, 2 glutelins and 3 prolamins. Osborne doubts the existence of nucleoproteins to any considerable extent in seeds although the embryos contain more or less nucleic acid. Similarly, glycoproteins and phosphoproteins do not appear to exist in seeds.

The ultimate composition of the seed proteins shows a considerable range of variation. The mean composition and heat of combustion per gram of 19 seed proteins and the extreme range, as given by Osborne,[4] are:

Composition of Vegetable Proteins

	Mean	Maximum	Minimum
Carbon	52.11	55.03	49.91
Hydrogen	6.88	7.03	6.67
Nitrogen	17.68	19.03	15.84
Sulfur	0.73	1.67	0.32
Oxygen	22.60	23.40	20.84
	100.00		
Heat of combustion per gram	5,636 cals.	5,916 cals.	5,358 cals.

As appears in Chapter 2, while the heat of combustion is not notably different the percentage of nitrogen tends to be higher than in the animal proteins.

On acid hydrolysis, the vegetable proteins yield qualitatively the same products as the animal proteins, viz.: substantially amino acids and some ammonia. No amino acids peculiar to the vegetable proteins have been obtained as yet. Quantitatively, however, a distinct difference appears between the two classes. The vegetable proteins yield, in particular, relatively large amounts of glutamic acid, while many of them are comparatively rich in prolin and arginin, to which is due their relatively high percentage of nitrogen. The prolamins, on the other hand, are notably poor in arginin, as well as glycin, lysin, histidin, and tryptophan. Some of

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[2] For a detailed discussion, compare Haas and Hill, "An Introduction to the Chemistry of Plant Products," London, 1917.

[3] "The Vegetable Proteins," London, 1916, pp. 73-81.

[4] *Loc. cit.*, p. 49.

these differences are illustrated in Table 1 which has been compiled chiefly from the results of T. B. Osborne and E. Abderhalden.

TABLE 1

Cleavage Products of Proteins

	Gliadin from Wheat	Gluten from Wheat	Zein from Maize	Legumin from Pea	Egg Albumin	Lactalbumin	Casein from Cow's Milk	Ox Muscle	Chicken Muscle
	%	%	%	%	%	%	%	%	%
Glycin	0.02	0.89	0.00	0.38	0.00	0.00	0.45	2.06	0.68
Alanin	2.00	4.65	9.79	2.08	2.22	2.50	1.85	3.72	2.28
Valin	0.21	0.24	1.88	?	2.50	0.90	7.95	0.81	+
Leucin	5.61	5.95	19.55	8.00	10.71	19.40	9.70	11.65	11.19
Phenylalanin	2.35	1.97	6.55	3.75	5.07	2.40	3.88	3.15	3.53
Tyrosin	1.20	4.25	3.55	1.55	1.77	2.20	4.50	2.20	2.16
Serin	0.13	0.74	1.02	0.53	?	?	0.50	?	?
Cystin	0.45	0.02	?	....	?	?	0.07	....	....
Prolin	7.06	4.23	9.04	3.22	3.56	4.00	7.63	5.82	4.74
Aspartic acid	0.58	0.91	1.71	5.30	2.20	1.00	1.77	4.51	3.21
Glutamic acid	42.98	23.40	26.17	16.97	9.10	10.10	10.77	15.49	16.48
Tryptophan	1.00	+	0.00	+	+	+	1.50	+	+
Arginin	3.16	4.72	1.55	11.71	4.91	3.23	3.81	7.47	6.50
Lysin	1.33	1.92	0.00	4.98	3.76	9.16	5.95	7.59	7.24
Histidin	0.58	1.76	0.43	1.69	1.71	2.06	2.50	2.66	2.47
Ammonia	5.11	4.01	3.64	2.05	1.34	1.32	1.61	1.07	1.67
Total	73.77	59.66	84.88	62.21	48.85	58.27	64.44	68.20	62.15

The individual proteins of some important agricultural crops lack certain amino acids. Thus the zein of maize lacks glycin, tryptophan and lysin and the gliadin of wheat lacks glycin. Practically all seeds, however, contain a mixture of more than one protein and it has not been shown that any one of the amino acids is entirely lacking in the case of total proteins of seeds excepting diamino-tri-oxydodecanic acid which is found only in casein. In brief, the mixed proteins consumed by farm animals may at times be unbalanced as compared with the body proteins, but probably never incomplete.

Non-Proteins. Besides the proteins, plants contain a variety of non-protein nitrogenous compounds. These have been designated collectively as non-proteins, this being an abbreviation for non-protein nitrogenous matter. The more important groups included under non-protein are the nitrogenous lipoids, nitrogenous glucosides, alkaloids and organic bases, amino acids, nitrates, and amids and ammonium salts. Occasionally somewhat considerable amounts of the latter compounds are found in vegetable materials but they are to be regarded rather as accidental materials than as constituting part of the plant. Of the organic compounds the amino acids and amids are of most significance in relation to the nutrition of animals. E. Schulze,[5, 6, 7] to whose researches the larger part of our knowledge in this field is due, enumerates seven nitrogenous glucosides and ten amino acids, viz.: valin, leucin, isoleucin, phenylalanin, tyrosin, prolin, tryptophan, arginin, lysin, and histidin, besides the purin bases, xanthin, hypoxanthin, adenin and guanin, as well as guanidin, allantoin and carnin, as having been isolated from various vegetable materials. Hart and Bentley[8] found that from 50 to 70 per cent of the water-soluble nitrogen of a variety of feeding stuffs existed as amino acids or peptids, while the amid nitrogen proper amounted to only 10 to 20 per cent of the whole.

Non-proteins are most abundant in the plant, as would be expected, where proteins are being built up, i.e., in those parts of the plant where active growth is taking place, and, on the other hand, under conditions where proteins are being broken down by fermentation, as in silage. They are likewise abundant in roots, where they serve as a nitrogenous reserve for the second year's growth.

It should not be assumed that non-proteins are of little or no use to the animal as a source of protein. It is certain that those which are of peptid or amino acid form may be just as useful as protein matter itself for the latter material must yield such products—peptids and amino acids—on digestion. However the assortment of amino acids may be much less complete in the non-proteins.

Carbohydrates. Agricultural crops as a whole are pre-eminently a source of carbohydrates. Pearl[9] computes that, of the total digestible matter contained in the primary foods produced in the United States for the seven years 1911-12 to 1917-18, inclusive, 83.5 per cent consisted of carbohydrates, while for the grain and hay consumed by domestic animals during the same period the corresponding percentage was 78.

Carbohydrates being products of the synthetic activity of chlorophyll bearing plants, beginning probably with the formation of formaldehyde, CH_2O, one naturally finds almost all classes represented in vegetable feeding stuffs but only the pentose and hexose groups occur in significant amounts.

Of the monosaccharoses, dextrose and levulose are found in small amounts in many forage plants, either free or in the form of glucosides. Of the disaccharoses, sucrose is the chief representative, occurring in not

[5] *Jour. f. Landw.*, 52 (1904), 305.
[6] *Ztschr. physiol. Chem.*, 45 (1905), 38.
[7] *Ibid.*, 47 (1906), 507.
[8] *J. Biol. Chem.*, 22 (1915), 477.
[9] "The Nation's Food," Philadelphia and London, 1920, pp. 54 and 262-268.

inconsiderable amounts in such crops as the sweet sorghums, sugar beets, etc. Maltose is found in small amounts in the cell sap and likewise in germinating seeds. Of the trisaccharoses, raffinose has been found in a few feeding stuffs. Rhamnose, a substituted pentose, occurs in some plant material.

It is the polysaccharids, including both hexosans and pentosans, however, which constitute the great bulk of the carbohydrates of feeding stuffs. Of the hexosans, cellulose and starch are the important members, the latter constituting the larger share of the carbohydrates of cereal seeds. Galacatans are found in the legumes in small amounts and mannans in various seeds, while a levulan, inulin, replaces starch in certain *compositae.* Of the pentosans, xylan, araban and the pectins are the chief representatives. In addition to these compounds, feeding stuffs, especially the roughages, contain in the cell wall substances such as the hemicelluloses and the gums which on hydrolysis yield both pentoses and hexoses, but whether they are compounds or only mixtures is uncertain. In the indurated cell wall[10] of mature plants are also found certain incrusting substances, designated collectively as lignin, which apparently are substituted celluloses containing methoxyl and ethoxyl groups in considerable amount. Such cell walls also contain small amounts of the cutin group whose chemical nature is little known.

Fats. Fats and other lipoids are very widely distributed in the vegetable kingdom. Many of the common true fats are mixed triglycerides of oleic, palmitic or stearic acids, although other acids are found in fats of commercial importance such as the erucic acid of rape oil and the linoleic acid of the drying oils.

Of lipoids other than the fats may be mentioned the waxes, the cholesterols, and the lecithins, while fat solvents remove from the vegetative organs of plants the green chlorophyll to which they owe their characteristic color.

Ash. This term is used rather loosely to designate all the elements contained in the plant other than carbon, hydrogen, nitrogen and oxygen. It includes both those present as electrolytes and those combined with the carbon compounds. The list includes sulfur, phosphorus, chlorine, sodium, potassium, calcium, magnesium, iron, iodine, bromine, zinc, manganese, and copper. Those following iodine in the list given are of rare occurrence and need not be considered further here. Silica is also frequently found in plant and animal material. These ash ingredients may be combined with organic matter or be taken by the animal in inorganic form.

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[10] Compare König: *Landw. Vers. Stat.,* 65 (1907), 55.

Vitamins. Concerning vitamins, or food hormones, very little need be said in a study of the efficiency of the animal as a converter. This is not because of their unimportance in the processes of nutrition, for they are like the vital spark in the gasoline engine without which the fuel and engine itself are impotent. It is largely for the reason that the energy and matter content of them is so small and partly because an adequate presentation of the subject would occupy too much space here. Three types are recognized at present: The fat soluble vitamin, or vitamin A, without which growth of animals is impossible: the antineuritic vitamin, or vitamin B, the absence of which causes nervous disorders and paralysis and results in poor growth; and the antiscorbutic vitamin, or vitamin C, the absence of which causes scurvy. For greater detail reference should be made to "The Vitamins" by Sherman and Smith and to similar works.

Feeding Stuffs Analysis.

The conventional scheme of feeding stuffs analysis makes no attempt to separate the vast number of individual compounds occurring in plants but seeks in rather crude fashion to determine the five groups of compounds named in the preceding paragraph. The results have been commonly reported in five rubrics: ash, crude protein, ether extract, crude fiber, and nitrogen free extract. This scheme dates back substantially to the early investigations at the Weende Experiment Station by Henneberg and Stohmann [11] and G. Kühn,[12, 13] and the analytical methods employed have been summarized by Wolff in 1875 [14] and 1876.[15]

Ash signifies the residue left after complete burning of the material in air or oxygen. Any portions of unburned carbon contained in the residue and usually its CO_2 contents are deducted, leaving what is known as the net ash. The ash includes both materials originally present as electrolytes and also some originally combined with the various carbon compounds of the plant, while on the other hand certain elements, notably sulfur and chlorine and to a smaller degree sodium and potassium, are liable to be partially volatilized in the ashing process.

Crude protein signifies the total nitrogenous matter of the feeding stuff. Its amount is computed from the total nitrogen as determined

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[11] "Beiträge zur Begründung einer rationellen Fütterung der Wiederkauer," I (1860), 140; II (1864), 25.

[12] Kühn, Gustav, Aronstein, L., and Schultzé, H., "Neue Versuche über die Ausnutzung der Rauhfutterstoffe durch das volljährige Rind" (1863 and 1864). In *Jour. Landw.,* Jahrgang 13, 283.

[13] *Ibid.,* Jahrgang 14, 269.

[14] "Anleitung zur chemischen Untersuchung. landw. wichtiger Stoffe," Berlin, 1875, 171.

[15] "Die Ernährung der landw. Nutzthiere," Berlin (1876), 25-37.

analytically by multiplying by the conventional factor, 6.25. This method is, of course, based upon the two assumptions that all the nitrogen of the material exists in the form of protein and that protein contains on the average 16 per cent of nitrogen. As pointed out in a subsequent paragraph, neither of these assumptions is strictly correct.

Ether extract, or crude fat, comprises all the substances soluble in dry ethyl ether. The method was intended to determine the amount of fat present but the extract includes also numerous other substances, especially in the case of coarse fodders.

Crude fiber, or woody fiber, is the non-nitrogenous organic matter insoluble in boiling dilute acids and alkalies, alcohol and ether. The method of determination is a purely conventional one, the strength of the solutions and the time of action, as well as the fineness of grinding of the material, being exactly prescribed. The crude fiber includes not only cellulose but a variety of other relatively insoluble carbohydrates, both hexosans and pentosans, as well as other material. Schulze also devised a method for the determination of cellulose but it was very time-consuming and has never come into general use.

Nitrogen-free extract is determnied by difference. It includes all the dry matter not contained in the four preceding groups. It includes starches and sugars but also a host of other ingredients.[16]

Modifications of Feeding Stuffs Analysis. On the whole the foregoing scheme of feeding stuffs analysis has undergone comparatively little change since it came into general use some half century ago, the principal modifications relating to the nitrogenous constituents.

Non-Proteins. It was of course clearly recognized by the earlier analysts that plants contain nitrogen compounds other than proteins but it was assumed that their amounts were too small to be of material significance. Later investigations, however, have shown the error of this assumption. Since the discovery of asparagin in asparagus by Vauquelin and Robiquet in 1805 numerous students of plant physiology have demonstrated the wide occurrence of this class of compounds in plants, but Kellner [17] appears to have been the first to call attention to the significance of the results for the analysis of feeding stuffs. He found in various forage crops that from 7.5 per cent to 38.5 per cent of the total nitrogen existed in the non-protein form, while the results of others cited by him showed even larger proportions in roots and tubers. These results have been fully confirmed by many later analyses. The present scheme of

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[16] Compare Tollens: *Jour. f. Landw.*, 45 (1897), 295.

[17] *Landw. Jahrb.* 8 (1879), 1, 243. This paper contains a somewhat extended bibliography of the subject.

feeding stuffs analysis, therefore, includes the separation of the nitrogen contained in proteins from that existing in the non-protein form. The usual method assumes that substantially all the non-proteins are soluble in water. The material is extracted with hot water, some precipitant is added to throw down any proteins, the soluble matter is filtered off and the nitrogen of the insoluble residue determined and considered to represent the protein nitrogen.

Nitrogen Factors. Both the protein and the non-protein of feeding stuffs are determined by the use of conventional factors. As already noted the factor 6.25 has been chiefly used for protein. As is apparent, however, the percentage of nitrogen in the vegetable proteins although quite variable is on the whole greater than 16. The following factors have been proposed by Atwater and Bryant,[18] and have been used to some extent. The factor employed in any given case should of course be specified if it is other than the conventional 6.25.

Animal foods	6.25
Wheat, rye, barley, and their manufactured products	5.70
Maize, oats, buckwheat, rice, and their manufactured products	6.00
Dried seeds of legumes	6.25
Vegetables	5.65
Fruits	5.80

Ordinarily the factor 6.25 has also been used for the computation of the non-proteins although the choice is naturally arbitrary. Armsby has used tentatively the factor 4.7, corresponding to the composition of asparagin, although this choice also is purely arbitrary.

Carbohydrates. The heterogeneous mixture of carbohydrates and other substances included under the terms crude fiber and nitrogen-free extract has also been the subject of study, notably by Tollens[19] and by König.[20] It has been shown that both contain pentosans in amounts depending upon the nature of the feeding stuff. Their amount is determined by conversion into furfurol by boiling with hydrochloric acid. König divides the crude fiber into three groups, cellulose, lignin, and cutin, and describes methods for the determination of each; while elaborate studies of the cellulose have been made by Cross and Bevan.[21] Tollens gives an extended list of substances, both carbohydrates and non-carbohydrates, found in the nitrogen-free extract. That the latter is not composed exclusively of carbohydrates was shown by the earlier work of Stone[22] and has been confirmed by many subsequent investigators.

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[18] Storrs, Conn., Agr. Expt. Sta. Report 12 (1881), 79.
[19] *Jour. f. Landw.*, 45 (1897), 99 and 295; *Expt. Sta. Rec.*, 8 (1896-7), 639.
[20] *Landw. Vers. Stat.*, 65 (1906-7), 55.
[21] "Cellulose," London, 1918.
[22] *Jour. Amer. Chem. Soc.*, 19 (1897), 183.

With the exception of the distinction between proteins and non-proteins and the occasional determination of pentosans, comparatively little use has been made in agricultural laboratories of the more recent advances in plant chemistry. There appear to be two principal reasons for this apparent neglect. In the first place, the time required for many of these determinations forbids their use where large numbers of analyses have to be made. In the second place, and more important, it is difficult to make any practical use of the information acquired by more complete analysis on account of our present lack of knowledge of the physiological functions of the substances determined. As a natural result, the great bulk of the feeding stuffs analyses is still made substantially by the Weende method. The methods recommended by the Association of the Official Agricultural Chemists (so-called "official methods") are described in detail in the reports[23] of that body. For more complete data regarding feeding stuffs analysis, compare Wiley's "Principles and Practices of Agricultural Analyses."

Compilations. A number of compilations of feeding stuffs analyses and tables of average composition have been prepared. The earliest of these is the familiar one by Dietrich and König.[24] Subsequent tables of the average composition of European feeding stuffs have been published by Wolff in the *Landwirtschaftlicher Kalendar* of Mentzel & v. Lengerke, "Die landwirtschaftliche Fütterungslehre."

The first compilation of American feeding stuffs analyses was by Jenkins[25] in 1879. Goessmann[26] published in 1887 a compilation of the feeding stuffs analyses made at the Massachusetts Station. This was continued by Lindsey with additions and modifications in subsequent reports, the last appearing in 1911.[27] The most recent and complete compilation of this sort is that by Henry and Morrison[28] published in 1922.

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[23] "Official and Tentative Methods of Analysis of the A. O. A. C.," published by the A. O. A. C., Washington, D. C., 1920.

[24] "Zusammensetzung und Verdaulichkeit der Futterstoffe," Berlin, 1874.

[25] Conn. Agr. Expt. Sta., Report, 1879, 132-159.

[26] Mass. (State) Expt. Sta., 5th Report, 1887, 181-203.

[27] 23rd Report, 1911, 247-265.

[28] "Feeds and Feeding," Madison, Wis., 1922.

Chapter 2.

The Animal and the Finished Products—Meat, Milk and Eggs.

From the raw materials considered in Chapter 1 the food-producing animal manufactures body tissue, milk, and eggs which are utilized for human nutrition. So far as the animal is concerned these are the finished products. They are, of course, subjected to additional manipulation at the hands of man. Edible body tissue is separated mechanically from inedible, while milk constitutes the raw material of the dairy industry.

Components. As in the case of feeding stuffs, animal products, although containing a great number of individual compounds, may be regarded from the present point of view as consisting chiefly of proteins, non-proteins, carbohydrates, fats, and ash. They differ widely from feeding stuffs, however, in the proportions in which these major groups are present and as to the separate compounds making up each group.

Animal Proteins. Like the proteins of plants, the single animal proteins show distinct differences among themselves in ultimate composition, in amino-acid makeup, and in chemical and physical properties. But nevertheless they all possess the general characteristics of proteins. The distinction between animal and vegetable proteins relates, in general, to origin and not to general properties. The nucleic acids derived from the nucleo-proteins of vegetable and animal origin show distinct differences in composition, however, which are characteristic of the plant kingdom or animal kingdom.[1] Those of plant origin yield on hydrolysis phosphoric acid, guanin, adenin, cytosin, uracil and a pentose group while those of animal origin yield phosphoric acid, guanin, adenin, cytosin, thymin and levulinic acid, which latter is formed from a hexose group in their molecule.

Table 2 shows the average ultimate composition of the more important animal proteins, the results being means of the single analyses reported by Cohnheim[2] and by Samuely.[3] The last column of the table indicates the

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[1] Jones, "Nucleic Acids," London, 1914, 11.

[2] "Chemie der Eiweisskörper," Braunschweig, 1904.

[3] In Oppenheimer, "Handbuch der Biochemie des Menschen und der Tiere," Jena, 1909, 1, 274-346.

page of references cited and the author, "C" meaning Cohnheim and "S" Samuely. A comparison of the mean, maximum and minimum figures of Table 2 (shown below) with those reported in Chapter 1 for the vegetable proteins shows about an equal degree of variability for both. The most distinct difference between the two is the lower percentage of nitrogen in the animal proteins. This difference is even more striking in the case of the simple proteins with the exception of histones which show a relatively high percentage of nitrogen, as do also the albuminoids.

Composition of Animal Proteins

	Mean	Maximum	Minimum
Carbon	52.12	54.97	49.77
Hydrogen	7.07	7.58	6.47
Nitrogen	16.06	18.35	12.01
Sulfur	0.93	1.90	0.27

That the amino-acid make-up of animal proteins shows marked quantitative differences from that of the vegetable proteins has been already noted in Chapter 1.

Non-Proteins. As in the case of plants, the animal body and its secretions contain a great variety of non-protein nitrogenous compounds. Some of the most familiar of these are the muscle extractives, including creatin, creatinin, xanthin, and hypoxanthin, the lecithins, and the great variety of cleavage products arising temporarily from the breaking down of proteins in digestion and in the subsequent anabolism and catabolism of body proteins. Quantitatively, however, the non-proteins are much less significant than in feeding stuffs and the total nitrogenous matter of the animal body may be regarded as consisting substantially of proteins.

Carbohydrates. Carbohydrates are especially plant products, the two particular representatives in the animal body being glycogen and lactose. Glycogen is found in rather small amounts in the liver and muscles of animals and to a less degree in other parts of the body. It has been estimated that the entire body of a man contains approximately 300 grams of glycogen and that of a 1200-pound steer approximately 2200 grams. It has important functions in the carbohydrate metabolism of the animal and likewise in connection with the production of muscular work.

Lactose is produced in relatively large amounts in the mammary gland but is not found elsewhere in the body. Average cow's milk contains approximately 4.9 per cent of lactose, so that the moderate daily yield of 12 kilograms of milk would contain about 588 grams of this carbohydrate. In the nucleo proteins of animal origin there is contained a carbohydrate radical of the hexose group.

TABLE 2

Ultimate Composition of Animal Proteins

	C	H	N	S	P	Fe	Reference
Simple Proteins							
Albumins and Globulins							
Serum albumin	53.01	6.78	15.97	1.90	....	....	C. 161
Ovalbumin	52.57	7.18	15.30	1.47	....	....	C. 162
Lactalbumin	52.19	7.18	15.77	1.73	....	....	S. 283
Serum globulin	52.71	7.01	15.83	1.15	....	....	C. 168
Thyreoglobulin	51.85	6.88	15.49	1.87	....	....	C. 170
Fibrinogen	52.93	6.90	16.56	1.19	....	....	C. 182
Mean	52.54	6.99	15.82	1.55	....	....	
Albuminoids							
Elastin	54.15	7.16	16.77	0.27	....	....	S. 334
Collagen	50.75	6.47	17.86	....	....	....	S. 335
Gelatin	50.08	6.86	18.07	0.51	....	....	C. 287
Mean	51.66	6.83	17.57	0.39	....	....	
Histones							
Globin	54.97	7.20	16.89	0.42	....	....	C. 206
Thymus histone	52.36	7.51	18.35	0.62	....	....	C. 204
Fish sperm histone	50.54	7.42	18.14	....	....	....	C. 206
Mean	52.62	7.38	17.79	0.52	....	....	
Conjugated Proteins							
Phospho and Nucleo Proteins							
Casein from cows' milk	53.33	7.07	15.70	0.78	0.83	....	C. 192
Pancreas nucleoprotein	51.35	6.81	17.82	1.29	1.67	....	C. 227
Ovovitellin	51.24	7.16	16.38	1.04	0.94	....	S. 303
Ichthulin	52.48	7.58	15.80	0.67	0.54	....	C. 199
Mean	52.10	7.16	16.43	0.95	0.99	....	
Mucins and Mucoids	49.77	6.88	12.01	1.58	....	....	S. 326
Hemoglobin	54.01	7.16	16.76	0.59	0.44	0.43	C. 232
Mean of all classes	52.12	7.07	16.06	0.93	....	....	

Fats. While the storage of energy in the plant is accomplished in the majority of cases by the formation of carbohydrates, surplus energy in the animal is stored substantially as fat. The large accumulation of fat in fattened animals or the great amounts of butter fat produced by exceptional milk animals are familiar to all.

The body fat of the animals consists essentially of the mixed triglycerides of stearic, palmitic, and oleic acids, the proportions of the three varying in different species but remaining relatively constant in individuals of the same species. The body fat of the horse differs markedly from the fats of the other domestic animals in yielding a semidrying[4] oil very high in olein and containing linolic and linolenic acids.[5] These triglycerides differ but little in elementary composition and accordingly the elementary composition of animal fats is very constant. Table 3 shows the results of the investigations of Schulze and Reinecke[6] together with the average reported by Benedict and Osterberg[7] for human fat.

TABLE 3

Composition of Animal Fats

		Carbon			Hydrogen			Oxygen		
	No. of Samples	Average %	Maximum %	Minimum %	Average %	Maximum %	Minimum %	Average %	Maximum %	Minimum %
Beef fat	10	76.50	76.74	76.27	11.91	12.11	11.76	11.59	11.86	11.15
Pork fat	6	76.54	76.78	76.29	11.94	12.07	11.86	11.52	11.83	11.15
Mutton fat ..	12	76.61	76.85	76.27	12.03	12.16	11.86	11.36	11.56	11.00
Average ...	28	76.50			12.00			11.50		
Dog		76.66			12.01			11.33		
Cat		76.56			11.90			11.44		
Horse		77.07			11.69			11.24		
Man		76.62			11.94			11.44		
Man—Average		76.08			11.78					

The average carbon content of body fat is usually taken as 76.5 per cent. Milk fat contains in addition to the triglycerides constituting body fat, glycerides of several of the lower acids of the aliphatic series, the principal ones being butyric, caproic, caprylic, capric, lauric, and myristic acids. In the body fats there have been found also higher acids of the same series, particularly arachnic acid. No ultimate analyses of milk fat seem to be on record.

The animal body in addition to fats contains small amounts of other lipoids such as cholesterins, lecithins and other phosphatides, cerebrosides, etc.

Ash. The ash of the animal contains the same elements found in the ash of the plant (Chapter 1). In vertebrate animals it is most obvious in the bones, the ash of which consists chiefly of calcium phosphate, and carbonate, with smaller amounts of magnesium, sodium, potassium and chlorine.

The composition of the ash of bones is shown in Table 4. The results reported by Gabriel are on the basis of the air-dry bone ash. All other

[4] Dunlop, Harry, *Analyst,* 32 (1907), 317.

[5] Kilmont, J., Meisl, E., and Mayer, K., *Analyst,* 40 (1915), 349.

[6] *Ann. d. Chemie und Pharmacie,* 142 (1867), 191.

[7] *Amer. Jour. Physiol.,* 4 (1901), 69.

TABLE 4

Composition of Bone Ash

	Teeth of Cattle[1]	Bones of Man[1]	Bones of Cattle[1]	Bones of Geese[1]	Leg Bone of Goat[2]	Leg Bone of Lamb[3]	Pigs' Bones[4]	Bones of Pigs[5]	Skeleton of Pigs[6]	Bones of Chickens[7]	Bones of Ducks[7]	Bones of Rabbits[8]
Fe_2O_3	....	....	....	....	....	....	....	....	....	....	....	....
CaO	50.76	51.31	51.28	51.01	53.55	52.34	54.59	52.73	52.82	51.96	52.68	52.86
MgO	1.52	0.77	1.05	1.27	1.20	0.98	1.17	1.15	1.68	1.42	1.49	1.16
K_2O	0.20	0.32	0.18	0.19	....	....	....	....	....	....	....	....
Na_2O	1.16	1.04	1.09	1.11	....	....	....	....	....	....	....	....
H_2O	2.21	2.46	2.33	3.05	....	....	....	....	....	....	....	....
P_2O_5	38.88	36.65	37.46	38.16	41.31	40.06	41.50	41.27	41.21	40.51	39.89	41.58
SO_3	....	....	....	....	....	....	1.24	....	....	....	....	....
CO_2	4.09	5.86	5.06	4.11	....	....	1.37	....	....	....	....	4.77
Cl	0.05	0.01	0.04	0.06	....	....	....	....	....	....	....	....
Total	98.87	98.43	98.49	98.99	....	....	99.87	....	....	....	....	100.37

[1] Gabriel, *Ztschr. physiol. Chem.*, **18** (1894), 257. Air-dry ash.

[2] Weiske, H., *Ztschr. f. Biol.*, **7** (1871), 179 and 333 (4 goats Os metacarpi).

[3] Weiske and Wildt, *Ztschr. f. Biol.*, **9** (1873), 541 (3 lambs Os metacarpi).

[4] Weiser, S., *Biochem. Ztschr.*, **66** (1914), 95 Math. average of 5 samples of bones of 3 pigs.

[5] Alway, F. J., and Hadlock, W. L., Nebraska Station Report, 1909, 32.

[6] Forbes, E. B., et al, Ohio Agr. Expt. Station Bul. 283 (1915), 129 (7 pigs 8 mo. old, 100 lbs.).

[7] Wheeler, N. Y. Agr. Expt. Sta. Bul. 468 (1919), (38 chickens, 29 ducks).

[8] Weiske, H., *Ztschr. f. Biol.*, **8** (1872), 239; Wildt, E., *Landw. Vers. Stat.*, **15** (1872), 404 (23 rabbits all ages).

results are on the basis of the dry ash. Phosphoric anhydride and lime form 90 to 95 per cent of the ash of bones. The effect of age on the composition of the ash of rabbit bones is shown by the results of Weiske and Wildt (Table 5) to be largely confined to an increase in calcium carbonate and decrease in magnesia.

TABLE 5

COMPOSITION OF BONE ASH OF RABBITS

Age	CO_2	CaO	MgO	P_2O_5
Shortly after birth[1]	3.65	52.17	1.38	42.05
3 days[1]	3.84	52.16	1.36	42.13
14 days[1]	3.99	52.10	1.26	42.19
4 weeks[2]	....	50.48	1.69	43.12
4 weeks[2]	....	51.99	1.51	42.65
1 month[1]	4.00	51.91	1.22	42.20
2 months[1]	4.52	52.10	1.09	41.64
2½ months[2]	....	53.52	1.22	42.17
2½ months[2]	....	53.38	1.23	42.29
3 months[1]	4.69	52.49	1.01	41.03
4 months[1]	4.92	52.60	1.02	40.80
5 months[2]	....	53.77	1.23	42.73
5 months[2]	....	53.68	1.24	42.01
5 months[2]	....	53.60	1.23	42.67
6 months[1]	4.94	52.64	1.05	40.80
8 months[1]	5.54	52.78	0.93	40.05
1 year[1]	5.71	52.61	0.91	40.04
2 years[1]	5.81	52.76	0.93	39.78
3 to 4 years[1]	5.66	52.84	0.83	39.80
Full grown[2]	....	53.94	1.06	40.03
Full grown[2]	....	54.21	1.09	42.08
Full grown[2]	....	53.93	1.06	42.00
Full grown[2]	....	54.16	1.09	42.02

[1] Wildt, E., *Landw. Vers. Stat.*, 15 (1872), 404.
[2] Weiske, H., *Ztschr. f. Biol.*, 8 (1872), 239.

The composition of the ash of flesh is strikingly different. Table 6 shows the ash constituents of the flesh of several species of animals. Phosphoric acid and potash together form 50 to 70 per cent of the ash. Sulfur and soda come next in relative quantity. Much sulfur is lost by ignition as is shown by the low results for it reported by Ali and Wolff. The other investigators determined sulfur by methods which did not permit of loss.

The composition of the ash of the total animal is given for seven species of mammal in Table 7. Aside from the results for a newborn dog the differences between the species are not marked.

The composition of the ash of the egg shell and the contents of the egg for the hen is reported by Buckner and Martin.[8]

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[8] *J. Biol. Chem.*, 41 (1920), 195.

TABLE 6

COMPOSITION OF ASH OF FLESH

	Pig[1]	Beef, Calf[2]	Swine[3]	Cattle[3]	Calf[3]	Chicken[3]	Deer[3]	Rabbit[3]	Dog[3]	Cat[3]	Frog[3]	Eel[3]	Pike[3]	Shell fish[3]	Human[3]	Flesh[4]
Fe_2O_3 .	....	1.00	0.64	2.87	0.87	0.78	1.07	0.53	0.48	0.98	0.71	0.97	0.45	0.62	1.64	0.70
CaO ..	3.65	9.38	0.87	0.23	1.39	0.88	0.96	1.79	0.71	0.89	1.93	5.53	4.03	2.29	0.81	2.82
MgO .	2.96	1.08	3.58	3.28	3.51	3.64	3.47	3.30	2.86	3.52	3.44	2.97	3.72	3.27	2.73	3.21
K_2O ..	27.26	16.81	23.32	36.20	31.85	33.02	29.14	33.34	27.69	33.81	32.70	29.14	36.27	30.02	29.94	41.27
Na_2O .	12.53	14.21	16.02	7.13	8.05	7.55	6.93	4.29	9.43	7.19	6.56	4.31	2.86	9.94	8.34	3.63
P_2O_5 .	33.07	36.48	37.12	31.59	35.00	34.19	40.99	40.29	37.56	34.24	37.58	40.79	35.09	23.34	36.16	42.54
S	16.34	1.97[5]	15.59	15.15	15.72	17.20	15.18	13.70	16.68	16.14	14.33	13.59	15.79	16.60	16.16	1.56[5]
Co_2 ...	....	9.55	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Cl	5.41	6.53	3.70	4.59	4.67	3.54	2.92	3.56	5.92	4.17	3.55	3.49	2.31	17.96	5.44	3.85
SiO_2 ..	....	1.40	....	....	....	....	....	....	....	....	....	....	....	....	....	1.11
Total.	101.22	98.41	100.84	101.04	101.06	100.80	100.66	100.80	101.33	100.94	100.80	100.79	100.52	104.04	101.22	100.69
O = Cl	1.22	1.48	0.84	1.04	1.06	0.80	0.66	0.80	1.33	0.94	0.80	0.79	0.52	4.04	1.22	0.87
Total.	100.00	96.93	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	99.82

[1] Forbes, *et al.*, Ohio Agr. Expt. Stat. Bul. 283 (1915), (Average calculated from 7 pigs).

[2] Ali, Mohammed Ahmed, Dissertation, A. M., Univ. of Mo., 1922 (Average of three animals).

[3] Katz, Julius, *Archiv. gesam. Physiol.*, **63** (1896), 1.

[4] Wolff, "Aschen Analysen" (1871), 158.

[5] Calculated as SO_3.

TABLE 7

COMPOSITION OF THE ASH OF ANIMALS

	Cattle[2]	Sheep[1]	Pigs[1]	Newborn Jersey Calf 11a[2]	Newborn Jersey Calf 11b[3]	Newborn Guinea Pig[4]	Newborn Dog[5]	Newborn Human Hugounenq[6]	Newborn Human Söldner[6]	Newborn Human Michel[6]	Newborn Human Cde. Lange[6]	Newborn Human Giacoso[6]
Crude Ash[7]	4.13	3.00	2.16	....	.....	....	....	....	....	....	....	....
Pure Ash[7]	4.09	2.91	2.15	4.10	4.29	....	....	....	....	....	....	....
Fe_2O_3	0.64	1.10	0.84	0.98	0.97	0.24	0.72	0.39	0.83	....	1.69	1.89
Lime CaO	45.28	44.00	39.54	43.11	41.07	32.18	29.52	40.48	38.08	41.39	38.89	41.92
Magnesia MgO	1.92	1.81	2.03	2.07	1.75	3.37	1.82	1.51	1.43	1.20	1.37	1.10
Potash K_2O	4.76	5.54	7.98	4.65	5.72	8.16	11.42	6.20	7.06	....	6.54	2.70
Soda Na_2O	3.31	3.78	4.26	6.23	5.96	6.92	10.64	8.12	7.67	....	8.80	10.23
Phosphoric Acid P_2O_5	40.13	38.89	40.13	39.38	38.46	42.07	39.42	35.28	37.66	38.02	37.61	37.65
Sulfuric Acid SO_3	0.91	1.20	2.24	1.11	3.11	....	....	1.50	2.02	....	....	....
Carbonic Acid CO_2	1.81	1.56	0.90	0.19	0.75	....	....	1.89	0.53	....	....	....
Chlorine Cl	1.42	1.94	2.50	1.95	2.24	9.11	8.35	4.26	6.61	5.73	6.36	5.77
Silica SiO_2	0.15	0.61	0.16	0.64	0.30	....	....	....	0.06	....	....	....
Total	100.33	100.43	100.58	100.31	100 33	102.05	101.89	99.63	102.09[8]	....	101.26	101.26
O = Cl	0.33	0.43	0.58	0.44	0.52	2.04	....	0.96	1.49	....	1.43	1.30
Total	100.00	100.00	100.00	99.87	99.81	100.01	....	98.67	100.60	....	99.83	99.96

[1] Lawes and Gilbert, *Phil. Trans.*, 1883, Pt. III, 875.

[2] Vanatta, E. E., Dissertation, M. S. A., Univ. of Missouri, 1911.

[3] Hogan, A. G., Dissertation, M. S. A., University of Missouri, 1912, and Trowbridge, P. F., *Proceedings American Society of Animal Production*, 1914, 100.

[4] Abderhalden, E., *Ztschr. physiol. Chem.*, **27**, 356.

[5] Hugounenq, M. L., *Compt. Rendus., Soc. Biol.*, 1899, 523.

[6] Söldner, *Ztschr. f. Biol.*, **44**, 70.

[7] Per cent of fasted live weight.

[8] Including 0.11% Al_2O_3 and 0.03% Mn_3O_4.

Wheeler[9] reports the composition of the ash of the shells of hen and duck eggs. The egg shell is largely calcium carbonate which accounts for Buckner and Martin's strongly ignited ash showing 98 per cent of lime and Wheeler's failing to add to much over 50 per cent. Wheeler shows strontium replacing calcium to a considerable extent in the bones of his hens and ducks in chemically equivalent quantities. Strontium salts had been added to the diet. In calculating the averages given the strontium has been added to the calcium. The results are given in Table 8.

TABLE 8

Composition of the Ash of Egg Shells and Eggs

	Ash	CaO	MgO	P_2O_5
Buckner:	% in Fresh Material		% in the Ash	
20 shells of hen eggs	55.33	97.91	0.76	0.66
20 contents of hen eggs	0.91	7.97	1.29	41.86
Wheeler:			% in Dry Shell	
17 shells of hen eggs	....	50.24	1.43	0.35
11 shells of duck eggs	....	50.08	0.80	0.39

Composition of Entire Animal. A number of investigators have analyzed more or less fully the entire bodies of farm animals, determining the percentages of the chief groups of constituents enumerated above. Dry matter and fat have been determined in all cases and in a considerable number of instances also the total nitrogen and ash. The results of these analyses, so far as available, are included in Tables 9 to 19. In those cases in which nitrogen was determined, the protein is equivalent to nitrogen x 6.25. Where the nitrogen was not determined, the protein is equivalent to fat- and ash-free dry matter. Generally these analyses fail to add up to 100 per cent. This is due mainly to two causes. First, the factor 6.25 does not apply to all animal proteins and is even not necessarily a good average figure for the entire bodies. Second, there are other materials in the body which will not appear as water, fat, protein or ash. For example, glycogen may be as much as 0.5 per cent of the flesh of cattle and dextrose and other non-fatty, non-nitrogenous materials may be present. As far as possible the results are given on the empty weight basis, i.e., the live animal minus the contents of the digestive and excretory tract. The difference between the sum of the analytical parts and the empty animal is considered to be water and is added to the analytical weight of water.

The results on cattle are rather extensive. Haecker's results are for

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[9] New York (Geneva) Agr. Expt. Station, Bul. 468 (1919).

TABLE 9

Composition of Entire Bodies of Miscellaneous Animals

	Kind of Animal	Age	Condition	Water %	Fat %	Nitrogen %	Ash %	Fat Free Basis Water %	Fat Free Basis Nitrogen %	Fat Free Basis Ash %
Pfeiffer, *Ztschr. f. Biol.*, **23** (1887), 340.	Fat dog	......	....	55.25	20.65	....	....	69.63	....	....
	Thin dog	......	....	61.90	9.40	....	....	68.32	....	....
	Fat rabbit	......	....	60.30	15.70	....	....	71.53	....	....
	Thin rabbit	......	....	63.50	8.60	....	....	69.47	....	....
	Fat hen	......	....	53.00	27.75	....	....	73.36	....	....
	Thin hen	......	....	65.20	5.40	....	....	68.92	....	....
Chaniewski, *Ztschr. f. Biol.*, **20** (1884), 179	Goose I	Grown	Normal	66.89	7.03	3.63	3.58	71.95	3.90	3.85
	Goose II	Grown	Fattened	63.86	13.53	3.18	3.40	73.85	3.68	3.93
	Goose III	Grown	Fattened	58.93	21.04	2.77	2.98	74.63	3.51	3.77
	Goose Ib	Grown	Starved	74.03	3.46	2.73	....	76.68	2.83	....
	Goose IIb	Grown	Fattened from starved	63.36	17.06	2.46	....	76.39	2.97	....
Schulze, *Landw. Jahrb.*, **11** (1882), 57.	Goose 1	Grown	Very fat	59.60	25.94	2.35	....	80.48	3.17	....
	Goose 2	Grown	Very fat	56.91	28.11	2.24	....	79.16	3.12	....
	Goose 3	Grown	Very fat	56.28	28.47	2.40	....	77.60	3.31	....
	Goose 4	Grown	Very fat	53.43	30.88	2.36	....	77.30	3.41	....
	Goose 5	Grown	Very fat	57.99	27.89	2.32	....	80.42	3.22	....
	Goose 6	Grown	Very fat	56.95	27.79	2.29	....	78.87	3.17	....
	Goose 7	Grown	Fat	61.05	20.29	2.86	....	76.59	3.59	....
	Goose 8	Grown	Fat	63.48	17.35	2.82	....	76.81	3.41	....

The figures for the composition of the geese are for the feather-free empty animal.

TABLE 10

COMPOSITION OF ENTIRE BODIES OF CATTLE—EMPTY WEIGHT BASIS

(Lawes and Gilbert[1]—Jordan[2])

								Fat Free Basis		
	Age, Days	Condition	Water %	Fat %	Protein %	Ash %	Nitrogen %	Water %	Nitrogen %	Ash %
Lawes and Gilbert	63-70	Fat	65.10	15.30	15.90	3.90	2.54	76.86	3.00	4.60
Lawes and Gilbert	1460	Half fat	56.10	20.80	18.40	5.00	2.94	70.83	3.72	6.31
Lawes and Gilbert	1460	Fat	48.40	32.00	15.40	4.20	2.46	71.18	3.62	6.18
Jordan	665	....	59.44	17.64	18.91	4.13	3.03	72.17	3.67	5.01
Jordan	731	....	57.39	18.97	18.95	4.81	3.03	70.83	3.74	5.94
Jordan	984	....	53.99	23.00	18.26	4.86	2.92	70.12	3.79	6.31
Jordan	1054	....	53.70	23.53	18.12	4.77	2.90	70.22	3.79	6.24

[1] *Phil. Trans.*, 1885, Pt. II, 493.

[2] Maine Agr. Expt. Station Report, 1895, Pt. II, 36, Jordan's results are without the skin. The above figures include the skin using Jordan's weights and the average composition of steer hides of a similar age, weight, and condition as reported by Moulton, *et al. seq.*

TABLE 11

Composition of Entire Bodies of Cattle—Empty Weight Basis

(Haecker[1])

Weight, Lbs.	No. of Individuals	Age, Days	Water %	Fat %	Protein %	Ash %	Nitrogen %	Fat Free Basis Water %	Fat Free Basis Nitrogen %	Fat Free Basis Ash %
Normal condition										
100	5	38	71.84	4.00	19.90	4.26	3.18	74.84	3.32	4.44
200	4	141	70.43	6.01	19.14	4.42	3.06	74.93	3.26	4.71
300	4	225	65.74	11.19	18.77	4.30	3.00	74.03	3.38	4.83
400	5	316	65.79	10.56	19.31	4.34	3.09	73.55	3.45	4.86
500	5	377	62.90	13.73	19.15	4.22	3.06	72.91	3.55	4.89
600	3	430	61.20	15.04	19.40	4.36	3.10	72.08	3.61	5.33
700	4	514	60.35	16.57	18.60	4.48	2.98	72.33	3.57	5.36
800	3	591	58.44	18.52	18.80	4.24	3.01	71.72	3.69	5.20
900	3	615	54.10	24.08	17.66	4.16	2.83	71.25	3.72	5.48
1000	4	632	52.03	26.91	17.11	3.95	2.74	71.18	3.75	5.41
1100	3	665	47.77	32.03	16.38	3.82	2.62	70.25	3.86	5.62
1200	3	828	47.96	32.32	16.02	3.70	2.56	70.88	3.79	5.46
1300	1	699	47.93	32.50	15.79	3.78	2.53	71.00	3.74	5.60
1400	1	832	47.76	32.58	16.15	3.51	2.58	70.84	3.83	5.21
1500	1	1036	43.48	37.59	15.72	3.21	2.52	69.66	4.03	5.14
From Pasture										
600	2	516	64.43	11.01	19.51	5.05	3.12	72.40	3.51	5.67
700	2	598	61.56	14.57	19.30	4.57	3.09	72.06	3.61	5.35
800	1	618	56.20	21.35	18.35	4.10	2.94	71.46	3.73	5.21
1000	1	635	58.40	18.05	19.06	4.49	3.05	71.26	3.72	5.48
1200	1	749	52.50	27.11	16.73	3.66	2.68	72.03	3.67	5.02

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[1] Minnesota Agr. Expt. Station, Bull. 193 (1920).

TABLE 12

Composition of Entire Bodies of Cattle—Empty Weight Basis

(Moulton, Trowbridge, and Haigh[1])

		Percentage Composition						Fat Free Basis		
Age	Condition	Water %	Fat %	Protein %	Ash %	Phosphorus %	Nitrogen %	Water %	Nitrogen %	Ash %
185 days	Embryo	84.80	2.36	10.46	1.78	0.283	1.67	86.85	1.71	1.82
232 days	Embryo	78.70	2.57	12.57	3.18	0.370	2.01	80.78	2.06	3.26
279 days	Embryo	74.19	3.38	17.09	4.06	0.688	2.74	76.79	2.83	4.20
Birth[2]	Normal	73.58	3.54	17.77	4.39	0.817	2.84	76.29	2.95	4.56
3 months	Fat	66.03	9.49	19.80	4.76	0.848	3.17	72.95	3.50	5.26
3 months	Medium	67.56	7.23	19.84	4.89	0.853	3.18	72.83	3.42	5.28
3 months	Thin	71.52	4.32	20.01	4.30	0.729	3.20	74.74	3.35	4.49
5.5 months	Fat	57.21	20.77	17.03	4.00	0.723	2.73	72.21	3.44	5.05
5.5 months	Medium	64.39	10.36	19.33	4.94	0.870	3.09	71.83	3.45	5.51
5.5 months	Thin	67.80	6.69	20.13	4.81	0.857	3.22	72.66	3.45	5.15
8.5 months	Fat	61.23	15.64	18.34	3.91	0.700	2.94	72.58	3.48	4.63
8.5 months	Medium	63.06	13.70	18.26	4.31	0.784	2.92	73.06	3.39	5.00
8.5 months	Thin	66.51	8.44	19.24	4.92	0.897	3.08	72.64	3.36	5.37
11 months	Fat	57.56	20.44	17.61	3.74	0.610	2.82	72.34	3.54	4.71
		54.42	24.42	16.96	3.95	0.730	2.71	72.01	3.59	5.22
		58.76	17.83	18.28	4.81	0.904	2.93	71.51	3.57	5.85
11 months	Medium	63.01	13.25	18.54	4.62	0.771	2.97	72.63	3.42	5.32
		60.37	16.03	18.27	4.87	0.895	2.92	71.90	3.48	5.80
11 months	Thin	64.80	11.51	18.21	4.52	0.803	2.91	73.23	3.29	5.11
15.5 months	Thin	64.05	8.75	20.45	5.87	1.077	3.27	70.19	3.58	6.43
16.5 months	Fat	57.34	19.33	17.41	4.83	0.883	2.79	71.08	3.46	5.99
18 months	Fat	53.04	26.00	16.70	3.70	0.661	2.67	71.67	3.61	5.00
18 months	Medium	58.34	17.40	18.31	4.94	0.916	2.93	70.63	3.55	5.98
18.5 months	Thin	65.41	9.95	18.86	4.97	0.879	3.02	72.64	3.35	5.52
21 months	Fat	50.93	28.74	16.11	3.92	0.708	2.58	71.47	3.62	5.50
21 months	Thin	64.55	9.81	19.42	5.84	1.081	3.11	71.57	3.45	6.48
21 months	Very, very thin	69.80	2.16	20.59	6.99	1.245	3.29	71.34	3.36	7.14
26 months	Medium	61.96	14.40	18.57	5.08	0.861	2.97	72.38	3.47	5.93
26 months	Thin	64.12	11.34	19.29	4.86	0.801	3.09	72.32	3.48	5.48
34 months	Fat	46.60	35.57	13.54	3.67	0.582	2.17	72.32	3.36	5.70
3 years	Half fat	50.02	29.72	15.70	4.14	0.741	2.51	71.17	3.57	5.89

TABLE 12—*Concluded*

		Percentage Composition						Fat Free Basis		
Age	Condition	Water %	Fat %	Protein %	Ash %	Phosphorus %	Nitrogen %	Water %	Nitrogen %	Ash %
34 months	Medium	58.01	18.76	18.08	4.85	0.758	2.90	71.41	3.57	5.97
3 years	Thin	57.34	18.03	18.52	5.70	1.069	2.96	62.35	3.22	6.20
39.5 months	Very fat	39.83	44.56	12.38	2.97	0.497	1.98	71.84	3.57	5.35
38 months	Medium	54.58	23.28	17.30	4.66	0.790	2.77	71.14	3.61	6.07
40 months	Medium	56.56	19.69	18.48	4.79	0.853	2.96	70.42	3.68	5.96
40.5 months	Thin	63.49	10.20	20.36	5.63	0.979	3.26	70.71	3.63	6.27
44.5 months	Very fat	41.40	41.79	12.82	3.12	0.585	2.05	71.12	3.52	5.36
44.5 months	Medium	57.63	16.57	20.02	4.97	0.866	3.20	69.07	3.84	5.95
45 months	Thin	58.37	16.02	19.90	4.93	0.873	3.18	69.50	3.79	5.87
47 months	Very fat	39.84	43.56	12.27	3.27	0.577	1.96	70.58	3.48	5.79
48 months	Medium	52.67	23.70	17.99	5.01	0.891	2.88	69.02	3.77	6.57
48 months	Thin	58.14	16.85	19.59	4.97	0.866	3.13	69.93	3.77	5.98
5 years	Very fat	41.73	41.25	12.92	3.45	0.624	2.07	71.03	3.52	5.87

[1] Mo. Agr. Expt. Station, Research Buls. 28, 30, 38, and 55.

[2] Average of 13 beef calves at birth.

TABLE 13

Composition of Entire Bodies of Sheep—Empty Weight Basis

			Percentage Composition						Fat Free Basis		
	Age, Years	Condition	Ash %	Protein %	Fat %	Dry Matter %	Water %	Nitrogen %	Water %	Nitrogen %	Ash %
Lawes and Gilbert, *Phil. Trans.*, Part II (1859), p. 493.	6 months	Fat	3.2	13.4	31.2	47.8	52.2	2.14	75.87	3.11	4.65
	1 year	Store	3.4	15.8	19.9	39.0	61.0	2.53	76.15	3.16	4.24
	1¼	Fat	3.0	13.0	37.8	53.8	46.2	2.08	74.28	3.34	4.82
	1¾	Extra fat	3.1	11.6	48.3	62.9	37.1	1.86	71.76	3.60	6.00
	3¼	Half fat	3.5	15.5	25.9	44.8	55.2	2.48	74.47	3.35	4.72

"normal" condition cattle at the various 100-pound stages up to 1500 pounds. From one to five animals were analyzed at each stage and they weighed more or less than the even hundred pounds. The results are calculated to the average at the even 100 pounds. Fifteen different weights of "normal" cattle and five from pasture are given. Fifty-six cattle are included. Although Haecker determined nitrogen in all samples he reports only protein obtained by difference. His results then beg the question of the relation of nitrogen to protein and are valueless in computing a factor. He reports [10] that the factor runs from 5.69 for skin and hair to 6.59 for bone.

The work of Moulton, Trowbridge, and Haigh [11] is the most extensive on cattle. They report 56 cattle ranging in age from 185-day embryos to 5-year old cattle and representing 41 different ages and conditions.

For sheep the only figures for the composition of the entire body are reported by Lawes and Gilbert.[12] Henneberg,[13] Kern and Wattenberg,[14] Friske,[15] and Pfeiffer and Friske [16] have reported the composition of the soft parts of the carcass only.

Many investigators have worked with swine. Among the earliest were Lawes and Gilbert, Soxhlet, Tschirwinsky, and Weiske and Wildt. Their results are shown in Table 14. In the latter two investigations the dried bristles of the swine were classed as protein and added to the other protein of the body. This is largely true but not quite accurate as shown by unpublished work of the Missouri Agricultural Experiment Station. The hair and scurf of swine removed after scalding was found to contain from 0.4 to 1.4 per cent of ether soluble material, 4.9 to 8.4 per cent of nitrogen, and 1.1 to 3.3 per cent of ash with a water content of 46 to 68 per cent. Of course most of this water was introduced during the scalding process. In addition to the above error Tschirwinsky assumes that the fat and ash free dry bone is protein. The ash in the soft parts was not reported and a figure has been assumed for it in order to complete the calculations.

Wilson [17] and Washburn and Jones [18] have studied the nutrition of baby pigs and report the composition of pigs from birth to 100 days old. Wilson's results include the contents of the digestive and excretory tract

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[10] Minnesota Agr. Expt. Sta. Bul. 193 (1920), 107.

[11] Mo. Agr. Expt. Sta., Research Buls., 28 (1918); 30 (1919); 38 (1920), and 55 (1922).

[12] *Phil. Trans.*, 1859, Pt. II, 493.

[13] *Ztschr. f. Biol.*, 17 (1881), 295.

[14] *Jour. f. Landw.*, 26 (1878), 549, and 28 (1880), 289.

[15] *Landw. Vers. Stat.*, 71 (1909), 441.

[16] *Ibid.*, 74 (1911), 409.

[17] *Amer. Jour. Physiol.*, 8 (1902), 197.

[18] Vermont Agr. Expt. Sta. Bul. 195 (1916).

TABLE 14

COMPOSITION OF ENTIRE BODIES OF SWINE—EMPTY WEIGHT BASIS

			Percentage Composition						Fat Free Basis		
	Age, Days	Condition	Ash %	Protein %	Fat %	Dry Matter %	Water %	Nitrogen %	Water %	Nitrogen %	Ash %
Tschirwinsky,[1] *Landw. Vers. Stat.*, **29** (1883), 317	63	Unfattened	4.14	15.21	10.39	29.74	70.26	2.43	78.41	2.71	4.62
	70	Unfattened	3.51	14.30	10.27	28.08	71.92	2.29	80.15	2.55	3.91
	161	Fattened	3.90	11.70	27.77	43.37	56.63	1.87	78.40	2.59	5.40
	196	Fattened	2.62	11.08	40.92	54.62	45.38	1.77	76.81	3.00	4.43
Lawes & Gilbert, *Phil. Trans.*, Part II (1859), 493	330-365	Store	2.8	14.6	24.6	41.9	58.10	2.34	77.06	3.10	3.71
	330-365	Fat	1.7	11.4	43.9	57.0	43.00	1.82	76.65	3.24	3.03
Soxhlet, *Centbl. Agr. Chem.*, **10** (1881), 674	500	Fat	2.63	12.71	40.56	56.11	43.89	2.03	73.84	3.42	4.42
	575	Fat	2.44	12.92	35.69	51.56	48.44	2.07	75.32	3.22	3.79
	575	Fat	2.17	10.88	44.59	58.55	41.45	1.74	74.81	3.14	3.92
Weiske and Wildt,[2] *Ztschr. f. Biol.*, **10** (1874), 1	42	Unfattened	3.86	11.84	9.94	26.60	73.40	1.89	81.50	2.10	4.29
	277	Fattened on potatoes	1.64	8.50	26.12	37.80	62.20	1.36	84.19	1.84	2.22

[1] Dried bristles and fat and ash-free dry bone called protein. Ash not determined in the soft parts (assumed by difference).

[2] Dried bristles called protein.

TABLE 15

Composition of Entire Bodies of Baby Pigs—Live Weight Basis
Including Contents Digestive and Excretory Tract

										Fat Free Basis			
No. of Individuals	Diet	Age	Live Wt. Grams	Water %	Ash %	Protein %	Ash %	CaO %	Nitrogen %	Water %	Nitrogen %	Ash %	CaO %
		Wilson											
1		Birth	1044	80.35	1.31	12.19	...	1.85	1.95	81.42	1.98	...	1.87
1		Birth	1142	80.18	1.55	11.92	...	...	1.91	81.44	1.94	...	...
1		Birth	1016	79.54	1.60	12.51	...	1.92	2.00	80.83	2.03	...	1.95
1	Skim milk	16 days	2205	80.22	1.29	14.57	...	1.64	2.33	81.27	2.36	...	1.66
1	Skim milk and lactose	16 days	2435	79.64	1.43	14.78	...	1.63	2.36	80.80	2.40	...	1.65
1	Skim milk and dextrose	16 days	2471	79.96	1								
		Washburn and Jones			.35	14.13	...	1.63	2.26	81.05	2.29	...	1.65
24	Mother's milk...	28-35 days	8326	66.62	14.51	15.30	3.17	...	2.45	77.93	2.86	3.71	...
6	Milk and grain..	78-85 days	26790	66.19	17.36	12.90	2.42	...	2.06	80.09	2.50	2.93	...
16	Homogenized at 85°	68-75 days	40110	56.84	25.46	14.50	3.10	...	2.32	76.25	3.11	4.16	...
15	5% milk	74-81 days	28780	57.56	25.96	14.07	3.15	...	2.25	77.74	3.04	4.25	...
6	Normal milk ...	77-84 days	17710	67.29	13.38	15.21	3.15	...	2.43	77.68	2.81	3.64	...
6	Evaporated milk	77-84 days	19430	66.19	16.19	14.20	3.05	...	2.27	78.98	2.71	3.64	...
6	Sweet cond. milk	77-84 days	14610	61.90	21.61	12.57	2.86	...	2.01	78.96	2.57	3.65	...
27	2.5% milk	78-85 days	24350	63.08	18.60	14.67	3.23	...	2.35	77.49	2.88	3.97	...
16	Skim milk	79-86 days	23720	66.08	13.94	16.13	3.62	...	2.58	76.78	3.00	4.21	...
6	Diluted and undiluted	79-86 days	20840	67.74	13.23	15.53	3.10	...	2.48	78.07	2.86	3.57	...
10	Homogenized at 185°	95-102 days	19170	68.68	13.33	14.03	3.16	...	2.24	79.24	2.59	3.65	...
29	Malnutrition ...	73-80 days	14540	69.55	10.70	15.62	3.58	...	2.50	77.88	2.80	4.01	...

TABLE 16

Composition of Entire Bodies of Swine—Empty Weight Basis

(Swanson)—Duroc Jersey Swine

	Age, Days	Empty Wt., Lbs.	Water %	Fat %	Protein %	Ash %	Nitrogen %	Fat Free Basis		
								Water %	Nitrogen %	Ash %
VI Check	69	21.72	68.32	15.15	13.44	2.81	2.15	80.52	2.53	3.31
III Corn + protein-free skim milk	294	28.06	64.75	15.02	15.20	4.34	2.43	76.19	2.86	5.11
VI Corn alone	249	28.60	70.45	11.40	14.30	3.81	2.29	79.51	2.58	4.30
VI Corn + synthetic ash	249	34.37	69.94	15.51	12.08	2.59	1.93	82.78	2.29	3.07
V Check	61	34.63	66.30	14.87	15.42	3.06	2.47	77.88	2.90	3.59
III Check	107	37.65	56.28	29.00	11.98	2.79	1.92	79.27	2.70	3.93
IV Check	122	40.97	55.67	25.30	16.35	5.92	2.62	74.52	3.50	7.93
III Corn + synthetic ash	294	45.62	59.60	23.65	11.28	3.44	1.80	78.06	2.36	4.51
II Check	137	50.38	57.52	27.39	13.03	3.30	2.08	79.22	2.87	4.54
IV Alfalfa pasture	302	51.25	60.35	15.43	19.39	4.53	3.10	71.36	3.67	5.36
V Corn alone	261	62.71	46.77	40.50	11.48	2.22	1.89	78.61	3.09	3.73
III Corn alone	294	63.28	53.02	34.46	11.44	2.69	1.83	80.90	2.79	4.10
III Alfalfa pasture	294	63.60	73.36	5.27	16.41	3.96	2.63	77.44	2.77	4.18
VI Corn + ash-free blood protein	249	72.18	45.18	37.26	14.11	2.09	2.26	72.01	3.60	3.33
IV Corn + synthetic ash	302	86.40	45.03	40.83	12.08	2.88	1.93	76.10	3.27	4.87
IV Corn alone	302	105.25	40.82	47.16	10.94	2.57	1.75	77.25	3.31	4.86
II Corn + bone ash	417	122.80	40.77	48.42	11.25	2.71	1.80	79.04	3.50	5.25
IV Corn + protein-free skim milk	302	127.45	38.10	50.95	9.59	2.27	1.53	77.68	3.13	4.63
V Corn + casein every seventh day	261	139.84	40.10	48.78	10.45	1.63	1.67	78.29	3.26	3.18
V Corn + corn germ	261	140.44	48.71	38.37	12.03	1.83	1.92	79.04	3.12	2.97
II Corn alone	417	141.49	35.86	49.91	9.88	2.16	1.58	71.59	3.16	4.31
VI Corn, ash-free blood protein, + synthetic ash	249	156.86	44.31	40.44	13.02	2.63	2.08	74.40	3.50	4.42
VI Corn, starch, casein, + synthetic ash	249	159.35	43.82	38.55	12.20	2.43	1.95	71.31	3.18	3.95
IV Corn + milk albumin, small amounts	302	180.99	36.61	52.31	10.95	1.75	1.75	76.77	3.67	3.67

TABLE 16—*Concluded*

	Age, Days	Empty Wt. Lbs.	Water %	Fat %	Protein %	Ash %	Nitrogen %	Fat Free Basis Water %	Fat Free Basis Nitrogen %	Fat Free Basis Ash %
VI Corn, casein reducing + synthetic ash	249	192.20	41.64	44.20	12.30	2.61	1.97	74.62	3.53	4.68
VI Corn, casein 1 to 1½ + synthetic ash	249	195.66	45.59	40.72	12.03	2.46	1.92	76.91	3.25	4.15
VI Corn, casein 1 to 3 + synthetic ash	249	199.71	44.26	40.84	12.69	2.74	2.03	74.81	3.43	4.63
IV Corn + Milk protein every seventh day	302	209.95	36.49	51.21	10.81	1.96	1.73	74.79	3.55	4.02
V Corn + casein 1 to 3	261	211.22	39.92	46.71	12.65	2.10	2.02	74.91	3.80	3.94
V Corn + milk albumin. large amounts	261	245.15	39.69	46.30	11.33	2.02	1.81	73.91	3.38	3.76
IV Corn + casein 1 to 3	302	282.58	39.67	47.63	9.28	1.92	1.48	75.75	2.84	3.67
III Corn + milk protein	294	318.93	37.03	52.42	10.37	1.60	1.66	77.83	3.49	3.36
III-V Corn + synthetic ash	923	364.52	33.34	56.75	8.32	1.71	1.33	77.09	3.08	3.95
III-V Corn + protein-free skim milk	923	366.42	35.72	53.46	9.87	2.05	1.58	76.75	3.39	4.40
II Corn + black blood albumin.	417	378.20	31.53	59.08	9.22	1.47	1.48	77.05	3.60	3.59
II Corn, black blood albumin, + bone ash	417	389.26	30.68	61.53	8.51	1.76	1.36	79.75	3.54	4.57

and Washburn and Jones seem to have done likewise. Evvard[19] reports the average composition of pigs at birth. Roberts[20] in early work reported the composition of the carcasses of a thin and a fat Yorkshire sow. Table 15 shows the results of the first two investigators.

Swanson[21] reported the work of the Kansas Agricultural Experiment Station on the effect of corn with and without supplement of ash, or protein, or both, on growing pigs.

Only those animals which received both supplements can be considered normal. Of the thirty-six animals reported fifteen add up to less than 90 or more than 100 per cent in composition. The method of calculation accounts for this. The empty weight used is in most cases the weight of the dressed animal plus the weight of the blood and the dressed internal organs. The analytical samples do not add up to this weight. But the weights of water, fat, protein and ash found by analysis were divided by the "Empty weight" to give the results reported. Consequently the water content is invariably too low and the results for water are valueless. The other constituents are, however, strictly correct. The author has kindly furnished the data necessary to recalculate the composition of the swine to the true empty-weight basis assuming that the loss in preparation is water. The published results have been recalculated on this basis and are shown in Table 16.

In experiments II and III the contents of the digestive and excretory tract seem to have been determined directly and the water loss is rather accurately determined. In experiment IV the contents and the loss in preparation for analysis were determined together by difference. No recalculation therefore was possible and the results given are not comparable to the others. In experiments V and VI the empty animal was apparently determined by difference between the weight before slaughtering and the sum of the weights of parts analyzed and of portions not included in analysis. There are, therefore, three different methods involved and the recalculated results in the table, while probably nearer the truth, can hardly be used in the calculation of the true water content or the nitrogen in the water-, fat-, and ash-free matter.

Emmett, Grindley, Joseph and Williams[22] report the work of the Illinois Station on the effect of high and low protein diets on growing pigs. Seven young Berkshire pigs were analyzed. Table 17 gives the results. The dry substance was determined by summation (using protein = nitro-

[19] *Proceed. Amer. Breeders Assn.*, **8** (1912), 549.

[20] Cornell Agr. Expt. Station, Bul. 5 (1889).

[21] *Jour. Agr. Research*, **21** (1921), 279.

[22] Illinois Agr. Expt. Station, Buls. 168 (1914); 169 (1914); 171 (1914), and 173 (1914).

TABLE 17

Composition of the Entire Bodies of Swine—Analytical Animal

Illinois Work—Berkshire Breed

								Fat Free Basis			
Age, Days	Ration	Empty Wt., Lbs.	Water %	Fat %	Nitrogen %	Ash %	Phosphorus %	Water %	Nitrogen %	Ash %	Phosphorus %
127	Check	58.4	63.39	17.20	....	3.38	0.595	76.56	....	4.08	0.719
128	Check	52.5	60.99	20.88	....	3.01	0.532	77.09	....	3.80	0.672
300	Low Protein ...	169.1	45.39	35.89	2.349	4.03	0.708	70.80	3.66	6.29	1.104
300	Medium Protein	232.2	44.04	38.18	2.244	3.75	0.658	71.24	3.63	6.07	1.064
280	Medium Protein	188.8	44.19	37.16	2.261	4.52	0.671	70.32	3.60	7.19	1.068
299	High Protein ..	235.2	43.31	38.02	2.373	3.84	0.672	69.88	3.83	6.20	1.084
280	High Protein ..	175.6	45.36	36.72	2.278	3.68	0.652	71.68	3.60	5.82	1.030

gen × 6.25) and therefore the percentages of water are valueless in any comparison or computation.

Forbes [23] reported the composition of parts of a few swine including the carcasses of seven hogs. The total animal was not reported.

Table 18 gives the unpublished results of the Missouri Agricultural Experiment Station [24] on twenty-four different swine including two embryos. The results of Evvard and of Wilson on newborn pigs are included for comparison.

O. Wellman [25] reports the composition of the flesh of eight little pigs and the entire bodies of five little pigs. His results have been recalculated assuming that the loss in killing and cutting up is water. On this empty weight basis his pigs had the composition shown in Table 19.

In addition to the above data on swine there are those reported by O. Wellman [26] on twelve Berkshire pigs fed fat rich and carbohydrate rich milks of varying protein content. It has been impossible to secure the original publication, but reference must be made to the work here for the sake of completeness.

It is evident from the foregoing tables that fat is relatively the most variable component of the animal body, its amount varying with the age and especially with the condition of the animal. When the analyses are computed to fat-free substance the results show less variation.

Composition of the Fat-free Body. Since fat is the large variable and by its presence masks other changes in composition it is best to study the composition of animals on the fat-free, or protoplasmic, basis. Greene [27] and Moulton [28] have emphasized the value of this method, and Moulton, Trowbridge and Haigh [29] have shown what light is thrown upon changes in the composition of cattle with increasing age by using this method. Moulton [30] has shown that the water content of mammals decreases rapidly from the early embryo to birth and on to an age called the age of chemical maturity. Thereafter the decrease becomes rather suddenly very markedly less and decreases but slightly with further advancing age. The protein and ash content (on the fat free basis) show just the reverse condition, namely a marked increase in relative content until chemical maturity is

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[23] Mo. Agr. Expt. Station, Bul. 81 (1909); Ohio Agr. Expt. Sta., Bul. 283 (1915).

[24] Mo. Agr. Expt. Station, Bul. 197 (1922), page 37, gives a preliminary report of part of this work.

[25] *Landw. Jahrb.*, 46 (1914), 499.

[26] Kiserletügyi, Kozlemenyek, 19, I, 86-164 (Communications of Agr. Stations of Hungary).

[27] *J. Biol. Chem.*, 39 (1919), 435.

[28] *Ibid.*, 43 (1920), 67.

[29] Mo. Agr. Expt. Station, Research Bul. 55 (1922).

[30] *J. Biol. Chem.*, 57 (1923), 79.

TABLE 18

Composition of Entire Bodies of Swine—Empty Weight Basis

			Missouri Work						Fat Free Basis			
No. of Individual	Treatment	Age, Days	Empty Wt., Grams	Water %	Fat %	Nitrogen %	Ash %	Phosphorus %	Water %	Nitrogen %	Ash %	Phosphorus %
4	Normal embryo	88	522	86.87	1.13	1.32	2.20	0.391	87.87	1.33	2.22	0.395
10	Normal embryo	113	842	85.06	1.19	1.52	2.52	0.408	86.09	1.54	2.55	0.413
2	Newborn	Birth	900	82.47	1.27	2.12	3.88	0.351	83.53	2.15	3.93	0.356
1	Newborn	1	920	77.44	3.63	3.08	4.25	0.712	80.35	3.20	4.41	0.739
	Evvard[1]	Birth	...	78.85	1.50	1.93	4.10	....	80.05	1.96	4.16	....
3	Wilson	Birth	...	80.02	1.49	1.95	...	....	81.23	1.98	...	....
			Duroc-Jersey Gilts.									
1	Open	242	65970	56.35	25.34	2.60	3.05	0.540	75.48	3.48	4.09	0.723
1	88 days in gestation ...	344	101559	50.87	31.07	2.50	2.20	0.399	73.80	3.63	3.19	0.579
1	1 day postpartum	366	101128	48.21	34.67	2.41	2.48	0.442	73.79	3.69	3.80	0.677
1	Open	368	92705	48.08	35.15	2.41	2.73	0.501	74.14	3.72	4.21	0.773
1	113 days in gestation ..	380	97005	48.33	34.05	2.43	2.22	0.411	73.28	3.68	3.37	0.623
1	68 days postpartum, suckling two pigs	384	99100	49.94	31.63	2.65	2.58	0.448	73.04	3.88	3.77	0.655
1	2 days postpartum	390	104829	48.32	35.72	2.32	2.23	0.383	75.17	3.61	3.47	0.596
1	Open	419	108068	48.90	33.41	2.60	2.16	0.388	73.43	3.90	3.24	0.583
1	68 days postpartum not suckling pigs	431	117566	46.52	35.70	2.43	2.27	0.389	72.35	3.78	3.53	0.605
1	68 days postpartum suckling five pigs ...	442	74157	57.83	21.55	2.91	2.73	0.481	73.72	3.71	3.48	0.613
			Poland-China Hogs.									
1	60 B	123	38102	66.62	16.22	2.40	3.14	....	79.52	2.86	3.75	....
1	6 B	183	69490	56.12	29.05	2.24	2.83	....	79.10	3.16	3.99	....
1	12 B	206	86364	54.18	28.54	2.32	2.66	....	75.82	3.25	3.72	....
1	40 S	229	112536	51.30	32.16	2.14	2.75	....	75.62	3.15	4.05	....
1	10 B	264	133673	42.56	42.64	1.86	2.07	....	74.20	3.24	3.61	....
			Yorkshire Hogs.									
1	13 B	127	41594	65.00	17.12	2.36	2.88	....	78.43	2.85	3.47	....
1	3 B	176	68900	57.22	26.03	2.21	2.79	....	77.36	2.99	3.77	....
1	53 B	198	84912	52.43	30.60	2.31	2.66	....	75.55	3.33	3.83	....
1	33 S	226	107410	47.93	36.85	2.02	2.62	....	75.90	3.20	4.15	....
1	33 B	275	127413	42.41	42.81	1.89	2.16	....	74.16	3.30	3.78	....

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[1] The results of Evvard and Wilson on new born pigs are included here simply for comparison.

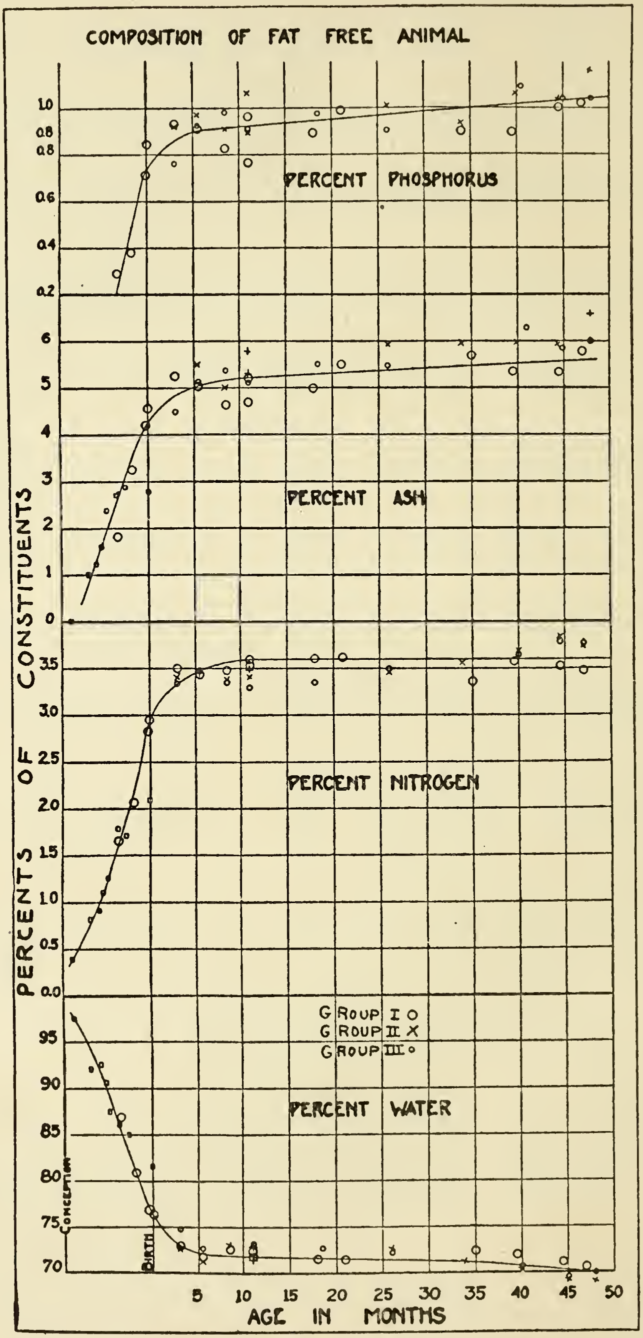

Fig. 1.—Effect of age on the composition of cattle. Data of Moulton and data on human embryos.

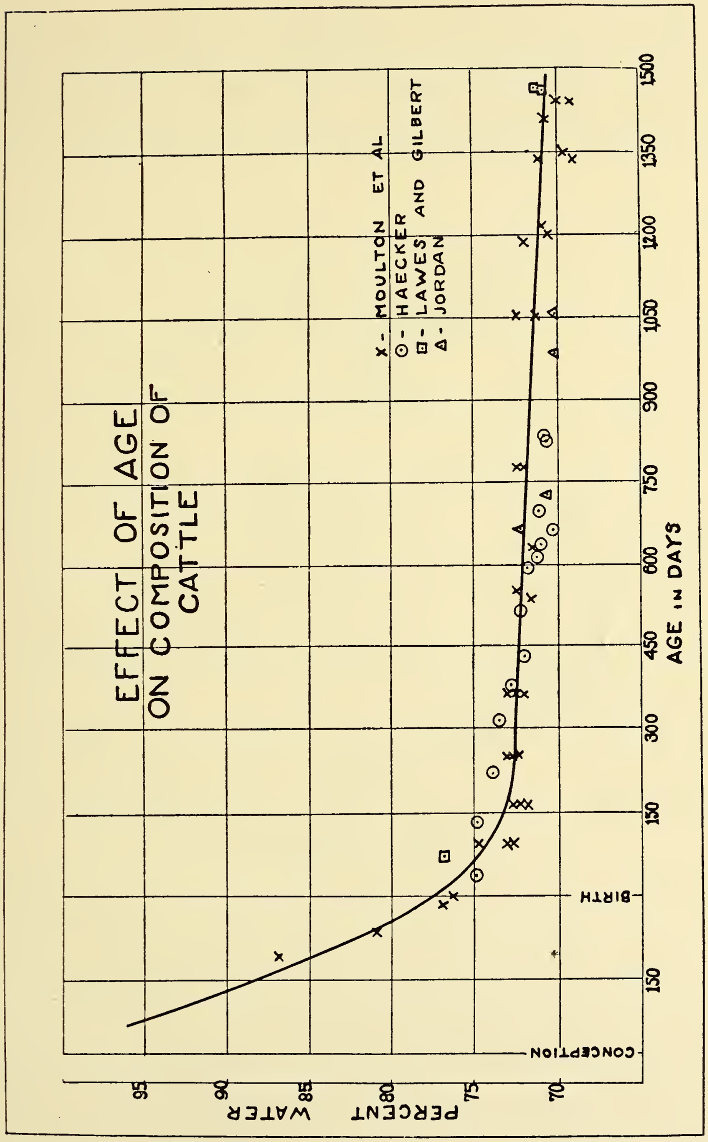

FIG. 2.—Effect of age on water content of cattle. Data of Moulton, Haecker, Lawes and Gilbert, and Jordan.

reached and then little or no change thereafter. For cattle the age of chemical maturity is about 5 months post partum and for swine it is 5 to 10 months.

The figures showing the results graphically are reproduced here (Figures 1 to 4). In studying the variations from the ideal curve drawn it should be borne in mind that hide, or skin, muscle, fatty tissue, and bone all have a different water, protein, and ash content on the fat-free basis. The relative amounts of these tissues vary in animals of the same breed even, depending upon the flesh and fatty tissue development. It is, therefore, more to be wondered at that the agreement is as close as it is than that there is variation from the ideal curve.

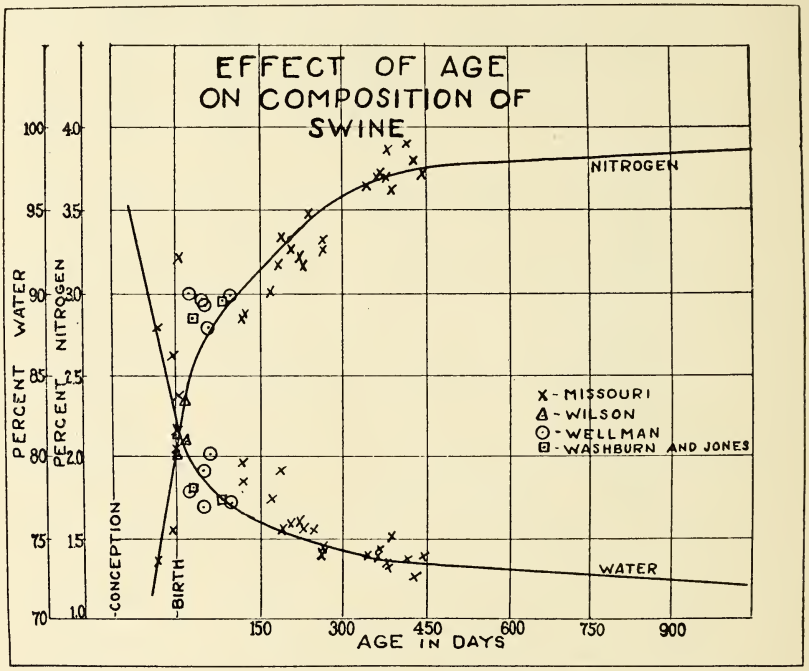

FIG. 3.—Effect of age on composition of swine—water and nitrogen.

Composition of the Fat- and Ash-free Dry Matter of the Body. Special interest attaches to the composition of the fat- and ash-free dry matter of the body on account of its relation to the experimental methods described in a subsequent chapter. Tables 20 to 22 show the percentage of fat- and ash-free dry matter and of nitrogen in those cases in which nitrogen, fat, ash, and total moisture in the empty animal were determined.

The computed percentage of nitrogen in the fat- and ash-free dry matter is given also. The percentages vary from 13.99 in the embryos reported by Moulton, Trowbridge and Haigh to 16.31 in Chaniewski's geese. Omitting the embryos and the results of Soxhlet and Weiske and Wildt, the latter two on account of certain unjustifiable assumptions in the calculations, an average of 15.97 per cent nitrogen is obtained. This compares very closely with the average for animal proteins, 16.06. If it is assumed that there is 0.5 per cent of glycogen, flesh acids, and other non-fatty, nonnitrogenous organic matter in the fat-free animal the percentage becomes 16.05 (15.97 ÷ .995).

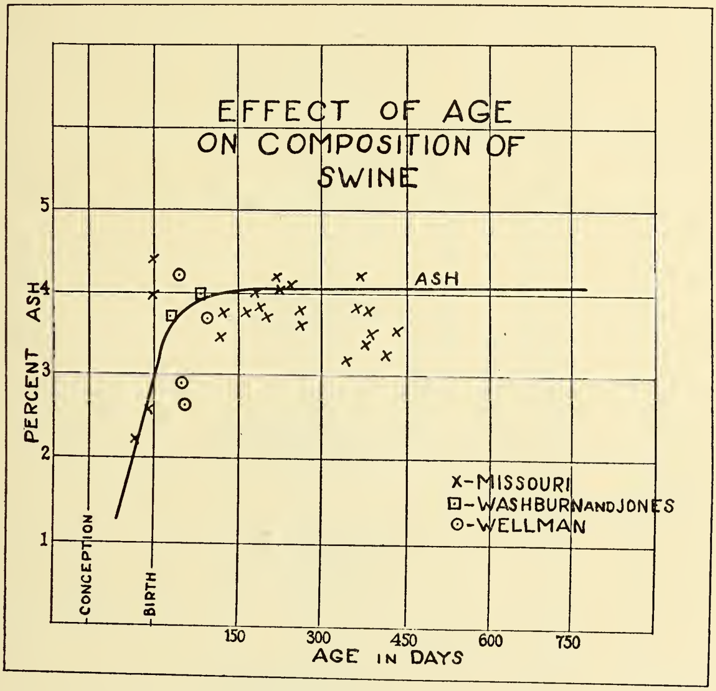

Fig. 4.—Effect of age on composition of swine-ash.

The value of 16 per cent is further confirmed by the work of Mendel[31] with white mice. He reported the composition of 36 normal and 4 abnormal mice of various ages and on various diets. The 36 normal mice had 15.98 per cent nitrogen in the water-, fat- and ash-free matter of the body (minus the abdominal viscera and contents, but including the liver). The range was between 15.0 and 16.9 per cent with one value at 14.2 per cent.

[31] *Biochem. Ztschr.*, 11 (1908), 281.

TABLE 19

Composition of Young Pigs—Empty Weight Basis

(Wellman)

Age, Days	Animal No.	Live Wt., Grams	Empty Wt., Grams	Water %	Fat %	Nitrogen %	Ash %	Fat Free Basis Water %	Fat Free Basis Nitrogen %	Fat Free Basis Ash %
48	VIIa	4350	3986	71.92	6.54	2.76	3.94	76.95	2.95	4.22
96	VII	18068	17057	66.94	13.38	2.58	3.19	77.28	2.98	3.68
26	VIII-IXa	4656	4371	69.02	11.38	2.66	3.13	77.88	3.00	3.53
49	VIII	8040	7420	71.62	9.51	2.67	2.61	79.15	2.95	2.88
59	IX	12037	11374	73.86	7.91	2.56	2.42	80.20	2.78	2.63

The four abnormal mice had only 14.48 per cent nitrogen. Zuntz[32] obtained similar results with the rat at birth. From 45 litters containing 281 individuals he found 15.94 per cent nitrogen in the water-, fat-, and ash-free matter. However, the rats were too young to be developed chemically and the fat was obtained by difference. The figure obtained is, therefore, valueless for the present purpose.

TABLE 20

Nitrogen in Fat- and Ash-Free Dry Matter

		Empty Weight Contained		
		Fat- and Ash-Free Dry Matter	Nitrogen	Nitrogen in Fat- and Ash-Free Dry Matter
Chaniewski	Geese[1]	22.50	3.63	16.13
	Geese[1]	19.21	3.18	16.55
	Geese[1]	17.05	2.77	16.25
Jordan	Cattle	18.79	3.03	16.13
	Cattle	18.83	3.03	16.09
	Cattle	18.15	2.92	16.09
	Cattle	18.00	2.90	16.11
Lawes and Gilbert	Cattle	15.70	2.537	16.16
	Cattle	18.10	2.95	16.30
	Cattle	15.40	2.466	16.01
	Fat lamb	13.40	2.150	16.05
	Sheep	15.70	2.525	16.08
	Sheep	15.40	2.486	16.14
	Sheep	13.00	2.085	16.04
	Sheep	11.50	1.857	16.15
	Pig	14.50	2.342	16.15
	Pig	11.40	1.830	16.05
Soxhlet	Swine	12.92	2.03	15.71
	Swine	13.43	2.07	15.41
	Swine	11.79	1.74	14.76
Weiske and Wildt	Swine	12.80	1.89	14.77
	Swine	10.04	1.36	13.55
Washburn and Jones	Swine	15.70	2.45	15.61
	Swine	14.03	2.06	14.68
	Swine	14.60	2.32	15.89
	Swine	13.33	2.25	16.88
	Swine	16.18	2.43	15.02
	Swine	14.57	2.27	15.58
	Swine	13.63	2.01	14.75
	Swine	15.09	2.35	15.57
	Swine	16.36	2.58	15.77
	Swine	15.93	2.48	15.57
	Swine	14.83	2.24	15.10
	Swine	16.17	2.50	15.46

[1] Less feathers.

A number of analysis of fat- and ash-free muscular tissue (lean meat) have been made which show a distinctly higher percentage of nitrogen.

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[32] *Archiv Gynaekologie,* 110 (1919), 244.

TABLE 21

Nitrogen in Fat- and Ash-Free Dry Matter, Missouri Cattle

		Empty Weight Contained		
	Cattle	Fat- and Ash-Free Dry Matter	Nitrogen	Nitrogen in Fat- and Ash-Free Dry Matter
Moulton, Trowbridge, Haigh...	Embryos	11.06	1.67	15.10
	Embryos	15.55	2.01	12.93
	Embryos	18.37	2.74	14.92
	New born calves	18.49	2.84	15.36
	Cattle	19.72	3.17	16.07
	Cattle	20.32	3.18	15.65
	Cattle	19.86	3.20	16.11
	Cattle	18.02	2.73	15.15
	Cattle	20.31	3.09	15.21
	Cattle	20.70	3.22	15.56
	Cattle	19.22	2.94	15.30
	Cattle	18.93	2.92	15.43
	Cattle	20.13	3.08	15.30
	Cattle	18.26	2.82	15.44
	Cattle	17.21	2.71	15.75
	Cattle	18.60	2.93	15.75
	Cattle	19.12	2.97	15.53
	Cattle	18.73	2.92	15.59
	Cattle	19.17	2.91	15.18
	Cattle	21.33	3.27	15.33
	Cattle	18.50	2.79	15.08
	Cattle	17.26	2.67	15.47
	Cattle	19.32	2.93	15.17
	Cattle	19.67	3.02	15.35
	Cattle	16.41	2.58	15.72
	Cattle	19.80	3.11	15.71
	Cattle	21.05	3.29	15.63
	Cattle	18.56	2.97	16.00
	Cattle	19.68	3.09	15.70
	Cattle	14.16	2.17	15.32
	Cattle	16.12	2.51	15.57
	Cattle	18.43	2.89	15.68
	Cattle	18.93	2.96	15.64
	Cattle	12.64	1.98	15.66
	Cattle	17.48	2.77	15.85
	Cattle	18.96	2.96	15.61
	Cattle	20.68	3.26	15.76
	Cattle	13.69	2.05	14.97
	Cattle	20.83	3.20	15.36
	Cattle	20.68	3.18	15.38
	Cattle	13.33	1.96	14.70
	Cattle	18.62	2.88	15.47
	Cattle	20.04	3.13	15.62
	Cattle	13.57	2.07	15.25

TABLE 22

Nitrogen in Fat- and Ash-Free Dry Matter, Missouri Swine

		Empty Weight Contained		
	Swine	Fat- and Ash-Free Dry Matter	Nitrogen	Nitrogen in Fat- and Ash-Free Dry Matter
Missouri	Embryos	9.80	1.32	13.47
	Embryos	11.23	1.52	13.54
	New born	12.38	2.12	17.12
	New born	14.68	3.08	20.98
	Swine	15.26	2.60	17.04
	Swine	15.86	2.50	15.76
	Swine	14.64	2.41	16.46
	Swine	14.04	2.41	17.17
	Swine	15.40	2.43	15.78
	Swine	15.85	2.65	16.72
	Swine	13.73	2.32	16.90
	Swine	15.53	2.60	16.74
	Swine	15.51	2.43	15.67
	Swine	17.89	2.91	16.27
	Swine	14.02	2.40	17.12
	Swine	12.00	2.24	18.67
	Swine	14.62	2.32	15.87
	Swine	13.79	2.14	15.52
	Swine	12.73	1.86	14.61
	Swine	15.00	2.36	15.73
	Swine	13.96	2.21	15.83
	Swine	14.31	2.31	16.14
	Swine	12.60	2.02	16.03
	Swine	12.62	1.89	14.98

Earlier analyses by Rubner, Stohmann and Langbein, and Argutinsky gave the results shown in Table 23.

TABLE 23

Composition of Water-, Fat- and Ash-Free Muscular Tissue of Cattle

	Carbon %	Hydrogen %	Nitrogen %	Oxygen and Sulfur %	Heat of Combustion per Gram, Cals.
Rubner	53.40	8.04	16.30	22.19	5.6569
Stohmann & Langbein	52.02	7.30	16.36	24.32	5.6409
Argutinsky	52.33	7.30	16.15	24.22	.....
Köhler	52.69	7.17	16.57	23.57	5.7008

Köhler[33] found the figures shown in Table 24 after allowing for the minimal amounts of fats not removed by ether extraction. Köhler's figures for cattle are also included above.

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[33] *Ztschr. physiol. Chem.*, 31 (1901), 479.

TABLE 24

Composition of Water-, Fat- and Ash-Free Lean Meat of Domestic Animals

	No. of Samples	Carbon %	Hydrogen %	Nitrogen %	Sulfur %	Oxygen %	Heat of Combustion per Gram., Cals.
Cattle	4	52.69	7.17	16.57	0.52	23.05	5.7008
Sheep	2	52.53	7.19	16.64	0.69	22.96	5.6387
Swine	2	52.71	7.17	16.60	0.59	22.95	5.6758
Horse	3	52.64	7.10	15.55	0.64	24.08	5.5990
Rabbit	2	52.83	7.10	16.90	...	....	5.6166
Hen	2	52.36	6.99	16.88	0.50	23.28	5.6173

While the foregoing figures show some variations, they make it clear that the amounts of substances other than water, fat, protein and ash contained in the animal body are comparatively insignificant so far as they affect the quantitative composition.

The Schematic Body. This conception of considering the animal body to be, aside from negligible amounts of glycogen, merely water, fat, protein, and ash is a very useful one. That it cannot be far from correct is shown by comparing the figure 15.97 with 16.06. The figure 16 for the percentage of nitrogen gives a protein factor of 6.25. For the proteins of lean flesh alone the factor 6 is perhaps more accurate.

From this point of view it is evident that the effect of any feeding stuff or ration in causing a gain or preventing a loss of fat, protein, and ash (and glycogen) is indicative of its aggregate nutritive effect. Since the organic matter of the body may be looked upon as stored energy, a still simpler expression of the nutritive effect may be obtained by determining the effect of the feed upon the store of protein and of chemical energy in the body. The demonstration is not entirely complete, however, unless stock is taken of each different kind of protein in the body and its location. This stock must be maintained. In addition it must be demonstrated that all the energy containing material derived from the feed is actually capable of yielding up its energy to the organism. No considerable storage of unavailable energy in the body has been recognized and, especially on a mixed diet, it may be assumed that, if the body maintains its stock of protein, each particular kind is practically maintained.

The comparative slaughter test relies upon this conception of the schematic body.

Composition of Carcass. The foregoing figures, except those for the composition of muscular tissue, refer, as stated, to the entire animal and include the offal parts as well as the commercial meat. The composition of the latter is of great interest.

Lawes and Gilbert[34] report the composition of the total commercial carcasses of their ten animals, including the kidneys and kidney fat but none of the other edible organs. Their results are shown in Table 25.

TABLE 25

Composition of Carcasses of Animals

(Lawes and Gilbert)

	Per Cent. in Carcass				
Description of Animal	Mineral Matter	Dry Nitrogenous Compounds	Fat	Total Dry Substance	Water
Fat calf	4.48	16.6	16.6	37.7	62.3
Half-fat ox	5.56	17.8	22.6	46.0	54.0
Fat ox	4.56	15.0	34.8	54.4	45.6
Fat lamb	3.63	10.9	36.9	51.4	48.6
Store sheep	4.36	14.5	23.8	42.7	57.3
Half-fat old sheep	4.13	14.9	31.3	50.3	49.7
Fat sheep	3.45	11.5	45.4	60.3	39.7
Extra fat sheep	2.77	9.1	55.1	67.0	33.0
Store pig	2.57	14.0	28.1	44.7	55.3
Fat pig	1.40	10.5	49.5	61.4	38.6
Mean of all	3.69	13.5	34.4	51.6	48.4
Mean of 8; namely, of the half-fat, fat, and very fat animals	3.75	13.3	36.5	53.6	46.4
Mean of 6; namely, of the fat and very fat animals	3.38	12.3	39.7	55.4	44.6

From the data reported by Trowbridge, Moulton and Haigh[35] it may be computed that the lean and fat flesh plus the skeleton of their four steers had the following composition:

	Weight of Lean and Fat Flesh and Skeleton, Grams	Water %	Fat %	Protein[1] %	Ash %
Steer 18	217,799	53.24	20.44	18.40	7.35
Steer 121	362,045	46.60	31.96	15.78	5.50
Steer 48	538,621	38.82	43.11	12.77	4.45
Steer 197	325,537	50.57	26.55	16.72	5.90

[1] Protein = Nitrogen x 6.25.

Haecker[36] found the average composition of the edible portion (including edible offal) of five calves at 100 pounds and five at 400 pounds live

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[34] *Phil. Trans.*, Part II (1859), 520.

[35] Mo. Agr. Expt. Station, Res. Bul. 30 (1919), 92-95.

[36] *Amer. Soc. Anim. Production, Proc.*, 1916, 169.

weight, respectively, corresponding to the approximate ages of 38 days and 316 days, to have the following composition:

Weight of Calves	Dry Matter %	Protein %	Fat %	Ash %
100 lbs.	24.94	19.27	4.60	1.07
400 lbs.	31.67	18.55	12.13	0.99

Moulton, Trowbridge and Haigh[37] give the composition of the edible portion of the carcasses of many cattle from birth to four years (Table 26). This edible matter gets very fat in the older, fatter animals. But, while it may be classed as edible, it is not likely that it will all be eaten.

TABLE 26

COMPOSITION OF THE LEAN AND FAT FLESH OF THE CARCASSES OF CATTLE
(Moulton, Trowbridge and Haigh)

Age, Months	Condition	Water %	Fat %	Nitrogen %	Ash %	Phosphorus %
Birth	Normal	77.03	4.01	2.707	0.989	0.167
3	Fat	70.59	9.14	3.088	1.128	0.184
3	Medium	73.19	5.94	3.121	1.166	0.191
3	Thin	76.42	3.26	3.078	1.100	0.189
5½	Fat	58.12	24.82	2.484	0.855	0.155
5½	Medium	70.03	9.45	2.987	0.989	0.175
5½	Thin	73.75	4.73	3.197	1.054	0.192
8½	Fat	63.12	17.92	2.722	0.888	0.156
8½	Medium	66.53	14.30	2.834	0.943	0.185
8½	Thin	73.49	5.52	3.054	0.962	0.190
11	Fat	58.71	23.09	2.681	0.844	0.156
11	Medium	67.66	14.01	2.902	0.944	0.176
11	Thin	67.88	11.72	2.971	0.968	0.179
18	Fat	53.95	28.72	2.570	0.792	0.142
18	Thin	68.05	10.03	3.169	1.026	0.189
21	Fat	49.66	35.13	2.293	0.679	0.128
26	Medium	65.17	16.50	2.832	0.858	0.161
26	Thin	68.45	11.91	2.971	0.936	0.174
34	Fat	42.28	45.22	1.885	0.571	0.103
34	Medium	60.40	21.48	2.724	0.812	0.151
39½	Fat	37.34	51.80	1.633	0.486	0.089
40	Medium	59.20	22.38	2.758	0.833	0.152
40½	Thin	70.33	8.86	3.148	0.980	0.175
44½	Fat	38.66	49.37	1.704	0.514	0.093
44½	Medium	61.63	18.22	2.913	0.843	0.156
45	Thin	63.17	16.96	2.887	0.852	0.160
47	Fat	36.25	53.12	1.457	0.485	0.087
48	Medium	54.96	28.29	2.484	0.772	0.133
48	Thin	63.11	17.23	2.960	0.892	0.156

From the data presented by these workers, which include the composition of various offal parts, one may easily calculate the edible portion of the entire animal. The liver, kidneys, sweetbreads, kidney fat, and caul fat

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[37] Mo. Agr. Expt. Station, Research Bul. 55 (1922).

would be included. Many other parts of the offal are consumed however. The modern packinghouse converts a large part of the animal into edible products. The personal taste of the consumer enters largely into the question of edibility and much of the offal fat does not enter directly into human food. The failure of all of the animal to be used as human food should not be laid at the door of the animal. Therefore, it is not considered worth while to present other data here.

Henneberg, Kern and Wattenberg have reported the composition of the entire flesh of the various wholesale cuts of the carcasses of 8 sheep. From their work the composition of the flesh of the carcass can be calculated. The results are shown in Table 27. The flesh of these sheep did not get as fat as that of cattle or swine, the high value of fat being below 26 per cent.

TABLE 27

Composition of the Entire Flesh of the Carcasses of Sheep
(Henneberg, Kern and Wattenberg)

Age, Months	Condition	Empty Wt., Kilograms	Water %	Fat %	Nitrogen %	Ash %	Fat Free Basis Water %	Fat Free Basis Nitrogen %	Fat Free Basis Ash %
6½	Thin	14.91	68.45	13.08	2.75	1.06	78.75	3.16	1.22
12½	Fat	39.50	66.62	15.90	2.73	0.99	79.22	3.25	1.18
13	Plump	31.97	68.98	13.16	2.81	1.00	79.43	3.24	1.15
17½	Very fat	52.94	57.63	25.80	2.54	0.95	77.67	3.42	1.28
21½	Plump and fat	48.97	62.16	20.58	2.66	0.97	78.27	3.35	1.22
27½	Very fat	61.66	63.49	18.41	2.76	1.03	77.82	3.38	1.26
33	Almost plump	35.75	59.93	23.71	2.49	1.00	78.56	3.26	1.31
40	Very fat	51.90	66.29	14.98	2.89	1.04	77.97	3.40	1.22

Composition of Milk.

The cow is the milk producing animal of the western nations and by far the larger share of all available data regarding milk relate to the product of this animal.

Variation in Composition. Cow's milk varies widely in composition. The most important differences are due to breed and individuality on one hand and, on the other, to the stage of lactation, the season of the year and the age of the animal. This statement refers to the average composition for a series of milkings. In the same individual animal there are often notable fluctuations in the composition of the milk from milking to milking and from day to day. The most notable conditions causing these changes are the length of the interval between milkings, the completeness of the milking, cold or hot weather, moderate exercise after rest, the physical condition of the cow, and underfeeding for a time. Some idea of the principal differences in the composition of milk afforded by the analyses of milk of several breeds can be obtained from data compiled by Armsby.[38] Other important sources of information may be found below.[39]

Fat being the most valuable ingredient of the milk and being also readily determinable with a good degree of accuracy by the various rapid methods, very extensive data regarding the percentage of this constituent are on record. Fat is the most variable ingredient of milk. For the cow a minimum of 1.67 per cent is reported by König.[40] On the other hand occasionally 7 per cent is reached in cow's milk. Babcock[41] states that 9 per cent is the maximum observed for a cow giving 15 pounds of milk daily. These extremes are confirmed in a statistical study by Anderson[42] concerning the variations in fat content of the milk from cows on test.

The percentage of solids not fat may be computed with a considerable degree of accuracy from the percentage of fat and the specific gravity of the milk by means of the formulas proposed by Fleischmann,[43] Hehner,[44] Richmond,[45] and Babcock.[46] For a comparative study of formulas reference can be made to the more recent work of Shaw and Eckles.[47]

Relatively few determinations of other ingredients are available.

The average composition of cow's milk according to various authorities cited by Wing[48] is as shown in the last four columns of Table 28 while the first column shows the average as compiled by Van Slyke.[49]

The proteins of milk include casein, lactalbumin, paraglobulin and traces of peptones. According to König[50] the percentage of casein varies from 1.79 to 4.23 per cent and that of the other proteins from 0.25 to 1.44 per cent. Cooke[51] found that the total protein of milk varies slightly from 25 per cent of the total solids. The same conclusion may be drawn

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[38] "Nutrition of Farm Animals," New York, 1917, 473-4.

[39] "Milk and Its Hygienic Relations," Lane-Claypon, London, 1916. "Milk," Heineman, Philadelphia and London, 1919. "Manual of Milk Products," Stocking, New York, 1917. "Dairy Chemistry," Richmond, London, 1920. Eckles and his coworkers U. S. D. A., Bur. of Animal Ind. Buls. 134 (1911); 155 (1913); 156 (1913); 157 (1913). Univ. of Mo., Agr. Expt. Station, Bul. 100 (1912). U. S. Treasury Dept., Hygienic Lab., Bul. 41 (1908).

[40] "Nutrition of Farm Animals," Armsby, 460.

[41] *Ibid.*, 460.

[42] Mich. Agr. Expt. Station, Special Bul. 71 (1914).

[43] *Jour. f. Landw.*, 33 (1885), 251.

[44] *Analyst*, 7 (1882), 27 and 13 (1888), 26.

[45] *Proc.* 11th *Convention* (1884), A. O. A. C., U. S. D. A., Bur. of Chem., Bul. 43, 181.

[46] Annual Report, Wis. Agr. Expt. Sta., 1891, 292 and 1895, 120.

[47] U. S. D. A., Bur. An. Industry, Bul. 134 (1911).

[48] "Milk and Its Products" (1897), 17.

[49] Jordan: "The Feeding of Animals," New York, 1901, 305.

[50] "Nutrition of Farm Animals," 459.

[51] Vt. Experiment Sta., Report 1890, 97-100.

TABLE 28

Average Composition of Cow's Milk

	American (Van Slyke)	American (Babcock)	English (Oliver)	German (Fleischmann)	French (Cornevin)
Water	87.1	87.17	87.60	87.75	87.75
Fat	3.9	3.69	3.25	3.40	3.30
Casein	3.2[1]	3.02	3.40	2.80	3.00
Albumin	....	0.53	0.45	0.70	....
Sugar	5.1	4.88	4.55	4.60	4.80
Ash	0.7	0.71	0.75	0.75	0.75
	100.00	100.00	100.00	100.00	100.00

[1] Casein + Albumin.

from the composition of milk of different breeds referred to above and also from Haecker's[52] results from analyses of 544 individual samples of milk from the Minnesota Station herd. Accordingly, by assuming an average figure for the ash, the approximate composition of a milk may be computed from its fat content and specific gravity.

The ash of milk is quite similar in its make-up to the ash of the body except that the proportions of calcium and phosphorus are lower on account of the absence of bone tissue. Bunge[53] finds that the composition of ash of the milk of different species corresponds quite closely to that of the body and differs widely from that of the blood serum. His figures for cattle, to which have been added Lawes and Gilbert's figures for the ash of a calf, are given in Table 29.

TABLE 29

Percentage Composition of Ash of Blood and Milk of Cattle and of Body of Calf

	Serum of Cattle Blood	Cow's Milk	Body of Calf
K_2O	3.2	22.1	5.40
Na_2O	55.1	13.9	3.82
CaO	1.6	20.0	43.95
MgO	0.6	2.6	2.20
Fe_2O_3	0.1	0.04	0.53
Cl	47.1	21.3	0.12
P_2O_5	3.4	24.8	40.37

Table 30, largely after Heinemann,[54] gives the composition of the milk of various mammals. For further data see Schäfer's "Textbook of Physiology," Edinburgh and London, 1898, I, 125 and also Völtz in Oppenheimer's "Handbuch der Biochemie des Menschen und der Tiere," Jena, 1910, III, 1*er* Haelfte, 403.

[52] Minn. Agr. Expt. Sta., Bul. 140 (1914), 51.

[53] *Ztschr. Biol.,* 10 (1874), 301; 12 (1876), 191.

[54] "Milk," Philadelphia, 1919, 70.

TABLE 30

Composition of Milk of Mammals

Kind of Milk	Water	Total Solids	Proteins Casein	 Albumin	Total Protein	Fat	Lactose	Ash	Fuel Value per Lb.	Specific Gravity
Woman	87.58	12.42	0.80	1.21	2.01	3.74	6.37	0.30	310	1.0298
Cow	87.27	12.73	2.88	0.51	3.39	3.68	4.94	0.72	310	1.0313
Cow Colostrum ...	75.07	24.93	4.19	12.99	17.18	3.97	2.28	1.53	...	1.042
Goat	86.88	13.12	2.87	0.89	3.76	4.07	4.64	0.85	315	1.0305
Sheep	83.57	16.43	4.17	0.98	5.15	6.18	4.73	0.96	410	1.0355
Sow	83.94	16.06	...	...	7.23	4.55	3.23	1.05	...	1.038
Buffalo (Indian)...	82.16	17.84	4.26	0.46	4.72	7.51	4.77	0.84	...	1.035
Bitch	75.44	24.56	...	...	11.17	9.57	3.09	0.73	...	1.035
Zebu	86.13	13.87	...	...	3.03	4.80	5.34	0.70	...	.....
Elephant	79.30	20.70	...	...	2.51	9.10	8.59	0.50	...	1.0313
Camel	87.13	12.87	3.49	0.38	3.87	2.87	5.39	0.74	...	1.042
Llama	86.55	13.45	3.00	0.90	3.90	3.15	5.60	0.80	...	1.034
Reindeer	67.20	32.80	8.38	1.51	9.89	17.09	2.82	1.49	...	.....
Mare	90.58	9.42	1.30	0.75	2.05	1.14	5.87	0.36	...	1.0347
Ass	90.12	9.88	0.79	1.06	1.85	1.37	6.19	0.47	215	1.032
Rabbit	69.50	30.50	...	...	12.00	13.50	2.00	2.50	...	1.047
Dolphin	41.00	59.00	...	...	11.00	46.00	1.30	0.60	...	.....

Composition of Eggs.

Atwater and Bryant[55] report the average composition of hen's eggs as follows:

Shells	11.2
Contents	88.8
	100.00
Edible portion:	
Water	73.7
Protein (by difference)	14.8
Fat	10.5
Ash	1.0
	100.00

Unpublished data of the Missouri Agricultural Experiment Station show that eggs may contain 10.42 per cent shell and 89.58 per cent contents. The contents are 60 per cent white and 40 per cent yolk. The average composition of 30 samples of eggs is as follows:

	Water	Protein (Nitrogen × 6.25)	Fat	Ash
White	85.42	12.57	....	...
Yolk	53.92	16.11	27.82	1.56
Composite	72.82	13.99	11.13	...

Fat and ash were not determined in the egg white.

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[55] U. S. Dept. of Agr., Office of Expt. Sta., Bul. 28 revised (1906).

Chapter 3.

Digestion and Absorption.

Differences Between Feeding Stuffs and Animal Products. It is plain even to the most casual observation that the meat, milk and eggs which are contributed to the food supply by domestic herbivora and omnivora differ radically from the feeding stuffs consumed by them and that profound changes are involved in the conversion of hay and grain into animal products. The consideration, in Chapters 1 and 2, of the chemistry of feeding stuffs and of animal products serves to reinforce and render more precise this conclusion from common observation.

Quantitatively, the proportions of the three great groups of organic substances concerned, viz., protein, carbohydrates, and fats, differ widely in the two cases. While the green plant performs the indispensable function of manufacturing the proteins contained in its cells and stored in its seeds, nevertheless from the quantitative standpoint it is, broadly speaking, pre-eminently a producer of carbohydrates. From them it builds up its framework and with them it stores in most species the cells of its reserve organs. The animal body, on the other hand, is pre-eminently a storer of proteins and fats, utilizing the former as structural material and setting aside large amounts of the latter, often much more than is contained in its feed, as reserve material.

Qualitatively the differences between plants and animals are in a sense even more marked than the quantitative differences. While both contain proteins, carbohydrates and fats, the individual members of these groups differ markedly as to chemical composition, molecular structure, and physical properties.

The proteins of plants and animals differ relatively little in ultimate composition, the chief distinction being a tendency to a higher percentage of nitrogen in the former. In their amino acid makeup, on the other hand, very marked differences appear, the vegetable proteins tending to be, as already noted, relatively rich in glutamic acid and in prolin, while, on the other hand, several are deficient in one or more of the amino acids found in animal proteins. Finally, the demonstrated specific differences in animal proteins and the phenomena of immunity and anaphylaxis render it evident that some at least of the enormous possibilities for isomerism in the highly complex protein molecule are realized in the animal body and presumably in the plant as well.

The carbohydrates are but sparingly represented in animal products. Neither of their two chief representatives, glycogen and lactose, are found in feeding stuffs; while it is evident that such carbohydrates as starch and cellulose must require extensive chemical changes to fit them for use in the body.

The fats of the vegetable and animal kingdom show somewhat less striking differences than the proteins or carbohydrates, although fatty acids other than those of body fat occur in some feeding stuffs while the lower fatty acids of milk fat are peculiar to it.[1]

The quantitative and qualitative changes required for the conversion of vegetable into animal products are initiated in the process of digestion. Chemistry of digestion has been studied chiefly with carnivora.

The Organs of Digestion. Morphologically, the digestive tract of all animals is an invagination, or infolding, of the external surface of the body so that the contents of this tract are still outside the body proper. In very simple animals it consists merely of a cavity or tube having an opening for the entrance of food and for the exit of indigestible matter and provided with cells in its walls which excrete a digestive fluid or fluids. As we rise in the biological scale, the digestive organs become more numerous and complex and their functions are increasingly differentiated. In the higher animals, the digestive tract may be briefly described as a tube beginning at the mouth and ending at the anus and having various enlargements, folds, and diverticula together with numerous highly developed glands which pour their secretions into its cavity. In domestic animals it consists of the mouth, esophagus, stomach, and small and large intestines with the corresponding glands.

No extended description of the digestive organs is required here, since we are concerned chiefly with the chemistry of processes, but it is necessary to emphasize one respect in which the digestive tract of the common farm animals differs from that of man or of carnivora. Not only do the digestive organs of the herbivora correspond in size with the more bulky feed which these animals consume but they are especially characterized by certain diverticula in which the feed, so to speak, stagnates in its passage through the alimentary canal. These diverticula are enlargements of the esophagus or of the large intestine.

The crop of fowls is such an enlargement of the esophagus but the

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[1] See Ulzer and Klimont, "Allgemeine und physiologische Chemie der Fette für Chemiker, Mediziner und Industrielle," Berlin, 1906.

most marked example is the rumen, reticulum and omasum—the so-called first, second and third stomachs—of ruminants. In the horse the cardiac portion of the apparently simple stomach is also in reality an enlargement of the lower end of the esophagus, although separated from the true stomach only by a slight constriction. The same is true of the hog although the cardiac portion of the stomach is relatively much smaller than in the horse.

The other enlargement of the digestive cavity is the cecum, situated at the junction of the small and large intestines. The cecum is more or less supplementary to the esophageal pouches. It reaches its greatest development in the horse, where it represents about one-sixth of the total capacity of the digestive organs, thus compensating for the relatively small stomach of this animal, while the colon of the horse is also enormously developed. In ruminants, on the other hand, with their compound stomach, the cecum constitutes only about 2½ to 3 per cent of the total capacity of the digestive tract and in the hog only about 5½ per cent.

Agents of Digestion. The chemical and the consequent resulting physical changes which the food undergoes in the process of digestion are effected chiefly through the agency of enzymes, while the digestive cavities serve both as containers and as incubators. The digestive enzymes are contained in the secretions of the digestive glands and produce hydrolysis. The micro-organisms also present are apparently derived in the first instance from the food consumed and include various species of bacteria and protozoa. With a uniform food supply certain species acquire predominance and a comparatively stable balance becomes established. Radical changes in the food may effect more or less marked modification of the intestinal flora, yet under ordinary conditions the balance for any particular species of animal seems to be fairly well maintained.

The Digestive Enzymes. The enzymes of the digestive fluids are the major agents of digestion in all animals but are supplemented to a varying extent in different species by the action of the micro-organisms. In man and in carnivorous animals the latter is a small factor, while in the herbivora, on the contrary, it is one of considerable significance. With the possible exception of rennin, all digestive enzymes are hydrolytic.

The more important digestive enzymes are:

1. The amylases, ptyalin (in the saliva) and amylopsin (in the pancreatic juice), acting upon starch with the final production of maltose.

2. The invertases, sucrase, maltase and lactase (in the intestinal juice and mucosa) converting di-saccharoses to mono-saccharoses.

3. The proteases, pepsin (in the gastric juice), trypsin (derived from

trypsinogen in the pancreatice juice) and erepsin (in the intestinal juice and mucosa), acting upon proteins, ultimately giving amino-acids.

4. Nucleases and nucleosidases (in the intestinal juice) acting on nucleic acids.

5. The lipase, steapsin (in the pancreatic juice), acting upon the lipoids, or specifically the fats, giving fatty acids and glycerol. In some animals, at least, there seems to be a gastric lipase.

The Micro-Organisms. Of the micro-organisms, by far the most significant for the present purpose are those which bring about the methane fermentation of various carbohydrates. Their activitiy is especially evident in the herbivora, particularly in those portions of the digestive tract (rumen, cecum, and colon) in which the food stagnates, although it is not absent in other species, including even man, as has been shown by Fries.[2] Lower fatty acids are the utilizable products formed.

Of secondary importance are the putrefactive bacteria of the lower intestine giving rise to the production of ammonia and various substances of the aromatic series, especially indol, skatol and the phenols, derived from heterocyclic components of the protein molecule and which cause the offensive odor of the feces. These components are in part absorbed by the intestine and excreted through the urine, largely in the form of so-called ethereal sulfates, which are comparatively harmless products.

The Bile. The bile, a secretion, or excretion, of the liver, takes part in the digestion and absorption of the fats through its mulsifying power and its alkalinity. No enzymes occur in the bile. It is delivered into the small intestine at, or near, the point of entrance of the pancreatic juice.

The Digestion of Proteins.

Gastric Digestion. The first digestive fluid to act upon the proteins is the gastric juice. This fluid is produced by numerous tubular glands contained in the mucous membrane of the stomach and contains two enzymes, rennin and pepsin, together with hydrochloric acid. As has been shown by the brilliant research of Pawlow[3] and confirmed by subsequent investigators, the presence of food in the mouth or even the sight or odor of palatable food causes a "psychic" secretion even before the food is swallowed. Subsequently the products of the progressive digestion of the proteins (or the meat extractives) serve as a chemical stimulus to maintain the secretion. The mere introduction of food into the stomach (mechanical stimulus) as through a gastric fistula does not cause a flow of the gastric juice.

[2] *Amer. Jour. Physiol.*, 16 (1906), 468.

[3] "Die Arbeit der Verdauungsdrüsen," Wiesbaden, 1898.

Rennin is the active ingredient of rennet. It acts specifically upon the casein of milk, coagulating it and thus aiding to retain it in the stomach until it is acted upon by pepsin. Some authorities consider rennin and pepsin to be identical but the weight of opinion is greatly against this view.

The action of pepsin upon the proteins in an acid medium consists substantially of a series of hydrolytic cleavages, giving rise to substances belonging to the group of derived proteins according to the classification recommended by a Committee of the English Physiological Society[4] and by a joint Committee of the American Physiological Society[5] and the American Society of Biological Chemists.[6]

From the simple proteins the action of pepsin produces, first, metaproteins and successively proteoses and peptones and possible polypeptids. In actual digestion it does not appear that the action of pepsin goes so far as to produce amino acids although some of them may be secured by prolonged artificial digestion. The conjugated proteins undergo cleavage into the conjugate, nucleic acids for example, and the corresponding simple proteins which are then digested like other simple proteins.

Intestinal Digestion. The lower end of the stomach is closed by a sphincter muscle called the pylorus. As gastric digestion progresses and the contents of the stomach become more or less liquefied and also increasingly acid, the pylorus relaxes at intervals and the contractions of the stomach force or "squirt" the partially digested food in small portions into the upper portion of the small intestine, the duodenum. According to Cannon[7] this occurs whenever the difference between the normally alkaline reaction in the duodenum and the acid reaction of the stomach reaches a certain level. In the duodenum the protein cleavage products resulting from the peptic digestion in the stomach, together with any unaltered proteins, are subjected to the action of the pancreatic juice, the alkaline secretion of the pancreas, and of the intestinal juice secreted by numerous small glands in the walls of the intestine itself.

The pancreatic juice contains, along with other ingredients, a proferment, trypsinogen, which when acted upon by the enterokinase of the intestine yields the protease, trypsin. Especially in a neutral or alkaline solution trypsin effects cleavage of proteins, resulting not only in the production of proteoses and peptones but of relatively large amounts of amino acids. The cleavage into amino acids, however, is incomplete, even prolonged action leaving a considerable residue in which no amino acids are found but which on hydrolysis with strong mineral acids yields them

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[4] *Jour. Physiol.* (London), 35 (1907), XVII-XX.

[5] *Amer. Jour. Physiol.,* 21 (1908), XXVII-XXX.

[6] *Proc. Soc. Biol. Chemists,* 1 (1908), 142-145.

[7] *Amer. Jour. Physiol.,* 20 (1907), 283.

in abundance. Apparently trypsin is able to split off from the protein molecule certain amino acids with comparative readiness while other portions of the molecule are resistant to its attack.

The intestinal juice likewise contains a protease, erepsin, which does not act upon unaltered proteins, with the exception of casein and perhaps histones and prolamines, but hydrolyzes proteoses and peptones energetically, yielding amino acids. By the combined action of trypsin and erepsin, at least in artificial digestion, proteins may be more or less completely broken down.

Intestinal tissue also contains enzymes which act upon the nucleic acids resulting from the cleavage of nucleoproteins.

Extent of Proteolysis. So long as the essential feature of digestion was considered to be the dissolution of food ingredients it was believed that in natural digestion the soluble proteoses and peptones were quite promptly absorbed and the profound hydrolysis occurring in digestion *in vitro* was thought to have little physiological significance in the animal. As will appear on subsequent pages, the investigations of recent years have radically changed its point of view. It is now generally admitted that, while soluble proteoses and peptones may be absorbed, the products of the natural digestion of proteins are substantially the same as those obtained in artificial digestion, viz., the comparatively simple amino acids or "building stones" of the proteins.

Fermentation and Putrefaction. Reference has already been made to the important rôle played by the organized ferments in digestion, particularly with reference to the methane fermentation of carbohydrates in the rumen and cecum of herbivora. Kellner [8] has shown that, in cattle at least, the proteins are not attacked by the organisms causing the methane fermentation, while Voit and Pettenkofer [9] and Tappeiner [10] found earlier that at most only traces of methane are excreted by carnivora.

On the other hand, the proteins and their cleavage products are peculiarly subject to the action of the putrefactive organisms, particularly in the lower portions of the digestive tract. The chief products of putrefaction are ammonia and certain aromatic compounds, notably phenols, indol, and skatol. These are in large part resorbed and eliminated again in combination with sulfur and the so-called ethereal sulfates of the urine. The amount of these substances in the urine furnishes a more or less accurate index to the extent of intestinal putrefaction.

Fate of the Non-Proteins. As determined by the conventional

[8] *Landw. Vers. Stat.*, 53 (1905), 420.
[9] *Ztschr. Biol.*, 7 (1871), 433; 9 (1873), 2 and 438.
[10] *Ibid.*, 20 (1884), 52.

methods outlined in Chapter 1, the non-proteins consist of the water-soluble nitrogenous ingredients of feeding stuffs which are not precipitable by boiling nor by certain metallic compounds, usually cupric hydroxide. As was there stated, they appear to consist to a large extent of amino acids and amids.

So far as these substances are assimilable, it may be presumed that if they once reach the resorbing surface of the small intestine they will be taken up. In ruminants, however, another process intervenes. As already stated, the first stomach of these animals is the seat of extensive fermentation of the carbohydrates by micro-organisms. Zuntz [12] seems to have been the first to suggest that the readily soluble non-proteins may serve as a source of nitrogen to these organisms and thus be synthesized to proteins which in their turn may supply the needs of the host. This hypothesis was quite in harmony with the results of earlier experiments upon the nutritive value of non-proteins and its truth has been confirmed by numerous subsequent investigations.[13] For the present purpose it suffices to state as their general result that readily soluble nitrogenous compounds in the feed, especially simple ones like asparagin or even ammonium salts, stimulate the multiplication and activity of the micro-organisms in the rumen. The result is a more extensive fermentation of the carbohydrates with a correspondingly increased excretion of methane and a synthesis of considerable amounts of bacterial protein. The protein thus formed appears to be digested (to a greater or less extent), its apparent indigestibility, as observed by some investigators, being due seemingly to an increase in the amount of metabolic products contained in the feces.

Recent investigations by Völtz [14] have shown that the bacterial protein thus formed may be an important addition to the protein supply of the animal. As he puts it, the first three stomachs of the ruminant are a protein factory. However, this protein may be largely indigestible. This is discussed in later sections of this chapter.

The Digestion of the Carbohydrates.

Carbohydrates are the most abundant ingredients of the feed of farm animals and at the same time those which most obviously require chemical change, since they are only sparingly represented in the body. The polysaccharoses, including starch, cellulose, etc., constitute the large share of

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[12] *Archiv. Physiol.*, 49 (1891), 483.

[13] For citations of literature compare Armsby: "Principles of Animal Nutrition," New York, 1910, 52-58 and U. S. Dept. Agr., Bur. Anim. Indus., Bul. 139 (1921), 6-28.

[14] *Biochem. Ztschr.*, 102 (1920), 151.

the carbohydrates consumed. Disaccharoses are the next in abundance, while the amounts of monosaccharoses consumed are usually small.

Cellulose. That cellulose, contrary to earlier opinions, may be digested was first shown by Heubner[15] in experiments on cattle. His results were soon verified by Henneberg and Stohmann[16] while a long series of subsequent digestion experiments has established beyond question the fact that cellulose is digested to a greater or less extent both by herbivora and omnivora and the more tender forms even by man.

On the other hand no digestive enzyme (cytase) which acts upon cellulose has been found in the digestive fluids of higher animals nor in any significant amounts in the feed which they consume. The digestion of cellulose is effected by means of the organisms mentioned in the preceding section. That such was the case was conjectured by Zuntz[17] in discussing the earlier investigations of Wildt,[18] but Tappeiner[19] seems to have been the first to furnish experimental evidence of the fact, 4.7 grams of methane being produced per 100 grams of cellulose. His results have been fully confirmed by Markoff,[20] while Kellner[21] has shown that the consumption of a crude form of cellulose (straw pulp) increases the excretion of methane. The products of the fermentation are carbon dioxide, methane, possibly small amounts of hydrogen and various organic acids of the aliphatic series, chiefly acetic and butyric, which combine with the alkalies of the saliva or other digestive fluids. In ruminants this fermentation takes place especially in the first stomach, or rumen. In the horse its principal seat is the enormous cecum and colon. Kellner's investigations showed the production of 4.2 parts of methane per 100 parts of digested carbohydrates.[22] Armsby[23] confirms both of these figures showing the production of 4.8 parts per 100 of digestible carbohydrates.

Hemicelluloses and Pentosans. What is true of cellulose appears to be substantially true also of the other carbohydrate ingredients of the cell wall. No animal enzymes are known which attack the pentosans, or the galactans, levulans, etc., with which they are associated. On the other hand they are digested to a considerable extent by herbivora and

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[15] "The Nutrition of Farm Animals," Armsby, 1917, 89.

[16] "Beiträge zur Begründungen einer rationellen Fütterung der Wiederkauer," 1860 and 1864, "Neue Beiträge," etc., 1870.

[17] *Landw. Jahrb.*, 8 (1879), 101.

[18] *Jour. f. Landw.*, 22 (1874), 1.

[19] *Ztschr. Biol.*, 20 (1884), 52.

[20] *Biochem. Ztschr.*, 34 (1911), 211; 57 (1913), 1.

[21] *Landw. Vers. Stat.*, 53 (1900), 193, 300.

[22] *Loc. cit.*, p. 420.

[23] *Jour. Agr. Research*, 3 (1915), 450.

when added to the feed seem to increase the production of methane. It appears highly probable, therefore, that, like cellulose, they are fermented by micro-organisms and that they yield substantially the same products.

Starch. In contrast with the carbohydrates just considered, starch is acted upon in the animal by at least two amylases, ptyalin and amylopsin.

Ptyalin is the active ingredient of the mixed saliva of herbivora and omnivora but is absent from that of carnivora. Its action upon starch is most efficient in a neutral solution, while it is inhibited by more than minute amounts of alkalies but especially of acids. To acids combined with proteins it is less sensitive and less so to organic than to inorganic acids, the essential factor seeming to be the hydrogen ion concentration. Its action upon starch consists of a series of hydrolytic cleavages resulting in the production of soluble starch and a series of dextrins and finally as end product the disaccharose, maltose.[24]

The action of ptyalin can scarcely proceed to any significant extent in the mouth, while in the stomach the hydrochloric acid of the gastric juice tends to inhibit it and ultimately to digest the ptyalin itself, so that there has been a tendency to minimize its significance. As a matter of fact, it appears to play an important rôle in herbivora and omnivora. This arises from two facts. First, the contents of the stomach in these animals are semi-solid rather than liquid and are not extensively mixed by the peristaltic contractions of the stomach, as has been shown by the stratification observed in frozen sections. Second, the gastric juice is secreted only in the fundus and pyloric regions of the stomach and penetrates the mass of food rather slowly, giving ample opportunity for the saliva to continue its action in the cardiac portion of the stomach.

It has been shown especially by the extensive investigations of Ellenberger and Hofmeister [25] that the digestion of starch in the cardiac end of the stomach of the horse and the hog may continue for as much as four or five hours. The saliva of ruminants contains but little ptyalin but the considerable stay of the food in the rumen, together with the normally slightly alkaline reaction of its contents, must lead to a considerable digestion of starch except as it may be modified by a factor to be considered in the next paragraph.

The products of the gastric digestion of starch, together with such portions of the latter as escapes the action of ptyalin, are hydrolyzed energetically in the duodenum by the amylase of the pancreatic juice, amylopsin, the end product, as in the case of ptyalin, being maltose.

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[24] Carlson and Luckhart [*Amer. Jour. Physiol.*, 23 (1908-9), 149] state that both ptyalin and amylopsin produce dextrose from starch.

[25] *Jahresb. f. Thierchem.*, 15 (1885), 284 and 16 (1886), 260, 261.

The Disaccharoses. The disaccharoses, being crystalline and readily soluble and diffusable, would, according to the older conceptions of the digestive process, require no further action. But although soluble, they are not assimilable. They are not found in the animal body and when injected into the circulation are treated like foreign substances and excreted in the urine.

Both the maltose resulting from the digestion of starch and the disaccharoses, such as sucrose and lactose, contained in the food are further hydrolyzed by the invertases (maltase, sucrase, lactase), contained in the intestinal juice or in the epithelial cells of the small intestine and resorbed as the resulting monosaccharoses (see succeeding chapter).

Fermentation of Soluble Carbohydrates. In addition to the enzymatic digestion of starch and the more soluble carbohydrates just described, these substances are likewise attacked by the micro-organisms which cause the methane fermentation of cellulose. This is especially true of ruminants, in which the action upon cellulose is most marked, and has important bearings upon the utilization of feed by these animals. Among the extensive series of respiration experiments upon cattle by G. Kühn[26] and by Kellner[27] are a considerable number in which starch was added to a basal ration. The result was a marked increase in the amount of methane excreted along with a decreased digestibility of cellulose (crude fiber). The fact that the digestibility of the crude fiber is usually decreased by the addition of starch or other readily soluble carbohydrates indicates that the activity of the micro-organisms is diverted more or less from cellulose to starch or to the products of its hydrolysis. The same facts have been observed in a few experiments by Armsby and Fries[28] and Kellner[29] likewise mentions experiments in which the same effects were produced by sucrose while the investigations of Kühn, of Kellner, and of Armsby and Fries have shown that the evolution of methane is, in general, proportional to the total digestible crude fiber and nitrogen free extract.

It would appear that digestion in the rumen is a combination of enzymatic and bacterial actions. As already noted, the conditions appear to be favorable to the action of ptyalin on starch and it is at least a plausible conjecture that much of the increase of the methane production is due to the fermentation of the resulting maltose.

No sufficient data are available from which to estimate the proportion

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[26] *Landw. Vers. Stat.*, 44 (1894), 257.
[27] *Ibid.*, 3 (1900), 423.
[28] *Jour. of Agr. Res.*, 15 (1918), 269.
[29] "Ernährung der landw. Nutztiere," 6th Ed., 93.

of the more soluble carbohydrates which is fermented in the rumen but it clearly is very considerable. Some approximate estimate may be based upon the figures reported by Kellner[30] as the average of his own and of Kühn's investigations, just cited, and including also his unpublished results. He finds that for each 100 grams of digestible carbohydrates there were produced:

	CH_4	Equivalent C
From starch	3.17	2.38
" straw pulp	4.45	3.34
" mixed rations	4.29	3.22

Estimating that the digestion of the straw pulp, consisting to the extent of 77 per cent of crude fiber, was effected solely by the micro-organisms and estimating further that the products of the fermentation of starch are quantitatively the same as those of straw pulp, it appears that the proportion of starch which underwent fermentation was $2.38 \div 3.34 = 71.2$ per cent.

Markoff[31] reports as the mean of six discordant determinations of the gases evolved in the anaerobic fermentation of the fresh liquid portion of the contents of the rumen of an ox, the ratio of CH_4 to CO_2 as, by volume, 1 to 7.844, by weight, 1 to 21.57. Markoff's results show great discrepancies, the ratio by volume varying from 1:5.63 to 1:19.88. Kellner's individual results show a wide range, the methane carbon per 100 of carbohydrates ranging from 2.14 to 4.11. Armsby and Fries' figures are in general higher than Kellner's and in particular show that the extent of the fermentation increases, as would be expected, as the amount of feed consumed diminishes. In a few trials with starch given as part of a light ration, they observed a higher relative production of methane than in any of the experiments previously cited. It is clear that the extent of the fermentation may vary rather widely under varying conditions of amount and kind of feed and that the foregoing computations have little quantitative value. They suffice, however, to show that, even under normal conditions, a very considerable share of the more soluble carbohydrates in the feed of ruminants is fermented and not hydrolyzed.

In the horse and hog, starch and similar carbohydrates are largely or wholly digested by the action of the digestive enzymes before the feed reaches those points in the digestive tract where it can stagnate. Consequently, the methane fermentation in these species is substantially limited to the less soluble carbohydrates. Experiment shows that the horse is

[30] "Ernährung der landw. Nutztiere," 6th Ed., 89-95.
[31] *Biochem. Ztschr.*, 57 (1913), 1.

capable of digesting crude fiber in particular to a considerable extent, although not as well as do ruminants. The action no doubt occurs chiefly in the cecum and colon. Lehmann, Zuntz and Hagemann,[32] as the average of eight somewhat discordant experiments on a horse, observed a production of 4.73 grams of methane per 100 grams of digested crude fiber. This figure is in close agreement with Tappenier's results and likewise with those on cattle just mentioned, thus indicating that the crude fiber was the source of the methane and that there could have been no considerable fermentation of other carbohydrates. In later experiments von der Heide, Steuber, and Zuntz[33] observed the methane excretion per 100 grams of digested crude fiber to be 9.06 grams on hay and 2.28 on straw pulp.

The amounts of methane excreted by the hog are insignificant. Fingerling, Köhler and Reinhardt[34] found the amounts of combustible gases excreted too small to be determined with their form of Pettenkofer apparatus. Von der Heide and Klein[35] in three experiments with a Regnault-Reiset apparatus obtained the following results:

EXCRETED BY SWINE PER 100 GRAMS DIGESTED CARBOHYDRATES

	Methane, Grams	Hydrogen, Grams
Period I	0.62	0.11
Period II	0.65	0.07
Period III	0.68	0.04
Average	0.65	0.07

Effect of Fermentation upon the Respiratory Quotient.

Fermentation of carbohydrate material not only gives rise to methane (with small amounts of hydrogen) but also results in the production of carbon dioxide. Fries[36] has pointed out that there is a great difference in the volume, composition, and origin of the gases eliminated by the herbivorous animal. In the ruminant the respiratory quotient is influenced to a large degree by the gases of fermentation, as much as one-tenth or more of the total carbon dioxide coming from the paunch and intestine.

Møllgaard and Andersen,[37] as a result of elaborate respiration experiments conducted with a cannula healed into the trachea of a milking cow,

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[32] *Landw. Jahrb.*, 23 (1894), 125.
[33] *Biochem. Ztschr.*, 73 (1916), 161.
[34] *Landw. Vers. Stat.*, 84 (1914), 197.
[35] *Biochem. Ztschr.*, 55 (1913), 195.
[36] *Amer. Jour. Physiol.*, 55 (1921), 53.
[37] Kungl. Veterinaer og. Landbohøjskoles Laboratorium for landøkonomiske Forsøg. 94de Beretning fra Forsøgslaboratoriet, Copenhagen, 1917.

determined accurately the pulmonary gas exchange as well as the methane and carbon dioxide of fermentation. The ratio of methane to carbon dioxide was 1:2.81 by volume.

Markoff[38] had obtained earlier data concerning the gases of fermentation by taking samples of gas directly from the paunch. The observed ratio of methane to carbon dioxide was 1:3.68. He assumed that carbon dioxide was absorbed from the alimentary tract and excreted through the lungs and derived a corrected ratio of 1:5.19. Klein[39] has done some work on oxen similar to that of Møllgaard and Andersen. He used a respiration apparatus of the Regnault-Reiset type. With a cannula in the trachea of the oxen he carried out pulmonary exchange experiments of very short duration. This latter fact renders the ratios of methane to carbon dioxide obtained by him valueless.

The facts brought out in the paragraphs just above have a bearing on the determination of the energy production by means of the respiratory quotient or the total carbon dioxide production. The respiratory quotient cannot be used for this purpose with cattle. This question is dealt with again in Chapter 5.

The Digestion of Fats.

The digestion of fats appears to be entirely enzymatic. They do not seem to be fermented to any extent in the digestive tract and when fed to cattle have not been found to increase the excretion of methane. Their digestion has been studied chiefly on carnivora. Their digestion consists substantially of two processes, *viz.:* saponification and emulsification, effected by the combined action of the pancreatic juice and the bile.

Saponification. Some cleavage of the fats seems to occur in the stomach of the carnivora but the principal action is in the duodenum, brought about by the lipase, steapsin, of the pancreatic juice. This enzyme splits the fats into glycerol and fatty acids, the latter uniting with the alkalies of the pancreatic juice and bile to form soaps. The bile salts aid in the action of the steapsin and accelerate the cleavage of the fats. They also facilitate the absorption of the fatty acids.

Emulsification. The process of saponification is expedited by the emulsification of the fats, the two processes mutually promoting each other. Most native feeds contain more or less free fatty acid while such cleavage as occurs in the stomach adds to it. In the duodenum these free fatty acids combine with the alkalies present and the soaps thus formed help to emulsify the fats. The emulsification in its turn, by vastly increasing

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[38] *Biochem. Ztschr.*, 57 (1913), 1.
[39] *Ibid.*, 72 (1916), 169.

the surface of the fat, tends to aid the hydrolytic action of the steapsin, while in turn the products of the latter action assist in further emulsification. As already noted, the bile accelerates the cleavage, while it is also capable of dissolving the fatty acids and their calcium and magnesium soaps.

Extent of Cleavage. The extent to which the fats undergo cleavage in natural digestion was once the subject of much controversy, many physiologists regarding the emulsification as the essential process. This is now regarded as chiefly an aid to the cleavage which is essential to the assimilation of fat.

Digestion of Other Ingredients.

Ash Ingredients. The sulfur of the proteins is contained in organic combination chiefly in the amino acid, cystin, which appears to be one of the end products of the digestion of proteins and to be absorbed without change. The phosphorus of the nucleo-proteins and phospho-proteins is present as the P_2O_5 radicle but opinions differ as to whether it is split off as phosphoric acid in the course of digestion or absorbed still in "organic" combination as a nucleoside. To what extent other ash ingredients are taken up in organic combination it is scarcely possible to say, although it may be regarded as not improbable. The sulfur, phosphorus and other ash elements present as electrolytes are probably dissolved by the hydrochloric acid of the gastric juice and absorbed to a greater or less extent in that form.

Coloring Matters. Certain coloring matters, having no apparent nutritive value in themselves, are of commercial importance through their influence on the appearance and market value of the products. This is particularly true in the case of the dairy cow and the hen. Palmer and Eckles [40] have shown that the yellow color of cow's milk and of human milk as well as of the body fat and skin secretions of the cow is due to the yellow pigments, carotin and xanthophyll, found accompanying chlorophyll in all green plants and in other plants and animals. These substances are not produced in the body of the animal, but are taken up with the feed and subsequently secreted or stored in the body fat. In the case of the cow they consist chiefly of carotin. In the case of the hen, on the contrary, subsequent investigations by Palmer and his associates [41] have shown that it is chiefly xanthophyll. For further information on these coloring matters consult "Carotinoids and Related Pigments: The Chromolipins," Leroy S. Palmer, in this series of Monographs.

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[40] *J. Biol. Chem.*, 17 (1914), 191-249.
[41] *Ibid.*, 23 (1915), 261; 39 (1919), 331.

Summary of Digestive Changes.

As stated in the opening paragraphs of this chapter, digestion is the first stage in the conversion of feeding stuffs into animal products. Having considered the changes wrought in the principal groups of nutrients by the digestive processes, it is now desirable to summarize the facts from a more general point of view so as to secure a clear conception of the rôle of digestion in that conversion.

Hydrolytic Cleavages. As appears from previous paragraphs, digestion in the narrower sense of the action of the enzymes of the digestive fluids consists essentially of a series of hydrolytic cleavages. The proteins are ultimately split into their amino acids. The nucleo-proteins likewise yield the amino acids of the protein components with the addition of phosphoric acid, purin bases, and pentose. Fats are split into the corresponding fatty acids and glycerol, while the carbohydrates yield ultimately the corresponding monosaccharoses.

Fermentation. To the enzymatic cleavages of digestion in the more limited sense, there is added in herbivora the fermentation resulting from the activity of micro-organisms, especially the methane fermentation of the carbohydrates. Besides the escaping gases this fermentation yields some of the lower fatty acids of the aliphatic series.

Ingredients of Digested Matter. Through these various processes the heterogeneous materials consumed by herbivora in particular yield a qualitatively uniform material for absorption into the blood current consisting substantially of amino acids, purin bases, monosaccharoses (chiefly dextrose), acids of the aliphatic series derived on the one hand from cleavage of fats and on the other from the fermentation of carbohydrates, and finally soluble ash ingredients. The supplying of this uniform nutritive material to the cells of the body is one of the chief functions of the digestive apparatus.

Molecular Simplification. The digestive process is obviously one in which large molecules are split into much smaller ones. This has two important consequences.

First, such a change is generally accompanied by greater solubility in water and a higher osmotic pressure of the solution. In other words, the direction of the change is from the colloid to the crystalloid condition. Such a change obviously tends to facilitate the passage of digested feed from the digestive cavity into the blood stream, although it is far from being the only factor in this process.

Second, the various feed constituents being thus split up, the body tissues are supplied with comparatively simple molecules or "building stones" out of which, as will appear later, they are able to construct the specific substances which compose them and which, as pointed out at the beginning of this chapter, differ widely from the ingredients of the feed. A good example of this is furnished by the disaccharoses which are readily soluble and diffusible but whose molecules evidently cannot be fitted into the structure of the cell protoplasm. The most striking illustration, however, is found in the proteins. As already pointed out, the body proteins show specific differences among themselves and differ widely from those of the feed. For their construction the body needs to be supplied, not with proteins as such, but with the constituents (amino acids) out of which the specific body proteins may be built up.

Absorption.

The process by which digested feed is transferred from the digestive cavity to the body fluids (blood and lymph) is called absorption.

Organs and Mechanisms of Absorption. Absorption takes place chiefly in the small intestine, the active agents being the epithelial cells with which it is lined. The extent of absorbing surface is greatly increased by a vast number of finger-shaped projections from the intestinal wall called villi, giving the wall a velvety appearance. The villi are covered with epithelial cells and contain in their interior blood capillaries and a small lacteal.

Since digestion results in the formation of soluble and diffusible substances there has been a certain tendency to regard the transfer of the latter to the body fluids as being effected simply by osmosis. That osmosis plays an important part in absorption, as it does in other vital phenomena, cannot be doubted, but the process cannot be explained by a simple analogy with the parchment diffusion tube of the laboratory. It is a function of the living epithelial cells and is clearly a highly complicated physico-chemical process. Perhaps its most marked feature is the fact that the permeability of the epithelial cells is chiefly in the direction from the digestive cavity to the interior of the villi. Absorption might be briefly characterized as a reverse secretion.

Paths of Absorption. The amino acids, etc., resulting from the digestion of the proteins and the monosaccharoses and organic acids produced in the digestion and fermentation of carbohydrates, as well as the soluble ash ingredients, appear to pass from the epithelial cells to the blood capillaries of the villi, being carried from thence through the portal vein to the liver capillaries and thence into the general circulation. Somewhat earlier, the amino acids were believed to be synthesized to proteins (serum protein) in the epithelial cells but it now appears well established that they enter the blood substantially unchanged.

Most of the fat, on the contrary, passes through the epithelial cells into the lacteals in the form of microscopic globules and enters the general circulation through the lymphatic system. There is, however, some indication that a part of the fat finds its way directly into the blood stream. The saponification of fats is a necessary preliminary to their absorption and the fat globules observed in the epithelial cells and the lymph are the result of resynthesis.

The Feces. The indigestible portion of the feed, as well as the actually undigested and unabsorbed portion, together with a greater or less amount of intestinal products, are finally voided as the feces. The latter, therefore, are to be regarded as both a feed residue and an excretory product. The excretory products comprise such portions of the digestive fluids and their decomposition products as may fail to be absorbed again and likewise direct products of intestinal activity such as mucus, worn out epithelial cells, leucocytes, etc., together with dead micro-organisms. The intestine also serves as an excretory organ, notably for salts of calcium and of iron and in herbivora of phosphoric acid in combination with calcium and magnesium. These various ingredients of the feces are often described collectively as metabolic products.

According to Völtz, *et al.,* proteins produced by the micro-organisms in the rumen of ruminants are indigestible and thus add to the fecal nitrogen. This is considered in the next section.

In carnivora these metabolic products constitute the bulk of the feces. In herbivora, on the contrary, they make up but a relatively small part of them, by far the larger portion consisting of indigestible feed residues. The omnivorous hog as well as man occupies an intermediate position in this respect. On a concentrated diet their feces tend to resemble those of carnivora while on diets containing much of the less digestible vegetable materials, notably those rich in fiber, the feed residues constitute the larger proportion of the feces.

Digestion Experiments.

Method. In studies on animal nutrition the term "digestible" signifies the percentage of the feed or of any single ingredient of it which the animal is able to extract and absorb during its passage through the digestive tract. As a rule this can be determined only by direct trial with the animal. Such a trial is known as a digestion experiment. In a digestion experiment the weight of the feed consumed and of feces voided is determined and samples of each are analyzed by the methods indicated in Chapter 1. The income and outgo of dry matter and of its several ingredients having been thus determined, a simple subtraction shows the amounts which have disappeared and may be regarded as having been digested. For a detail plan for work of this nature see *Bulletin of the National Research Council,* Vol. 2, Pt. 4, No. 2, June, 1921.

Aside from accuracy in weighing, sampling, and analysis, the essential conditions of accuracy are: first, that the weights taken show the true average amounts of feed consumed and excreta voided, and, second, that the feces must be derived from the feed experimented upon. To satisfy the first condition the ration is made as nearly identical as possible from day to day and the collection of the feces is continued long enough to compensate for irregularities of excretion and secure the true avergae daily amount. For ruminants a period of ten days appears to be the minimum for this purpose. For swine probably a somewhat shorter period suffices, while for man and for carnivora three or four days are often regarded as sufficient. To secure representative feces in the case of herbivora there is necessary a preliminary feeding period upon the feed to be investigated sufficiently long to expel all residues of previous feeds from the digestive tract. In herbivora a period of seven to ten days is required to assure this. In experiments on carnivora and on man it is possible to use some colored substance as a marker and thus to separate mechanically the feces from different days. A satisfactory digestion experiment with ruminants therefore requires approximately three weeks of which the last ten days serve as the digestion period proper.

Influence of Metabolic Products of Feces. The foregoing method obviously regards the feces as consisting solely of undigested feed, while in point of fact, they contain not insignificant amounts of the so-called metabolic products. Consequently, the percentage digestibility, as computed from an experiment such as that just described, is too low, the error being greatest for those ingredients which are least abundant in the feed and most abundant in the feces. These are substantially ash, ether extract, and protein. No method is available for distinguishing between the ash ingredients of feed residues and those excreted by the intestine itself. The ether soluble ingredients of feces are derived largely from the bile and methods for their approximate estimation have been worked out although not very satisfactorily. The fats usually play such a subordinate rôle in the nutrition of herbivora that the error involved is not a serious one. In the case of protein, however, it is possible to determine with a fair degree of accuracy the amount of error involved in including the metabolic products by means of experiments *in vitro.*

Artificial Digestion. Acting upon earlier suggestions by Stockhardt and by Hofmeister, Stutzer[42] devised a laboratory method for determining the digestibility of the protein of feeding stuffs by treating them *in vitro* with a solution of pepsin and hydrochloric acid under specified conditions and determining the undissolved nitrogen in the residue. Subsequently Stutzer,[43] on the basis of the results of Pfeiffer[44] and of further investigations of his own, modified his method by the addition of a digestion with alkaline trypsin following that with pepsin-hydrochloric acid. G. Kühn and his associates[45] conclude that this additional treatment with trypsin was not necessary if the pepsin digestion were somewhat more prolonged and their method has been the one in use since. More recently, however, Morgen and his associates[46] have found that in many cases it yields too low results and recommend that the treatment with trypsin be revived.

Determination of Fecal Metabolic Products. The accuracy of a method of artificial digestion of protein can be determined only by comparison with the results of natural digestion. Such a comparison, however, requires a knowledge of the amount of nitrogenous metabolic products in the feces in order that the true digestibility by the animal may be determined and this problem has necessarily formed a prominent part of the investigations just cited as well as of others. This problem was attacked by Kellner[47] and especially by Pfeiffer (*loc. cit.*) and by G. Kühn (*loc. cit.*) by treating the feces with pepsin-hydrochloric acid in the same manner as in the artificial digestion of feeding stuffs on the presumption that the metabolic products would prove to be soluble in pepsin. The result of these investigations was to confirm this presumption. The nitrogenous metabolic products of the feces proved to be soluble while the pepsin-insoluble nitrogen of the feed was recovered as the pepsin-insoluble nitrogen of the feces. In other words, artificial and natural digestion of protein yielded comparable results when the latter was computed on the basis of pepsin-insoluble nitrogen of the feces. Subsequent very extensive investigations by Morgen and his associates[48] upon the nutritive value of the non-protein seemed fully to confirm this conclusion. As already indicated, however, more recent results by the same investigators[49] upon sheep and swine have served to modify this conclusion somewhat. Not

[42] *Jour. f. Landw.*, 28 (1880), 195 and 435, 29 (1881), 473.
[43] *Ztschr. physiol. Chem.*, 9 (1885), 211.
[44] *Jour. f. Landw.*, 31 (1883), 221; 33 (1885), 149; 34 (1886), 425.
[45] *Landw. Vers. Stat.*, 44 (1894), 188.
[46] *Ibid.*, 85 (1914), 1.
[47] *Centbl. Agr. Chem.*, 9 (1880), 763.
[48] *Landw. Vers. Stat.*, 65 (1906-7), 413; 68 (1908), 333; 71 (1909), 1; 73 (1910), 285.
[49] *Ibid.*, 85 (1914), 1.

only do they find that the use of trypsin is necessary in the laboratory determination of the digestibility of feed protein but also that the same is the case in the determination of the metabolic products in the feces. They estimate that, in the latter case, the average increase in the amount of nitrogenous material thus dissolved from the feces as compared with pepsin digestion alone is approximately 33 per cent.

A method for the direct determination of the metabolic nitrogen in the feces and urine has recently been reported by Mitchell.[50] He devised a rather ingenious method for metabolism work with rats which permits of the separate collection of urine and feces. Using nitrogen-free diets the production of fecal nitrogen was determined. This was shown to be dependent upon the quantity of the ration eaten and to be increased in proportion when the ration contained more indigestible matter, such as filter paper. If the roughage content of the nitrogen-free diet approximates that of the protein-containing diet, Mitchell points out that the metabolic nitrogen content of the feces can be determined accurately by such a procedure. The increase in fecal nitrogen on a protein-containing ration above that calculated to be formed in the body as a result of the amount of food eaten is, then, the nitrogen left from the food.

Bacterial Protein in Feces. Mention has already been made of the formation of proteins from non-proteins by the micro-organisms of the digestive tract as well as of the possibility that the resulting proteins are but partially digested. This latter conclusion has been maintained especially by Völtz[51] supported by the results of Friedlander,[52] Just,[53] Kellner[54] and others.

In a considerable number of experiments using rations containing much non-protein nitrogen and but little protein, the feces were found to contain more protein nitrogen than did the feed. This was interpreted as showing a formation of indigestible bacterial protein from the non-protein of the feed. If this bacterial protein, however, were actually indigestible it should reappear in the feces as a part of the nitrogenous matter insoluble in pepsin or pepsin and trypsin. The investigations of Morgen and his associates, however, show that this apparent excess of protein in the feces is dissolved in the course of artificial digestion. It is, of course, possible that some of the bacterial protein might escape digestion for mechanical reasons but it appears more probable that this fecal protein was derived from the metabolic products of intestinal activity, rather than representing

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[50] *J. Biol. Chem.*, 58 (1923-4), 873.
[51] *Archiv. Physiol.*, 117 (1907), 514; *Biochem. Ztschr.*, 102 (1920), 151.
[52] *Landw. Vers. Stat.*, 67 (1907), 283.
[53] *Ibid.*, 69 (1908), 393.
[54] *Ibid.*, 72 (1910), 437.

indigestible bacterial protein. This probability is enhanced by the fact that Morgen's investigations show that the addition of readily soluble nitrogenous material, such as asparagin or ammonium salts, which must be presumed to stimulate the multiplication of the intestinal bacteria, cause a less marked increase in the protein nitrogen of the feces than do certain plant extracts containing less nitrogen but which, like the molasses or other materials used by Völtz, caused a very marked increase in the protein nitrogen of the feces. The latter experiments of Völtz in fact seem to show that the bacterial protein is largely digested and may be an important source of protein for the body.

Apparent Digestibility. The discussions of the last few paragraphs have dealt with the determination of digestibility in the physiological sense, *i. e.,* with the determination of the amounts of the several nutrients which can be actually hydrolyzed and absorbed in the digestive tract. As regards the nitrogenous ingredients, it appears possible to accomplish this with a fair degree of accuracy while for other ingredients this is far from being the case.

There is, however, another and important viewpoint. It might, for example, be determined by the methods already outlined that a kilogram of some feeding stuff contains 100 grams of protein capable of digestion and absorption. If, however, the digestive processes result in the excretion of 10 grams of protein (or its equivalent nitrogen) in the metabolic products of the feces, it is clear that the net result is the addition to the body's stock, not of 100 grams, but of only 90 grams of protein, *i.e.,* of the difference between the feed protein and the total protein of the feces. In other words, the nitrogenous products found in the feces are part of the cost of digesting the feed and the difference between the feed and feces will show how much of the several nutrients has actually been added to the store already present in the body. Most digestion experiments with farm animals have been made in this way, *i.e.,* without correction for the metabolic products in the feces, and their results show what has been called the apparent digestibility. From the economic or commercial standpoint this is in many respects the proverbial basis of comparison rather than the real digestibility.

Example of a Digestion Experiment.

A steer was fed 3.7 kilograms of clover hay per day for three weeks. During the last ten days of this time the average weight of the daily feces was 5.662 kilograms. Samples of each were analyzed and found to contain the following percentages of dry matter:

Clover hay	84.97 per cent
Feces	22.36 per cent

The 3.7 kilograms of hay, therefore, contained 3.144 kilograms of dry matter while the 5.662 kilograms of feces excreted contained only 1.267 kilograms of dry matter. The difference, 1.877 kilograms, which did not appear in the feces, is regarded as having been digested by the steer. This amount is 59.7 per cent of the 3.144 kilograms eaten. We say, then, that the percentage digestibility of the dry matter of this hay was 59.7 and this number is sometimes called its "digestion coefficient."

In precisely the same way the percentage digestibility of each ingredient may be computed from the results of analyses of the hay and of the feces shown in Table 31.

TABLE 31

Composition of Hay and Feces

	Hay %	Feces %
Water	15.03	77.64
Ash	5.49	1.92
Protein	10.24	3.13[1]
Non-protein	1.36	....
Crude fiber	28.61	9.29
Nitrogen-free extract	36.98	7.50
Ether extract	2.29	0.52
	100.00	100.00

[1] All the nitrogen of the feces is here assumed to exist in the form of protein, an assumption which is far from being true, but which does not affect the method of computation.

These figures, together with the weights of hay eaten and feces excreted per day, yield the results shown in Table 32.

TABLE 32

Results of a Digestion Experiment

	Dry Matter, Kgs.	Ash, Kgs.	Protein, Kgs.	Non-Protein, Kgs.	Crude Fiber, Kgs.	Nitrogen-Free Extract, Kgs.	Ether Extract, Kgs.
In hay eaten	3.144	0.203	0.379	0.050	1.059	1.368	0.085
In feces excreted	1.267	0.109	0.177	....	0.526	0.425	0.030
Difference = digested	1.877	0.094	0.202	0.050	0.533	0.943	0.055
Percentage digestibililty	59.70	46.48	53.19	100.00	50.27	68.94	65.02

Tables of Digestibility. A very large number of digestion experiments have been made both abroad (particularly in Germany) and in the

United States. Wolff,[56] in 1874, published a table giving the average percentage digestibility of a considerable number of feeding stuffs. This table has been continued and amplified in Mentzel and von Lengerke's "Landwirtschaftliche Kalendar" up to a recent date. Jordan,[55] in 1894, published a summary of the available results on American feeding stuffs and in 1896 Lindsey [58] published a similar compilation. In 1900 Jordan and Hall [59] amplified Jordan's previous publications by the inclusion of results up to that date, while Lindsey and his associates have likewise made revisions of their table in 1902,[60] 1906,[61] and 1911,[62] and Henry and Morrison [63] in the several editions of their "Feeds and Feeding" have likewise published an extensive table of digestion coefficients derived largely from the compilations already mentioned.

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[56] "Landwirtschaftliche Fütterungslehre," Berlin, 1874.

[57] *Expt. Sta. Record,* **6** (1894-5), 5.

[58] Mass. (Hatch) Agr. Expt. Sta., 9th Report (1896), 157.

[59] U. S. Dept. Agr., Office of Expt. Sta. Bul. 77 (1900).

[60] Mass. (Hatch) Agr. Expt. Sta., 14th Report (1902).

[61] Mass. (Hatch) Agr. Expt. Sta., 18th Report (1906).

[62] *Ibid.,* 23rd Report (1911).

[63] "Feeds and Feeding," Henry and Morrison, Madison, Wisconsin, 1922.

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Chapter 4

Metabolism.

General Conception. By the processes of digest outlined in Chapter 3 the various ingredients of the feed profound hydrolytic cleavages and there is transmitted to th lymph a qualitatively uniform material consisting substantially acids, monosaccharoses, simple organic acids and mineral ingr These substances, together with the oxygen taken up in the lungs blood, constitute the nutriment of the body cells and are carried by th circulation to all the body tissues. In a broad sense water is also a nutrient and should be considered as a vital part of the food of animals.

Metabolism might be briefly defined as the complex of chemical reactions which take place between these substances and the living protoplasm of the cells and through which the characteristic ingredients of the animal body considered in Chapter 2 are produced or excretory products formed by means of which vital activities are carried on.

Rôle of Enzymes. The part played by the extracellular enzymes in digestion is a familiar one and has already been considered in Chapter 3. More recently, the presence of intracellular enzymes of all the types there mentioned in all parts of the body has been recognized and the chemical changes constituting metabolism are now believed to be largely if not wholly enzymatic in nature, the enzymes acting substantially as catalyzers.

Anabolism and Catabolism. The chemical changes constituting metabolism are of two sorts. First, there are synthetic reactions, in which the exceedingly complex molecules of the cell protoplasm are built up out of the comparatively simple molecules absorbed from the digestive tract. Second, there are analytic reactions, in which the complex molecules of the protoplasm, or their precursors, yield relatively simple products. The term anabolism has been applied to the totality of the synthetic reactions, while the analytic reactions are grouped under the term catabolism. Metabolism, therefore, comprises both anabolism and catabolism.

Regarded as a whole, metabolism is an analytic and oxidative process, the final products being, in the main, the comparatively simple molecules of carbon dioxid, water, urea, and, in lesser amounts, of more complex nitrogenous compounds which constitute the excretory products.

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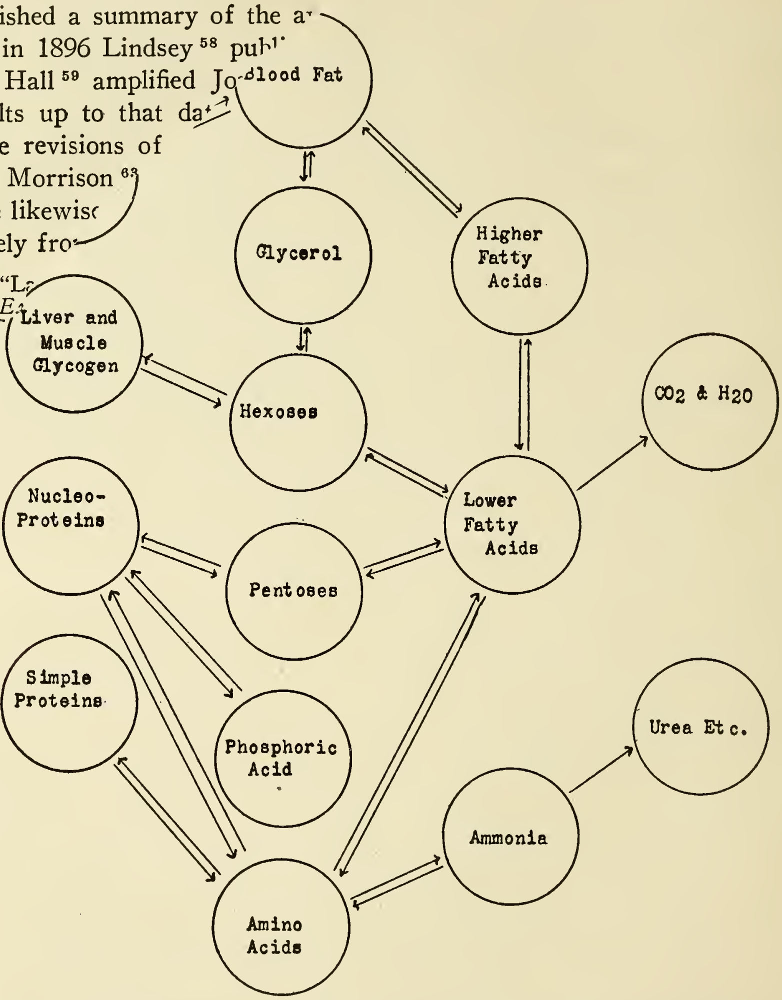

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FIG. 5.—A schematic suggestion summing up the processes of metabolism.

olism may store energy or may liberate energy depending upon whether anabolism or catabolism is taking place. Anabolic reactions are endothermic, *i.e.,* there is a storing up in the products of energy derived from the catabolism of other portions of the protoplasm or of the nutrients supplied to it. Conversely, catabolic reactions are exothermic, liberating energy which may serve to support anabolic changes or which may be expended by the organism in the form of heat or work. Accordingly, metabolism as a whole is exothermic and its function is in general to supply the energy for the constant output of work and heat which is the objective manifestation of life.

Metabolism a Gradual Process. Both anabolism and catabolism are gradual, *i.e.*, step by step processes. Between the substances absorbed from the digestive tract and the complex molecules of the protoplasm and between the latter and the excretory products, there are innumerable intermediate products, only relatively few of which have been identified. The metabolic changes through which the life of the organism is manifested vary from tissue to tissue and from cell to cell, as well as from time to time in the same cell, and the resulting products are correspondingly varied.

While the general course of metabolism is toward the production of more highly oxidized substances, it is not to be regarded as consisting in the direct union of oxygen with the materials supplied by the digestive tract or formed in the body cells. The basic processes in metabolism seem to consist, on the one hand, of synthesis of the cleavage products of digestion into the new compounds and, on the other hand, of hydrolytic cleavages along different lines, while only the relatively simple molecules resulting from these cleavages are directly oxidized.

The consideration, in the following paragraphs, of the metabolism of the chief groups of nutrients will serve to illustrate some of these facts.

Metabolism of Carbohydrates.

Glycogen. So far as the hexose carbohydrates escape fermentation in the digestive tract they are absorbed as monosaccharoses, chiefly dextrose, with minor amounts of levulose and galactose. With variations in the kinds and amounts of feed and in the frequency of its consumption, the influx of sugar to the blood will be more or less variable. On the other hand, the percentage of sugar in the blood is found to be remarkably constant and any material excess injected is promptly excreted through the kidneys.

The maintenance of this constancy of the blood sugar is effected chiefly in the liver and muscles by the formation or hydrolysis, as the case may require, of glycogen. Absorbed sugars, as noted in Chapter 3, pass by way of the portal vein to the liver capillaries before entering the general circulation. When the supply of sugar is in excess the liver is able to synthesize a portion of it into glycogen which is stored in its cells, while in the contrary case glycogen previously stored up is reconverted into sugar, the liver thus exercising a regulating function. The liver may also play a part in changing levulose and galactose to dextrose and glycogen.

The liver, however, is by no means the only organ concerned in the formation of glycogen. Indeed this substance seems to be a normal constituent of animal protoplasm, but next to the liver the chief seat of glycogenesis is the muscles. It has been estimated that roughly one-half of the total glycogen in the body is contained in the liver and by far the the larger share of the remaining half in the muscles, and these organs exercise the same regulative function as regards the blood sugar as does the liver. Muscle glycogen is of special significance in its relation to the performance of work. The energy of muscular contraction appears to be supplied in effect by the catabolism of the blood sugar and the resulting deficit of the latter is made good chiefly by the prompt mobilization of the muscle glycogen, *i.e.*, by its conversion into dextrose, while in the subsequent periods of rest the reverse reaction takes place and the store of glycogen is built up again.

Glycogenesis a Reversible Process. The foregoing facts afford one of the most familiar illustrations of the fact that the chemical reactions in metabolism are to a very large extent reversible, the particular case in question being represented by the equation

$$n\, C_6 H_{12} O_6 \rightleftarrows (C_6 H_{10} O_5)_n + n\, H_2O.$$

Furthermore, the conversion of glycogen into dextrose in the liver has been shown to be effected by an enzyme or enzymes. Since many if not all enzyme actions are regarded by good authorities as reversible[1] it would appear probable that the reverse change is effected by the same enzyme, the point of equilibrium being such as to maintain the normal concentration of dextrose in the blood. Numerous similar cases will be encountered later.

Formation of Fat. In one aspect, the formation of glycogen serves as a means of storing up surplus carbohydrates. The body capacity for storage in this form is limited, however, and a continued excess of carbohydrates in the feed must be otherwise disposed of. This is accomplished by the production of fat, which as a matter of common knowledge can be stored up in very large amounts, constituting a reserve which may be drawn upon in periods of scarcity.

Sources of Carbohydrates. The foregoing paragraphs have dealt with the carbohydrates digested from the feed. In case this supply is

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[1] Compare Bayliss: "The Nature of Enzyme Action," London, 1914, 49-70 and 146.

insufficient, however, the body is able to manufacture dextrose from the proteins and probably from the fats digested, as is most obvious in the case of the carnivora, and this dextrose is subject to the same reactions as that derived directly from the carbohydrates of the feed.

Catabolism. Aside from a more or less temporary storage as glycogen or fat, the blood sugar is the form in which the carbohydrates are made available as fuel material to supply the energy requirements of the body. This liberation of energy is accomplished by a series of catabolic reactions, together constituting what is known as the intermediary catabolism of the carbohydrates. The individual steps of the process are imperfectly known but they appear to be of the nature of hydrolytic cleavages with subsequent oxidation of the simpler products, especially lactic acid. That these changes, excepting the latter, are reversible and are catalyzed by enzymes may be regarded as probable and it has been shown that lactic acid may give rise to the formation of carbohydrates in the body. The following equations show some of the probable reactions:

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\begin{array}{l}
(C_6H_{10}O_5)_n \text{ (Glycogen)} + nH_2O \rightleftarrows nCH_2OH(CHOH)_4CHO \text{ (Dextrose)} \\
CH_2OH(CHOH)_4CHO \rightleftarrows 2CH_2OH.CHOH.CHO \text{ (Glyceric aldehyde)} \\
CH_2OH.CHOH.CHO - H_2O \rightleftarrows CH_3.CO.CHO \text{ (Pyruvic aldehyde)} \\
CH_3.CO.CHO + H_2O \rightleftarrows CH_3CHOH.COOH \text{ (Lactic acid)} \\
\qquad\qquad\qquad\qquad \text{or} \\
CH_3.CO.CHO. + O \rightleftarrows CH_3CO.COOH \text{ (Pyruvic acid)} \\
CH_3.CO.COOH + O \rightarrow CO_2 + CH_3.CHO \text{ (Acetaldehyde)} \\
CH_3.CHO + O \rightarrow CH_3.COOH \text{ (Acetic acid)}
\end{array}
$$

Pentose Carbohydrates. The foregoing paragraphs relate to the metabolism of the hexose carbohydrates. The feed of herbivora, however, contains also considerable amounts of carbohydrates of the C_5 series which disappear in part from the feed during its passage through the digestive tract and which are accordingly regarded as digestible.

Absorbed pentose sugars (in particular arabinose and xylose) are at least partially oxidized in the body although not so readily nor in as large amounts as the hexoses. Excessive amounts of either in the blood give rise to an excretion of sugar in the urine but the "limit of tolerance" is much lower for the pentoses than for the hexoses. The absorption of pentoses has also been shown to be followed by an increase in the liver glycogen, so that the effect must be regarded as an indirect one.

The pentose carbohydrates in stock feeds, however, consist chiefly or wholly of pentosans or their derivatives, no material amounts of pentose sugars being present. No digestive enzymes are known which act upon the pentosans and it appears highly probable that their apparent digestion is effected by the same methane fermentation which brings about the solution of cellulose. If such be the case, the products which are absorbed are not carbohydrates but chiefly organic acids (such as acetic, lactic and butyric acids) and the results of experiments with pentose sugars are not applicable to the feed of farm animals.

Organic Acids. It is evident that organic acids play a prominent rôle in the metabolism of herbivora. In the preparation of certain fermented feeds, notably silage, considerable quantities of these acids are produced at the expense of the more soluble carbohydrates.

In ruminants, a much more abundant source of organic acids is found in the extensive methane fermentation to which both the soluble and insoluble carbohydrates of the feed are subjected in the rumen and cecum, so that a large share of the "digested" carbohydrates may really be absorbed as organic acids. This is true to a far less degree of the non-ruminant herbivora but even here the fermentations in the colon and cecum yield considerable fatty acid.

Finally, as stated in a preceding paragraph, the catabolism of absorbed carbohydrates appears to consist of a series of hydrolytic cleavages resulting in the formation of organic acids which contain the larger share of the chemical energy of the carbohydrates and which are subsequently oxidized.

It would seem, then, as if it were the organic acids formed in one of the three ways just indicated from the carbohydrates rather than the latter substances as such, which serve directly as body fuel. This point of view is the justification for considering the metabolism of the organic acids along with that of the carbohydrates.

Catabolism of Organic Acids. Unfortunately but little is known concerning the catabolism of the simpler organic acids aside from the mere fact that they are oxidized to carbon dioxide and water.

Wilsing[2] and von Knieriem[3] have shown that organic acids such as result from the fermentation of carbohydrates are not found to any appreciable extent in the excreta, while the researches of Munk[4] and Mallevre[5] have shown that the sodium salts of butyric and acetic acids when injected into the blood are promptly oxidized, and Nencki and Sieber[6] have shown that lactic acid is readily oxidized, even by a diabetic patient.

Incomplete Catabolism. While the foregoing may be regarded as a fairly correct general outline of the catabolism of the pure carbohydrates, it must not be forgotten that the so-called "digestible carbohydrates" of

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[2] *Ztschr. f. Biol.*, 21 (1885), 625.
[3] *Ibid.*, 21 (1885), 139.
[4] *Arch. ges. Physiol.*, 46 (1890), 322.
[5] *Ibid.*, 49 (1891), 460.
[6] *Jour. f. pr. Chem., N. F.*, 26 (1882), 32.

stock feeds, especially of the roughages, include a variety of other substances. There seems to be good reason for believing that some of these, if catabolized at all, at least escape complete oxidation and are excreted in the urine. This belief is based upon the relatively high ratio of carbon and energy to nitrogen in the urine of herbivora.

As appears in the next section, the catabolism of the proteins gives rise to certain fairly well-known nitrogenous organic substances which are normally excreted in the urine. In the urine of carnivora and omnivora by far the larger part of its carbon and energy are contained in these substances and their ratio to the nitrogen content varies only within modest limits. In contrast with this the urine of herbivora, and especially of ruminants, carries relatively large amounts of carbon and energy as compared with its nitrogen and the ratio is quite variable. This arises in part from the fact that a considerable part of its nitrogen may exist in the form of hippuric acid but this is far from accounting for all the carbon and energy present. In extreme cases, on rations poor in protein, the carbon and energy content of the urine has even been observed to be greater than the entire amounts contained in the quantity of protein catabolized. The contrast between man and the ruminants in this respect may be illustrated by the following comparison (Table 33) of the average results upon men on a mixed diet reported by Benedict and Milner[7] and those reported by Kellner[8] upon an ox consuming meadow hay.

TABLE 33

CARBON AND ENERGY IN URINE OF MAN AND OX

	Men on Mixed Diet	Ox on Meadow Hay
Carbon per gram N	0.73	3.32 grams
Energy per gram N	8.07	31.74 cals.

No definite knowledge is yet available as to the nature of these non-nitrogenous ingredients of the urine of herbivora but apparently they must be derived from some of the nitrogen-free ingredients of the feed, particularly of the roughage.

Relation of Pancreas to Metabolism. The pancreas plays an important part in the metabolism of dextrose and so of all carbohydrate material. The Islets of Langerhans in this organ secrete a substance or substances which find their way into the blood and affect the power of the liver to convert dextrose to glycogen or to otherwise dispose of it. As a result when the cells of the pancreas which perform this function are

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[7] U. S. Dept. Agr., Off. Expt. Sta., Bul. 175 (1907), 144.

[8] *Landw. Vers. Stat.,* 47 (1896), 275.

no longer able to function, the animal body loses the power to utilize dextrose which then appears in the urine. This abnormal condition does not seem to be of great significance in the metabolism of our domestic animals. The material secreted by these Islets of Langerhans, which affects the body's ability to burn or otherwise utilize dextrose, is called insulin.

Metabolism of the Simple Proteins.

Anabolism. As stated in Chapter 3, it is now generally accepted that the simple proteins undergo extensive cleavage in digestion, the digestive products which are absorbed consisting chiefly of amino acids. Evidently these are rebuilt into the specific body proteins somewhere in the organism. Formerly this rebuilding was believed to occur in the epithelial cells of the intestines, yielding the serum albumin of the blood. The more refined analytical methods devised by Folin and Denis [9] and by Van Slyke and Meyer,[10] however, have revealed the presence in the blood and tissues of amounts of the amino acids sufficient to account for all that was absorbed while Abel [11] has succeeded in recovering considerable amounts of them by diffusion from the circulating blood of the living animal.

In the blood and lymph, then, we have the amino acids and other cleavage products brought into immediate contact with the living body cells. The latter, according to present conceptions, draw from this ever-present store of amino acids the particular kinds and proportions which each requires and build up from them their specific proteins while any surplus of single amino acids is catabolized.

Synthesis Reversible. It has already been noted that the synthesis of glycogen from monosaccharoses is a reversible process. This is true also of the synthesis of tissue proteins from amino acids. With a liberal supply of the latter to the blood, tissue proteins may be built up within the limits set by the capacity of the organism—consequently rapid in the young animal, which still retains the capacity for growth, but to a limited extent even in the mature animal. On the other hand, if the supply of amino acids to the blood is cut off, as in fasting, tissue proteins are hydrolyzed and the resulting amino acids are removed by the blood current. In other words, we apparently have here another instance of a reversible reaction, *viz.,*

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[9] *J. Biol. Chem.,* 11 (1912), 87.
[10] *Ibid.,* 12 (1912), 399.
[11] *Jour. Pharmacol. and Expt'l. Therap.,* 5 (1914), 275.

$$\text{Protein} \rightleftarrows \text{Amino acids,}$$

the point of equilibrium depending upon the relative concentration of the amino acids in the blood and lymph.

Reactions Enzymatic. The cleavage of tissue proteins just mentioned appears to be effected, or at least catalyzed, by intracellular enzymes (proteases), just as is the cleavage of the feed proteins by the enzymes of the digestive tract. The presence of such enzymes in animal tissues is most evidently shown by the process of autolysis, although there is much confirmatory evidence. Finely ground tissues, protected from infection by organized ferments, undergo fairly rapid change, or autolysis, with the production of amino acids and other products of protein cleavage. It is natural to suppose, therefore, that these proteases are active agents in the protein cleavage occurring in the living tissues. If, now, the belief that enzyme actions in general are reversible is justifiable, we have here a close parallel between the anabolism of the proteins and that of the carbohydrates. While this conception of the relations between the amino acids of the blood and lymph and the proteins of the various tissues confessedly lacks full experimental proof, it is in harmony with observed facts and has at least a schematic value.

Catabolism. The foregoing conception of protein synthesis as a complex of reversible reactions implies that the tissue proteins are being continually catabolized as well as synthesized. That such is indeed the case is most manifest in the fasting animal. With its external supply of protein cut off, the body suffers a continual loss of protein, more rapid in some tissues than in others, and continues to excrete the nitrogenous end products of protein catabolism. In the carnivora and omnivora, including man, urea is the most abundant of these end products, accompanied by lesser amounts of uric acid, allantoin, creatin, creatinin, ammonia, etc. In the herbivora, one of the products of protein cleavage, glycin, is coupled with the benzoyl radicle, giving rise to considerable amounts of hippuric acid, traces of which are likewise produced by carnivora and omnivora.

All these nitrogenous end products, as well as minute amounts of many others, are eliminated through the kidneys and excreted in the urine. It has been conclusively shown that the catabolism of protein does not give rise to an excretion of gaseous nitrogen.

The Non-Nitrogenous Residue. But while the nitrogenous end products of protein catabolism account for all the nitrogen of the proteins they contain only a portion of its carbon, hydrogen and oxygen. Thus the nitrogen of 100 parts of average protein (neglecting the sulfur) would be contained in 34.29 parts of urea while the latter would contain but 38 per cent of the oxygen, 33 per cent of the hydrogen and 13 per cent of the carbon of the protein, as the following computation shows (Table 34). The splitting off from proteins of the elements of the excretory products leaves a non-nitrogenous residue used as fuel or as a source of fat.

TABLE 34

DISTRIBUTION OF ELEMENTS IN PROTEIN BETWEEN UREA AND NON-NITROGENOUS RESIDUE

	Proteins	Urea	Residue
Carbon	53.0	6.86	46.16
Hydrogen	7.0	2.29	4.71
Oxygen	24.0	9.14	14.86
Nitrogen	16.0	16.00	....
	100.00	34.29	65.71

Intermediary Metabolism. As indicated in considering the nature of metabolism in general, the catabolism of the proteins is a step by step process. The first general stage of the process is the hydrolytic cleavage into amino acids expressed by the equation

$$\text{Protein} \rightleftarrows \text{Amino acids.}$$

The second general stage appears to be a deaminization of the amino acids, *i.e.,* a splitting off of the NH_2 groups, yielding ammonia and non-nitrogenous substances. The ammonia thus formed is believed to be the immediate antecedent of urea, into which it is rapidly converted, chiefly and perhaps exclusively in the liver.[12] The non-nitrogenous products of the deaminization have been regarded as being the hydroxy or the ketonic acids corresponding to the respective amino acids. It would appear, however, that the process may follow a different course in different amino acids. The investigations of Lusk [13] and his associates have shown that in the case of glycin and alanin all their carbon may, in the diabetic animal, be recovered as dextrose. In aspartic acid, on the contrary, only ¾ and in glutamic acid ⅗ of the carbon can be thus recovered, while still other amino acids yield no dextrose but instead oxy-acids. Remembering, however, that the carbohydrates appear to yield organic acids in their catabolism we may perhaps conjecture that the amino acids are ultimately catabolized to the corresponding acids, some via dextrose and others not, while it is certain that these acids are finally oxidized to CO_2 and H_2O.

Deaminization Reversible. Like the preliminary cleavage of the proteins, the deaminization of the resulting amino acids seems to be effected

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[12] Bollman, Mann and Magath, *Amer. J. Physiol.,* 69 (1924), 371.
[13] "The Science of Nutrition," Philadelphia, 1921, 171, 182 and 260.

by the agency of intracellular enzymes. Moreover, Knoop[14] and Embden and Schmitz[15] have shown that certain amino acids may be formed in the living animal or in the perfused liver from ketonic and hydroxy acids and ammonium salts, thus indicating that the reactions may be considered reversible. Assuming this, the reaction of the deaminization of alanin, *e.g.*, could be written thus:

$$CH_3.CHNH_2.COOH + H_2O \rightleftarrows CH_3.CHOH.COOH + NH_3$$

General Conception of Protein Metabolism. Recalling, now, that the catabolism of the carbohydrates appears to lead to the production of simple organic acids as the ultimate body fuel, and remembering also that some of the amino acids yield dextrose, it may be permissible to schematize still further and indicate in the following diagram the possible mutual relations of carbohydrate and protein metabolism.

$$\begin{tikzcd}
\text{Glycogen} \arrow[r, shift left] & \text{Dextrose} \arrow[l, shift left] \arrow[r, shift left] & \text{Organic acids} \arrow[l, shift left] \arrow[r] \arrow[d, shift left] & CO_2 \text{ and } H_2O \\
\text{Proteins} \arrow[r, shift left] & \text{Amino acids} \arrow[l, shift left] \arrow[r, shift left] & NH_3 \arrow[l, shift left] \arrow[u, shift left] \arrow[r] & \text{Urea}
\end{tikzcd}$$

The higher animals appear to be able to make very little use of such a process in synthesizing amino acids. Certain lower organisms do make use of some such process, converting end products of protein metabolism and even the nitrogen of the air into food for higher organisms.

Endogenous and Exogenous Metabolism. A study of the facts of protein metabolism has lead Folin[16] to distinguish between two kinds of protein metabolism which generally occur at the same time in the animal. The endogenous metabolism proceeds from the proteins of the animal's own body while the exogenous metabolism proceeds from the proteins of the food. The urea, uric acid, hippuric acid and other nitrogenous end products may vary more or less with the food intake. The creatinin output, on the other hand, is subject to much less variation. The amount excreted, allowing for the ingestion of creatin and creatinin in the food, is considered to be a fairly accurate measure of the endogenous protein catabolism.

Metabolism of the Conjugated Proteins.

The Nucleic Acids. In general, the conjugated proteins are split up into their constituents during digestion and the latter undergo substantially the same metabolic changes as if consumed separately. In view of the intimate relations of the nucleoproteins to the vital activities of the cell nucleus, however, the metabolism of their characteristic ingredients, the nucleic acids, calls for more detailed consideration.

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[14] *Ztschr. physiol. Chem.*, 67 (1910), 489.
[15] *Biochem. Ztschr.*, 29 (1910), 433.
[16] *Amer. Jour. Physiol.*, 13 (1905), 117.

Autogenesis. One of the most striking examples of the synthetic power of the animal organism is its ability to build up nucleic acids out of a food supply which lacks both purins and pyrimidins. Thus the eggs of birds and insects are practically free from these substances yet the bodies of their young contain normal amounts of nucleoproteins. Similarly, the milk consumed by a suckling mammal is very poor in purins and pyrimidins yet it sustains a rather rapid production of nucleo-proteins. Similarly, Osborne and Mendel[17] obtained a normal growth of two generations of white rats on purin- and pyrimidin-free feed.

Anabolism. Since the body possesses the power to build nucleic acids from purin- and pyrimidin-free materials, it appears natural to conclude that it can also synthesize them from their cleavage products when the latter are resorbed from the digestive tract. The validity of this conclusion, however, has been seriously questioned and a sharp distinction drawn between the endogenous and exogenous purin metabolism, based largely on the fact that the ingestion of nucleo-proteins results in a prompt increase in the excretion of the end products of their catabolism. The same thing is true, however, of the simple proteins, and it is difficult to understand why a cell which is able to build up a nucleic acid *de novo* should be unable to re-synthesize its cleavage products.

Catabolism. As with the simple proteins, the early stages of the catabolism of the nucleic acids consist of a series of hydrolytic cleavages which are substantially like those undergone in digestion and which result in the production of phosphoric acid, carbohydrate, and the purin and pyrimidin bases. Under the action of deaminizing enzymes the NH_2 group of the purin bases is split off as ammonia leaving xanthin and hypoxanthin which are oxidized by means of oxidases, yielding uric acid. Uric acid is the principal nitrogenous end-product of nucleic acid catabolism in man. In most other mammals the latter is largely oxidized by the enzyme uricase, yielding allantoin. In birds and reptiles, large amounts of uric acid are produced synthetically from ammonia and lactic acid by the liver.

Metabolism of Fats.

Anabolism

Blood Fat. As stated in Chapter 3, the prevailing opinion is that fats are resorbed from the digestive tract largely or wholly as soaps of the alkalies or in combination with the bile salts, but that they are re-

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[17] "Feeding Experiments with Isolated Food Substances," Carnegie Institution of Washington, Publication No. 156, Washington (1911), 85.

synthesized in their passage through the epithelial cells, appearing mostly in the lacteals as fat globules, but partly going directly into the blood.

But while the absorbed fat enters the general circulation via the thoracic duct and the anterior vena cava, the blood does not normally carry emulsified fats although its total fat content may rise to one per cent or more. Diverse views have been held regarding the form in which the blood fat exists. The researches of Bloor [18] have recently shown reasons for believing that it is contained in combination with phosphoric acid in some lecithin-like combination while cholesterol appears also to play a part in fat metabolism. His results appear to be confirmed by the investigation of Meigs, Blatherwick and Cary [19] upon the formation of milk fat.

Storage of Fats. All the active cells of the body contain in addition to fats at least small amounts of those complex lipoids (lecithins, cholesterins, cerebrosides, etc.) which seem to be essential ingredients of protoplasm, while the amount of the simple fats may be enormously increased in the cells of adipose tissue or excreted in milk. It has been shown that resorbed food fat may supply material for a deposit of fat in the body cells, effected presumably by a cleavage of the compounds which carry the blood fat, while the complex cell lipoids may be presumed to be derived from the same source. The deposits of true fat constitute a reserve of body fuel which may be drawn upon in a time of scarcity.

The Sources of Animal Fats.[20]

Feed Fats. That the ingestion of fat in the feed may serve to support the production of body fat has never been doubted and has been shown experimentally by the investigations of Hofmann,[21] of Pettenkofer and Voit [22] and of Rubner [23] while in numerous investigations in which foreign fats (vegetable fats, fats of other species) have been given in the feed it has been possible to identify their peculiar fatty acids or other characteristic ingredients in the body fat of the animal and to a less degree even in the milk fat.

On the other hand, the conversion of feed fat into body fat does not appear to be quantitative. In Pettenkofer and Voit's and Rubner's experiments from 66 to 92 per cent of the surplus fat consumed was stored in the body, while in Kellner and Köhler's [24] experiments on cattle with

[18] *J. Biol. Chem.*, 23 (1916), 317; 24 (1916), 447; 25 (1916), 577; 36 (1918), 49.
[19] *Ibid.*, 37 (1919), 1.
[20] For the literature up to 1894 compare Soskin: *Jour. f. Landw.*, 42 (1894), 157.
[21] *Ztschr. Biol.*, 8 (1872), 153.
[22] *Ibid.*, 5 (1869), 369.
[23] *Ibid.*, 19 (1883), 328-334; 30 (1894), 123.
[24] *Landw. Vers. Stat.*, 53 (1900), 112, 124, 199, 214.

peanut oil only 35 to 61 per cent was deposited in the body. The experiments with foreign fats, too, have been essentially qualitative. Their peculiar ingredients have been detected in the body fat but have not been quantitatively recovered. In the case of milking animals, addition of fats to fat-poor rations was found by Morgen and his associates[25] to exert a specific effect in increasing the production of milk fat in sheep and goats and Fingerling[26] has confirmed this conclusion. Experiments with cows on ordinary rations have sometimes given similar results but have often failed to do so. In none of the experiments with foreign fats does any considerable amount of them seem to have been transmitted to the milk and in many instances negative results were obtained.

On the whole, the conclusion seems warranted that the production of animal fat is a function of the cells of the adipose tissue or of the udder which may be *supported* by fats supplied in the feed but which does not consist to any large extent in their direct transfer to the tissues or the milk. Such a conclusion seems fully in accord with the facts concerning the manufacture of fats in the body which are treated in the following paragraphs.

Synthesis of Fats. Neither the extensive deposits of fat in the adipose tissues of meat animals nor the large amounts of butter fat secreted by good dairy cows, however, can usually be accounted for even by the total quantity of food fat consumed. Indeed herbivorous animals in general synthesize a large share of their fat from other components of their feed and other species, including man, possess the same power, as has already been indicated.

That such is the case was first asserted by Liebig,[27] on the basis of observation and general knowledge, and led to an extended controversy with the adherents of the then prevailing view according to which animal fats were derived solely from the fats of their feed. As the result of a large amount of experimental work,[28] however, the correctness of Liebig's view came ultimately to be accepted.

Fats from Proteins. Following the demonstration of the ability of the animal body to manufacture fats it was quite naturally assumed, without direct experimental proof, that the carbohydrates were the raw material for the process. Liebig designated the proteins as "plastic materials," serving to build up tissue, while the fats and carbohydrates were called "respiratory materials," serving as body fuel and, when in excess of the immediate needs of the organism, as sources of fat.

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[25] *Landw. Vers. Stat.*, 61 (1904), 1; 62 (1905), 251; 64 (1906), 93; 66 (1907), 63.
[26] *Ibid.*, 64 (1906), 299.
[27] *Ann. d. Chem. und Pharm.*, 45 (1843), 112; 48 (1843), 126; 54 (1845), 376.
[28] Compare "Principles of Animal Nutrition," 163.

But while this was long the prevailing view, numerous observations were reported from time to time [29] indicating that the proteins might also support fat production. Carl Voit,[30] however, was the first to present data attempting to prove that such was the case. His conclusion was based primarily upon the fundamental investigations of Pettenkofer and Voit [31] with the new respiration apparatus at Munich upon the functions of the organic nutrients which led to the general acceptance of the proteins as an important source of animal fat.

In the experiments upon protein, a dog was fed varying amounts of prepared lean meat freed as completely as possible by mechanical means of fat and connective tissue and the gain or loss of protein and fat by the animal computed from the balance of nitrogen and carbon in the manner described onp. 123. A considerable number of the experiments showed a greater retention of carbon by the animal than corresponded to the storage of protein and the difference was ascribed to a production of fat.

The seemingly conclusive nature of the experimental results, as well as Voit's authority as a physiologist, secured their general acceptance for more than two decades, despite more or less dissent. Their final fate affords a striking illustration of the hazardous nature of assumptions in scientific investigation. In 1872, Pflüger [32] pointed out that Pettenkofer and Voit estimated the carbon and nitrogen income of their dog, not upon actual analyses but on the assumption of average composition of the meat fed, while the carbon of the urine was computed from its nitrogen content. A recalculation by Pflüger of twenty-four of Pettenkofer and Voit's experiments, using what he considered more correct averages, resulted in showing either a loss instead of a gain of fat by the animal or a gain so small as to be within the limits of experimental error.

Pflüger's destructive criticism of the experiments which had served as the chief support of Voit's doctrine, naturally brought the whole matter into question, but a considerable number of more recent investigations [33] seem to have established beyond reasonable doubt the possibility of the formation of fat from protein in the body, although it should be

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[29] Compare "Principles of Animal Nutrition," 107-108.

[30] *Landw. Vers. Stat.*, **8** (1866), 23; *Sitzungsber. Bayr. Acad. d. Wiss.*, **2** (1867), 402; *Ztschr. Biol.*, **5** (1869), 79.

[31] *Ann. Chem. Pharm.*, II Suppl. bd., 1862 and 1863, 52 and 361; *Ztschr. Biol.*, **5** (1869), 369; **7** (1871), 489; **9** (1873), 1, 435.

[32] *Arch. Physiol.*, **51** (1892), 229.

[33] Positive results from experiments on animals have been reported by E. Voit: *Jahresber. Tier-Chem.*, **22** (1893), 34. Cremer: *Ztschr. Biol.*, **38** (1899), 309. Gruber: *Ztschr. Biol.*, **42** (1901), 409. Bogdanow: *Jour. Landw.*, **56** (1908), 53. Mimachi & Weinland: *Ztschr. Biol.*, **55** (1910), 1. Gigon: *Expt. Sta. Rec.*, **26** (1912), 158. Atkinson and Lusk: *Proc. Nat. Acad. Sci.*, **5** (1919), 246.

said that some of the experiments have been severely criticized by Pflüger [34] and that an almost equal number of investigators have failed to obtain satisfactory evidence of the formation of fat from protein in the animal.[35]

It is difficult, however, to secure the consumption by an animal of sufficient protein to leave any surplus above the maintenance requirement from which fat might be formed and such negative results are far less convincing than positive ones. Moreover it has been shown that dextrose may be produced in the catabolism of proteins and since it has been demonstrated that fat may be formed from carbohydrates no reason is apparent why the dextrose thus formed may not be available as a source of fat.

In the earlier controversies over this question much weight was laid upon the alleged formation of fat from protein in cases of phosphorus poisoning, in the ripening of cheese, in the fatty degeneration of muscular tissue, in the autolysis of proteins, etc., but the value of their evidence seems now to be generally discredited.

Fat from Carbohydrates. The results of Pettenkofer and Voit's experiments, not only led Voit, as shown in the preceding paragraph, to affirm the production of fat from proteins but also to regard as unproved and very improbable the tacit assumption by Liebig and his school that the carbohydrates were the source of the fat which they had shown to be manufactured in the body.

Voit's first announcement of this conclusion, at the Convention of German Agricultural Chemists at Munich in 1865, was promptly challenged by Lawes and Gilbert [36] in the following year on the basis of their determinations of the composition of the increase of fattening pigs. But while their results clearly demonstrated a formation of fat from carbohydrates they failed to secure the recognition which was due them and Voit's view soon came to be generally accepted as dogma. For years it dominated discussions of nutrition problems, particularly of domestic animals, and played a large part in leading to the formulation of the excessive estimates of their protein requirements embodied in the so-called "Feeding standards" of that period.

Gradually, however, results began to accumulate which were difficult to reconcile with Voit's view. In an increasing number of experiments

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[34] *Arch. Physiol.*, 68 (1897), 176; 71 (1898), 318.

[35] Negative results have been reported by: Kumagawa and Kaneda: *Expt. Sta. Rec.*, 8 (1896-7), 71. Rosenfeld: *Jahresb. Physiol.*, 6 (1897), 260. Taylor: *Ibid.*, 8 (1900), 249; *Jour. Exper. Medicine*, 4 (1899), 399. Athanasiu: *Arch. Physiol.*, 74 (1899), 511. Lindemann: *Ztschr. Biol.*, 39 (1900), 1. Lafon: *Jahresber. Agr. Chem.*, 56 (1913), 309.

[36] Rept. British Asso. Adv. Sci., 1866; *Phil. Mag.*, Dec., 1866.

the actual fat production, as measured either by analysis of the carcass or by means of the respiration apparatus, proved greater than could be accounted for even on the most liberal assumptions by the protein and fat consumed. Armsby has reviewed the literature of the subject elsewhere.[37] As a whole, the investigations demonstrated beyond question the formation of fat, often in large amounts, from carbohydrates while it has been as clearly shown that the rôle of the proteins in fat production is at best a minor one. It seems worth while also to note in passing that the establishment of this important physiological fact has been due largely to investigations at agricultural research institutions.

Catabolism.

Mobilization of Body Fat. The formation of body fat, as already indicated, is substantially a method of storing up surplus food material as a reserve in case of future scarcity and both common observation and exact experiments show that in the insufficiently fed or fasting animal fat is mobilized to support the internal and external activities of the body. Presumably this is effected by a process the reverse of that occurring during its storage, the body fat being reconverted into the compounds in which it exists in the blood.

Oxidation at the Beta Carbon Atom. During the catabolism of fats the fatty acids are split off and the glycerine is probably changed to dextrose or to glyceric aldehyde and lactic acid. In either case the ultimate fate is the same. The larger share of the energy of the fats is contained in the fatty acids and the catabolism of these substances is better known. Like the other cases already considered it appears to be a step-by-step process. The researches of Knoop, Embden, Dakin and others [38] have rendered it highly probable, if not certain, that the oxidation, at least in the case of the normal saturated acids, begins at the beta carbon atom (*i.e.*, at the second carbon atom from the COOH group) and results in the splitting off of two carbon atoms at a time. The final products of the oxidation are carbon dioxide, water and a fatty acid containing two less carbon atoms than the original one, and with which the same process of erosion is repeated. The intermediate stages of the reaction appear to be the corresponding beta-hydroxy and beta-ketonic acids and the general scheme for the beta oxidation of the fatty acids would be [39] as follows:

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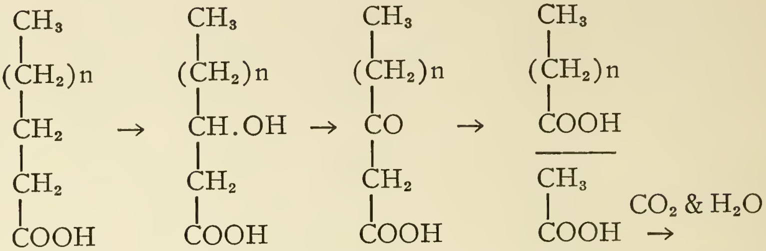
[37] "Principles of Animal Nutrition," 165-184.

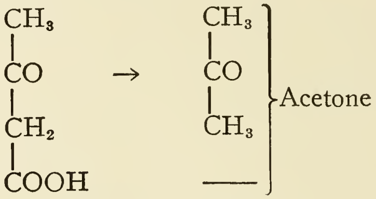
[38] Compare Dakin: "Oxidations and Reductions in the Animal Body," London, 1912, 17-47.

[39] The exact form in which the two carbon atoms are split off has not been demonstrated but it is a plausible hypothesis that the ketonic acid undergoes hydrolytic cleavage yielding acetic acid which is then oxidized, perhaps via formic acid, to CO_2 and H_2O.



$$CH_3{-}(CH_2)n{-}CH_2{-}CH_2{-}COOH \rightarrow CH_3{-}(CH_2)n{-}CH.OH{-}CH_2{-}COOH \rightarrow CH_3{-}(CH_2)n{-}CO{-}CH_2{-}COOH \rightarrow CH_3{-}(CH_2)n{-}COOH + CH_3{-}COOH \xrightarrow{CO_2 \,\&\, H_2O}$$

To a slight extent normally and to a considerable extent when excessive amounts of fat are being catabolized, as in fasting or diabetes, the aceto-acetic acid resulting from the oxidation of butyric acid may also split off CO_2, yielding acetone which is excreted.



$$\underbrace{CH_3{-}CO{-}CH_2{-}COOH}_{\text{Aceto-acetic acid}} \rightarrow \underbrace{CH_3{-}CO{-}CH_3}_{\text{Acetone}} + CO_2$$

Aceto-acetic acid CO₂

This scheme does not provide for the oxidation of the three lower acids of the series, propionic, acetic and formic, and in fact, while these acids are known to be freely oxidized in the body, the chemical mechanism of the process is little understood. According to Shaffer[40] aceto-acetic acid and similar acetone-forming bodies are probably oxidized after combination with a product of glucose oxidation. For more complete information concerning these ketone bodies and their significance in the intermediate metabolism see Shaffer's work on ketogenesis and antiketogenesis.[41]

Formation of Carbohydrates from Fats. When carbohydrates are absent from the feed the body is able to produce them from other substances. That they may be formed from the proteins has already been noted. The question whether they can also be formed from the fats has been much debated and much contradictory experimental evidence is on record. *A priori,* such conversion would seem probable enough. No obvious difficulties are suggested by the molecular structure while the fact that fats are largely formed from carbohydrates strongly suggest the possibility of the reverse process. Nevertheless, the weight of the experimental evidence appears to be against the possibility.

[40] *J. Biol. Chem.,* 47 (1921), 448 and 49 (1921), 144.

[41] *Ibid.,* 47 (1921), 433 and 449; 49 (1921), 143; 54 (1922), 399.

The earlier investigations of the question by Seegen[42] which were claimed to show a formation of dextrose from fats are not particularly convincing. The conclusion was, however, adopted by Chauveau and his school, who regard the carbohydrates as being the immediate source of energy to the animal organism. The more recent investigations of the question have been made chiefly on animals rendered diabetic by the removal of the pancreas or by the administration of phlorhizin. The results of these investigations have been elaborately discussed by Lusk.[43] Such animals cannot catabolize dextrose but excrete it in the urine. When such an animal has been freed from stored carbohydrates (glycogen) most investigators agree that the ratio of dextrose to nitrogen in the urine (the D : N. ratio) is constant, being about 2.8 : 1 in pancreatic diabetes and 3.65 : 1 in phlorhizin diabetes, and that this ratio is not materially changed when fat is fed or when body fat is catabolized in large amounts. From this it is argued that the sugar must be formed from the protein and that it is not produced from fats. The divergent results obtained by several experimenters are ascribed to the presence of a residue of glycogen in the body or to defective technique.

As regards the animal as a transformer, the importance of this lies in the fact that if fats are converted into dextrose before being oxidized as a source of energy rather more than one-third of their energy content would simply be converted into heat, and be unavailable for other purposes. This particular aspect of the question will be considered later. It may be noted, however, that as a rule farm animals consume relatively little fat.

Metabolism of Mineral Ingredients.

Forms. As already noted in Chapter 1, the so-called mineral elements, *i.e.,* those other than C, H, N and O, exist in feeding stuffs in two forms, *viz.,* as "organic" compounds and as electrolytes. Of the former, the most familiar examples are the sulfur of the proteins and the phosphorus of the nucleo- and phospho-proteins, although presumably other elements likewise exist in organic combination while all of them occur as electrolytes.

Anabolism. In the course of digestion and absorption (Chapter 3) it seems probable that the organic phosphorus is converted largely into the electrolytic form but that it may be resynthesized in the body to form nucleo-proteins as far as they are needed. The sulfur of the simple proteins appears to remain in organic combination in the amino-acid cystin. That cystin serves as one of the building stones of the body proteins seems

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[42] "Die Zuckerbildung in Thierkörper," 151.

[43] "The Science of Nutrition," Philadelphia, 1921, 445.

almost self-evident. Whether sulfur ingested as an electrolyte can be synthesized to organic compounds is not known. On the other hand, it is reasonably well established that phosphorus in electrolytes, *i.e.,* as phosphoric acid, can be synthesized to form the organic phosphorus compounds necessary for the organism.

Forbes[44] has given a very complete review of the literature of this subject. His general conclusion is that it has not been proven that a supply of organic phosphorus is essential, although he regards the proof that inorganic phosphorus can serve all the purposes for which any animal needs phosphorus as being incomplete. As regards the relative efficiency of the two, the facts noted in the following paragraphs regarding the importance of accessory substances, in particular the so-called growth substances, in nutrition strongly suggest that the apparent superiority of organic phosphorus which has been observed in some experiments may have been due to the presence of such substances accompanying the organic phosphorus compounds and not to the latter as such.

Catabolism. To the extent to which mineral elements exist in the body as electrolytes one can hardly speak of their catabolism in the sense of cleavages into simpler molecules. Their functions are performed by their presence rather than by their oxidation. The catabolism of organic molecules containing mineral elements results finally in the separation of the latter as the corresponding ions (SO_4, PO_4, K, Na, Ca, etc.) which, together with the carbonic acid arising from the catabolism of the organic nutrients, are thus added to the stock of electrolytes in the body, any surplus being excreted in the urine or feces.

Functions of the Nutrients.

Purpose of Metabolism. In the foregoing paragraphs the attempt has been made to sketch the broad features of metabolism as a chemical process. To get a full appreciation of the significance of the facts, however, it is necessary to turn from the chemical to the physical point of view and consider the purpose of metabolism and the part played by the several nutrients and its accomplishment.

Life, from the physical point of view, may be characterized as a manifestation or transformation of energy. The living organism is continually exerting force upon its environment. It is a prime motor, doing mechanical work, in moving itself and surrounding objects and also incidentally imparting heat to them. The supporting of this continual outflow of energy is the physical aspect of that which from the chemical viewpoint is called metabolism. By the various chemical reactions con-

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[44] Ohio Agr. Expt. Sta., Tech. Bul. 5 (1914), 318 to 365.

stituting catabolism, energy is liberated from the components of the protoplasm or of the cell fluids, appearing as heat or motion, while the anabolic processes serve to replenish the reserve supply from the substances absorbed from the food. The animal thus functions as a mechanism for the conversion of the stored solar energy originally contained in vegetable substances into mechanical work, while a surplus feed supply may result in production of valuable human food either by growth, fattening, egg production, or milk production. The latter, however, in its physiological aspect, is incidental to the prime purpose of metabolism which is the development and functioning of an organism or the liberation of energy for the vital activities.

Dual Function of Food. But while the food serves primarily as a carrier of the energy manifested by the living animal, the efficient functioning of the latter as a converter depends upon the building up and maintenance of an exceedingly complex mechanism, the body, the materials for which are supplied ultimately by the food. The food, then, has the double function of supplying both energy and matter.

The latter is sufficiently obvious as regards the proteins, fats, carbohydrates and mineral ingredients which make up the bulk of the organism. The food must either contain them ready-formed or supply materials out of which the body can construct them. But in addition to building up and maintaining the structural elements of the body, material must be available for the production of substances like the enzymes, hormones, endocrine secretions, vitamins and the like whose amount is minute as compared with that of the body as a whole but whose presence is essential to its normal functioning. So far as the food fails to contain them ready-formed or to supply the atomic groupings essential to their production by the body it is inadequate no matter how much protein and energy it may contain.

Functions of the Proteins. The proteins afford the most conspicuous example of the dual function of the food. The products of their digestion contain practically all the chemical energy of the original proteins while but a fraction of it appears in the products of their catabolism, the remainder being transformed in the body. They are therefore carriers of energy. At the same time they serve, during their intermediary metabolism to build up more or less temporarily the protein tissues of the body or as a source of milk or egg proteins, thus serving as building or repair material. Finally it may be at least plausibly conjectured that some of their constituents are utilized in the manufacture of the internal secretions, etc.

Functions of the Fats and Carbohydrates. In previous paragraphs of this chapter it has been shown that both fats and carbohydrates may support the formation of fat in the body or in the milk and thus serve as structural material. They are, however, pre-eminently sources of energy, by far the larger part of the supply to the body being carried by them or, in herbivora, in the products of their digestive fermentation.

Even here, however, specific differences appear. When the body is compelled to draw its energy supply chiefly from fats, as in prolonged fasting or in diabetes or when carbohydrates are absent from the diet, the catabolism of the fats is interfered with and incompletely oxidized products such as hydroxybutyric acid, acetoacetic acid and acetone are excreted in the urine. On the other hand, it has been claimed, and is still believed by some, that growth at least cannot be supported in the absence of a minimum of fat from the diet but it appears to be now generally admitted that this is due to lack of the so-called "fat-soluble A" vitamin and not to simple absence of the triglycerides.

Functions of Mineral Ingredients. In contrast to the "organic" nutrients, which act primarily as carriers of energy, the mineral ingredients of the food introduce no energy into the organism but do serve important purposes, both structural and functional.

Structurally, their importance is most obvious in the skeleton, the large amount of mineral elements which it contains imparting to it the necessary rigidity while they also serve as a reserve which may be drawn upon when the ash supply of the food is insufficient for the necessary functional uses, as Forbes[45] has shown to be true, *e.g.,* in the case of high-producing milk cows. It can hardly be doubted, too, that the lesser amounts of mineral ingredients contained in the soft tissues have also a structural significance. It is, however, in their functional relations that the greatest interest attaches to the mineral ingredients.

Single Elements. Comparatively little is known regarding the physiological functions of the elements contained in the ash or of the extent to which chemically similar elements may replace each other. We know that iron is an essential ingredient of the hemoglobin by means of which oxygen is introduced into the body. Iodine appears to be essential to the functioning of the thyroid glands. Fluorine is an essential ingredient of the dental enamel.

Certain general functions of the mineral elements as a whole can, however, be outlined.

Osmotic Pressure. The cells of the body are bathed by lymph which serves as a means of exchanging food and waste matter between the cells and the blood. For the normal functioning of the cells the osmotic

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[45] *J. Biol. Chem.,* 52 (1922), 281.

pressure of the body fluids must remain constant within very narrow limits. This pressure, estimated at about eight atmospheres, is due chiefly to the minerals present and its constancy is maintained by the excretory activity of the kidneys. These act like a sort of overflow valve, an excess of any ingredient in the blood over a certain minimum amount being promptly excreted in the urine. This is true of the organic products of metabolism, such, *e.g.*, as urea or dextrose, but notably of the electrolytes.

Ionic Concentration. The mineral ingredients in the body fluids are of course largely ionized and some of these ions have specific effects on cellular activities. Sodium ions, *e. g.*, sustain the irritability of muscle tissue while calcium or magnesium ions suspend it. Similar antagonistic actions have been observed in the development of the egg. In general, physiological activities seem to be conditioned on certain absolute and relative ionic concentrations.

Maintenance of Neutrality. An important special instance of the foregoing is found in the maintenance in the body fiuids of a definite concentration of H and OH ions, these concentrations in blood serum being approximately 0.4×10^{-7} and 7.2×10^{-7}, respectively. But this equilibrium is being continually disturbed by the production of acids (carbonic, phosphoric, sulfuric) in the catabolism of the organic nutrients. These acids are to a greater or less extent neutralized by the ammonia produced in the catabolism of the proteins but the investigations of L. J. Henderson have shown what an important rôle the mineral compounds of the blood serum play in the process while the basic salts of the skeleton may also be drawn upon in case of need.

The production of carbon dioxide or carbonic acid is continuous during the life processes. The blood stream must remove this substance from the cells where it is formed. This is largely done through the lungs. Carbon dioxide is carried by the blood stream in the form of $NaHCO_3$ and CO_2 about 93 per cent being in the form of the acid carbonate. The reaction between the normal alkalies of the blood and the carbonic acid is illustrated by the following equations:

$$Na_2CO_3 + H_2CO_3 \rightleftarrows 2NaHCO_3$$
$$Na_2HPO_4 + H_2CO_3 \rightleftarrows NaH_2PO_4 + NaHCO_3$$

These reactions are reversible and so the normal alkalinity of the blood is maintained. On the removal of carbon dioxide in the lungs the reaction goes in the direction of the formation of the alkaline salts.

These acids (carbonic, sulfuric, phosphoric) may also be neutralized by the ammonia split off during the catabolism of amino acids. The mineral acids, however, are largely eliminated by the kidneys as the sodium salts, NaH_2PO_4 and Na_2SO_4. Ammonia and carbonic acid react to form ammonium carbonate. They may also react to form ammonium carbamate which in turn is changed to urea and thus a proportion of acid-forming substance is removed.

$$2NH_3 + CO_2 \rightarrow NH_2 \cdot CO \cdot ONH_4$$
$$NH_2 \cdot CO \cdot ONH_4 \rightarrow NH_2 \cdot CO \cdot NH_2 + H_2O$$

Other precursors of urea may be ammonium lactate and glycocoll. The elimination of carbon dioxide along with ammonia would proceed when these compounds are chanegd into urea.

More recent work by Van Slyke[46] and his coworkers has shown that the salts must play a minor rôle in maintaining neutrality. He shows[47] that hemoglobin accounts for 73 to 79 per cent of the alkali reserve of the blood while bicarbonate accounts for but 7.4 per cent leaving 14.6 per cent to be accounted for by all other buffers. Buffers are substances which by their presence in solution increase the amount of acid or alkali that must be added to cause a unit change in the pH. Such substances combine with the acid or alkali added to form other substances which dissociate giving a much smaller concentration of hydrogen ions. The following equation illustrates such a reaction:

$$K_2HPO_4 + HA \rightarrow KH_2PO_4 + KA$$
$$KH_2PO_4 + KOH \rightarrow K_2HPO_4 + H_2O$$

Proteins possess this power to combine with either acid or alkali to a remarkable extent, forming salts which dissociate to a very slight extent and preventing any considerable change in the pH of the blood and body tissues.

Vitamins.

General Nature. As noted in Chapters 1 and 2, various vegetable and animal substances contain, in addition to the major groups of compounds there described, small amounts of other substances which neither build tissue nor yield energy, in the ordinary sense of the words, yet whose presence in the food is essential to the normal performance of the vital functions. Various names have been given to these substances by investigators but the name vitamin, proposed by Funk,[48] now appears to be generally accepted.

None of the vitamins have yet been isolated and practically nothing is known regarding their chemical nature. They are recognized by their effects, or perhaps it would be more exact to say by the effects of their

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[46] *J. Biol. Chem.*, 52 (1922), 525; 54 (1922), 121 and 149; 54 (1922), 481 and 507.
[47] *Ibid.*, 54 (1922), 512.
[48] *Jour. Physiol.*, 43 (1911), 50.

absence. The existence of such substances was first recognized in investigations by Eijkman[49] and by Funk,[50] upon the tropical disease called beri-beri and by Hopkins[51] on the feeding of growing animals upon purified food substances. Subsequent investigation has been largely along these two general lines, viz., the relation of vitamins to certain diseases and their significance in normal nutrition.

Present Knowledge. For the purpose of this discussion it would be unprofitable to attempt to follow in detail the later progress of investigation in a field which is still being actively explored[52] or to give more than a very general outline of present knowledge without specific citation of authorities.

Most authorities now appear to recognize at least three different vitamins (or perhaps classes of vitamins) as follows:

1. The fat-soluble A vitamin, associated with certain fats, notably those of milk and eggs and with liver fat but also with the body fat of animals. In the vegetable kingdom it is found in smaller amounts in seeds and more abundantly in leaves. It is essential to growth and its lack frequently induces a condition of the eyes called xerophthalmia. There is some evidence of a separate antirachitic vitamin associated with this growth vitamin.
2. The antineuritic, or water-soluble B vitamin, contained in a great variety of natural foods, notably in the leaves of plants, in the germs of seeds and in yeast, and extractable by water or alcohol. It also occurs in fruits, in fresh meats in small amounts, and in the edible glands of animals in appreciable amounts. This is the vitamin whose lack causes the disease beri-beri in man and the allied polyneuritis of birds, while it is likewise essential to the growth of young animals.
3. Antiscorbutic C vitamin, found especially in fresh fruits and vegetables and in much smaller amounts in fresh milk and fresh meat. The lack of this vitamin brings about the condition known as scurvy.

In addition to the diseases due to lack of the water-soluble and fat-soluble vitamins, certain other nutritional diseases, especially rickets and pellagra, have been classed among the so-called "deficiency diseases" and regarded as due in each case to lack of a specific vitamin. With regard

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[49] *Arch. Hyg.*, 58 (1906), 150.

[50] *The Lancet*, 2 (1911), 1266; *Ergeb. Physiol.*, 13 (1913), 125.

[51] *Jour. Physiol.*, 44 (1912), 425.

[52] Compare Sherman and Smith: "The Vitamins," New York, 1922. McCollum: "The Newer Knowledge of Nutrition," New York, 1922. Funk: "The Vitamines," Baltimore, 1922.

to rickets this is now apparently established, while in the case of pellagra the work of Goldberger [53] gives evidence that an amino acid deficiency may account for this disease.

Some very recent evidence points to the possibility of the existence of a vitamin required for reproduction. Evans and Bishop [54] have reported some extensive work indicating that the existence of such a vitamin may be considered as demonstrated.

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[53] *Public Health Reports* (U. S.) 39 (1924), 87; 40 (1925), 54.

[54] *Jour. Metab. Research,* 1 (1922), 319, 335; 3 (1923), 201, 233.

Part II.

THE QUANTITATIVE YIELD OF FOOD —EFFICIENCY OF CONVERSION.

The Quantitative Yield of Food.

Efficiency of Conversion.

In Part I there have been considered qualitatively the processes by which the raw materials contained in stock feeds are converted into animal substances. From the standpoint of the food supply, however, the thing of prime importance is the quantitative efficiency with which this conversion is accomplished, in other words, how much human food can be produced from a given amount of various raw materials by different varieties of live stock and under different conditions. The following chapters are devoted to a consideration of the several phases of this question, including an outline of the experimental methods which may be employed for its solution.

Chapter 5.

Methods of Investigation.

In order to judge of the validity and significance of the results of nutrition investigations, some knowledge of the nature and limitations of the experimental methods employed is essential. These are of three genral kinds: Live weight experiments, comparative slaughter tests, and balance experiments. For a discussion of the technical details of these methods, reference may be made to the report [1] of a sub-committee of the National Research Council upon methods of experimentation in animal production. Here it is merely attempted to outline their logical basis.

Live Weight Experiments.

Live Weight an Inadequate Measure of Results. At first thought it might seem that the efficiency of conversion might be measured quite simply by comparing the amount of feed consumed with the increase in live weight or with the weight of any particular product (milk, wool) obtained, since these are the factors which determine commercial results, and that no elaborate experimental methods are necessary. So far as concerns commercial questions this is true. The returns from feeding operations are determined by the weights of animals or of the products together with the market judgment upon their quality.

If, however, it is desired to investigate the quantitative efficiency of the animal as a converter, the live weight and to a less degree the weight of products is an inaccurate measure of the effect for two chief reasons.

Live Weight Fluctuating. The live weights of animals, particularly the herbivora, are subject to very considerable fluctuations from day to day even under apparently identical conditions. This is due chiefly to variations in the amounts of feed and especially of water contained in the digestive tract. The live weights of ruminants, even when fed on absolutely uniform rations, may vary by 3 or 4 per cent from one day to the next. In swine the variation is less but still considerable. The error involved may of course be reduced by taking the mean of several days,

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[1] *Bulletin of the National Research Council,* 6, Pt. 2, No. 33, Washington, 1923.

but even a ten-day mean, as Armsby has shown,[2] does not suffice to eliminate the fluctuations completely.

Composition of Increase Varies. Not only does the gain in live weight fail to show correctly the increase of the edible portion of the animal but the composition of that increase may differ from one case to another, while the variations in the composition of milk are more or less familiar to all. The increase in weight of actual body tissue may consist to a large extent of fat, having a high value as a fuel food, of protein with its function as a tissue builder, or to a considerable extent of water. Similarly, in samples of apparently normal milk, variations of the water content from 80 to 90 per cent and of the fat content from 2 to 8 per cent have been observed.

Comparative Slaughter Tests.

One method of eliminating the uncertainties attaching to live weight is by means of analyses of the entire bodies of the experimental animals, such as those cited in Chapter 2. In brief, two or more animals as nearly alike in every respect as can be determined are selected. One or more of these serves as the check animal and is weighed and slaughtered at the beginning of the experiment and the chemical composition of its body determined. The remaining animals are fed the ration whose effect is to be determined for a considerable period at the end of which they also are weighed, slaughtered and analyzed. If the check animals were exactly representative, it is evident that the results afford the means of computing the amount and composition of the increase. The uncertainty arising from differences in the content of the digestive tract may be eliminated by computing the results upon the empty weight basis, while the total increase in the amounts of any substances capable of accurate analytical determination, as well as their distribution between different parts of the body, can be computed.

The weak point of the method lies in the selection of the check animals. The assumed identity of composition of the animals cannot, in the nature of things, be proved and is very unlikely to be absolute. If individual analyses of several check animals are made, it is possible to form a good estimate of the error involved in assumptions of identity of composition. These errors are also greatly offset by employing a comparatively long feeding period so that the increase is large compared to the error. The percentage error may then be small. A later chapter shows that the net energy of a ration is practically the same when measured by the comparative slaughter test and by the respiration calorimeter.

[2] Penn. Agr. Expt. Sta., Bul. 42 (1898).

A great advantage of the method is that it permits of a direct and accurate determination of the product formed and, when accompanied by a balance experiment, of the income and outgo. The heat increment and similar losses are inferred. The respiration calorimeter and balance experiments infer the product formed while measuring income of food and outgo of excreta as well as the heat increment and similar losses. The slaughter method involves a smaller outlay in equipment. The larger number of animals used adds to the dependability of the results.

A few early analyses have been reported, the work of Lawes and Gilbert being for a long time the classical example. More recent and much more extensive work by Haecker, by Moulton, Trowbridge and Haigh, and by Swanson have been cited in Chapter 2. A somewhat larger number of carcass analyses are also on record. The work with pigs and cattle is rather extensive, but with other animals comparatively little has been done.

Balance Experiments.

The Balance of Nutrition. Another method of investigation is based upon the conception of nutrition as a balance between income and outgo.

As appeared in the discussion of metabolism in Chapter 4, the body substances are being continually catabolized, primarily to supply the energy required for the vital processes. To make good losses thus occasioned, the organism requires a supply of matter and its accompanying energy from outside in the form of food. Obviously the maintenance, increase, or decrease of body substance is determined by the relation between income and outgo.

The Schematic Body. Pending a complete knowledge of the physics and chemistry of the metabolic processes, studies of their aggregate effect upon the balance of nutrition as just defined may be made by utilizing the conception of the schematic body as set forth in Chapter 2.

This conception regards the body of an animal as consisting essentially of water, ash, protein and fat, together with small and rather constant amounts of glycogen, the amounts of other chemical compounds being so small as not to affect materially the truth of this view. The aggregate results of any ration or treatment can be measured by the increase or decrease of the store of the four principal substances contained in the body, or even more simply in terms of the gain or loss of structural materials (ash, protein) and energy. It will be convenient to consider first the balance of matter and second the balance of energy.

The Balance of Matter.

Balance of Mineral Ingredients. The increase or decrease of the mineral ingredients in the body may be very simply determined by a comparison of the amounts contained in the feed with those excreted in the feces and urine and in very accurate experiments in the losses of epidermal tissue.

Gain of Protein. Since the body does not normally excrete protein but only the products of its catabolism, it is not possible to make such a comparison of the intake and outgo as in the case of the mineral ingredients, but the same end may be reached by a similar comparison of the intake and outgo of its characteristic element, nitrogen.

It has been stated in Chapter 4 that no free nitrogen is produced in the catabolism of protein. This question has been the subject of a vast amount of investigation and controversy. The cumulative evidence, however, of the great number of experiments in which substantial equality between income and outgo of nitrogen have been observed under conditions which precluded the possibility of any gain or loss of body protein, together with the fact that the very careful and accurate investigations of recent years upon the excretion of free nitrogen in respiration have given negative results, amounts to a demonstration that food nitrogen leaves the body only in the combined form in the visible excreta.

It is only necessary, then, to add to a digestion experiment, as outlined in Chapter 3, a quantitative collection of the urine and determination of the nitrogen together with, in special cases, the amount of nitrogen in epidermal tissue. The difference between intake and outgo shows the amount of nitrogen gained or lost by the body which must have been substantially in the form of protein. The amounts of the latter can be computed by multiplying the nitrogen by the proper factor. The factor 6.25 has been most generally used. The data recorded in Chapter 2 appear to verify this factor for entire animals while the factor 6 is better for flesh alone.

Example of a Nitrogen Balance Experiment. The digestion experiment with clover hay used as an example in Chapter 3 may serve also to illustrate the nature of a nitrogen balance experiment. In that experiment the hay consumed daily contained 3.144 kilograms of dry matter and the daily feces 1.267 kilograms, while the average daily weight of the urine for 9 days was 5.449 kilograms. Analysis showed the following percentages of nitrogen:

In dry matter of hay	2.271 per cent
In dry matter of feces	2.240 per cent
In fresh urine	1.074 per cent

The brushings of the steer (hair, dandruff, etc.) were found to contain 1.87 grams of nitrogen per day. The daily nitrogen balance may accordingly be computed as in Table 35, showing a loss from the body which, of course, must be placed in the income column to complete the balance.

TABLE 35

EXAMPLE OF A NITROGEN BALANCE

	Income Grams	Outgo Grams
Nitrogen in hay	71.40	
Nitrogen in feces		28.40
Nitrogen in urine		58.50
Nitrogen in brushings		1.87
Nitrogen loss from body	17.37	
	88.77	88.77

These figures show a loss by the body of the animal of 17.37 grams of nitrogen daily, which, using the factor 6.25, is equivalent to 108.56 grams of protein.

Gain of Fat. If in addition to the nitrogen balance, the total income and outgo of carbon, including that contained in the gaseous excreta, be determined, the gain of fat by the animal may likewise be computed. The conception of the schematic body regards its carbon content as existing substantially in the two forms of protein and fat. The composition of body protein, however, varies but slightly and is sufficiently well established to permit the computation of the amount of carbon contained in the gain of protein as measured by the nitrogen balance. Any gain of carbon in excess of this amount is therefore regarded as showing an increase of body fat, the amount of which may be computed from its average composition.

TABLE 36

NITROGEN AND CARBON BALANCES OF A STEER

	Nitrogen		Carbon	
	Income Grams	Outgo Grams	Income Grams	Outgo Grams
6988 grams timothy hay	56.4		2831.7	
400 grams linseed meal	21.9		172.6	
16619 grams feces		33.5		1428.7
4357 grams urine		32.4		124.2
37 grams brushings		1.3		8.0
4730 grams carbon dioxide				1290.2
142 grams methane				106.6
Gain by body		11.1		46.6
	78.3	78.3	3004.3	3004.3

The average body protein of cattle contains 52.12 per cent of carbon and average animal fat 76.50 per cent. The computation is therefore as follows:

Total carbon gained	46.6 grams
Gain of protein $11.1 \times 6.25 = 69.4$ grams	
Carbon of protein gained $69.4 \times 0.5212 =$	36.2 grams
Carbon gained as fat	10.4
Equivalent fat $10.4 \div 0.765$	13.6

In making such computation, confusion may often be avoided by treating losses as negative gains.

Gain of Carbohydrates. The foregoing method assumes that there has been no significant change in the relatively small glycogen content of the body. In reasonably long periods this is probably substantially true but in short periods the discrepancy may be relatively important. If, however, there can be added to the determination of the nitrogen and carbon balances that of the balances of hydrogen and oxygen the means are afforded for calculating also the gain of carbohydrates, the method of computation being somewhat complicated.

The determination of the balance of matter naturally includes the balance of water, both that consumed as such and that produced by the oxidation of organic hydrogen in the body. Owing to technical difficulties, the determination of the outgo of water vapor is less exact than that of carbon dioxide or of the combustible gases. The amount of water produced from organic hydrogen, moreover, is relatively small compared with the amount of water simply evaporated, and consequently the error involved in its determination is relatively large.

A determination of the balance of matter, including water, should, of course, give a net result corresponding to the change in the live weight of the animal. Armsby has shown [3] that the correspondence is reasonably good.

The Respiration Apparatus. The determination of the carbon balance necessarily includes the determination of the carbon of the gaseous excreta and involves the use of some form of respiration apparatus, which in the case of herbivora must provide for the determination of the combustible gases excreted. Armsby [4] has described elsewhere some of the more important forms of respiration apparatus. The following summary is taken largely from the report of a joint committee [5] composed of members of the American Society of Animal Production and of the Committee on Food and Nutrition of the National Research Council.

Two general types of respiration apparatus are in common use, either being available for the determination of the total gaseous excreta.

a. The Regnault-Reiset, or Closed-Circuit Apparatus. In the

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[3] U. S. Dept. Agr., Bur. Anim. Indus., Bul. 143 (1912).

[4] "Nutrition of Farm Animals," pages 208-216.

[5] *Bulletin of the National Research Council,* 6, Pt. 2, No. 33, Washington, 1923.

closed circuit type of apparatus the animal breathes in a closed chamber of space, the carbon dioxide and water given off being absorbed by proper reagents and the loss of oxygen supplied from a gas holder or gas cylinder. In the earliest form[6] of this apparatus, which was intended for small animals, the subject was placed under a glass bell jar. Subsequently a larger form was devised for animals as large as sheep. Atwater and Benedict[7] were the first to describe a practical form of this apparatus for experiments on man, and Zuntz[8] subsequently constructed one for cattle.

A form for the investigation of the pulmonary exchange alone has also been devised by Benedict and is described, along with other forms, by Carpenter.[9]

b. The Pettenkofer, or Open-Circuit Apparatus. In this form of apparatus the animal breathes in a continuous measured current of out-door air whose content of water, carbon dioxide and combustible gases is determined on samples taken at the points of entrance and exit. It is that type which has been most commonly used in agricultural research.

The original chamber apparatus was constructed by Pettenkofer[10] at Munich for investigations upon man. A similar one for cattle was soon afterwards installed at Göttingen, and others later at Möckern and Leipzig. A form for the investigation of pulmonary respiration was likewise devised by Zuntz and Geppert. This form of apparatus was used by Zuntz[11] in his extensive investigations upon the working horse and Hagemann[12] has also applied it to sheep.

Determination of Oxygen Consumed. The determination of the oxygen consumed may be combined with the determination of the gaseous excreta by the respiration apparatus, although with considerable difficulties in practice.

a. Determination with the Closed-Circuit Apparatus. This requires in addition to the determination of the amount of oxygen admitted to the apparatus a determination of the amount contained in the apparatus at the beginning and at the end of an experiment. With a chamber apparatus, a determination of the latter is a decidedly difficult task. In the pulmonary form the problem is less difficult.

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[6] *Ann. de Chem. et de Physique,* 3ème Series, 26 (1849), 299.

[7] "A Respiration Calorimeter with Appliances for the Determination of Oxygen," Carnegie Institution of Washington, Publication No. 42, Washington, 1905.

[8] *Landw. Jahrb.,* 44 (1914), 776.

[9] "A Comparison of Methods for Determining the Respiratory Exchange of Man," Carnegie Institution of Washington, Publication No. 216, Washington, 1915.

[10] *Ann. der Chem. u. Pharm.,* Suppl. Bd. 2 (1862-3), I. Compare also, Atwater: U. S. Dept. Agr., Office of Expt. Stas., Bul. 21 (1895), 106.

[11] *Landw. Jahrb.,* 18 (1889); 27 (1898), Ergzbd. III.

[12] *Arch Anat. u. Physiol.,* 1899, Suppl. Band., 138.

b. Determination with the Open-Circuit Apparatus. With the pulmonary form of apparatus it is not difficult to determine the deficit of oxygen in the expired air with a good degree of accuracy.

The chamber apparatus is commonly used only for the determination of the expired gases. It is possible, however, to utilize it also for determining the amount of oxygen consumed by the animal, the difficulty lying only in the extremely accurate determinations of oxygen in the outgoing air which are necessary. Jaquet[13] has used the method for small animals while Møllgaard and Andersen[14] and Fries[15] have also applied it to cattle.

The principle of the Pettenkofer apparatus is also involved in the construction of the respiration calorimeter of Armsby and Fries. This apparatus has been used for work with cattle and has been described in some detail elsewhere.[16]

Møllgaard and Andersen of Copenhagen have recently done considerable work on a respiration apparatus of this type.[14, 17] Benedict and co-workers have developed a very inexpensive and rather efficient instrument for use with cattle at Durham, New Hampshire. This apparatus has been described rather fully by Benedict and co-workers.[18]

The Balance of Energy.

A storage of matter in the body signifies also a storage of chemical energy, and the amount of the latter may be computed from the composition of the gain determined by one of the methods already described, or it may be determined by the direct comparison of the income and outgo of energy.

The Income of Energy. The sole form of energy available to the animal is the chemical energy of its feed, the maximum amount of energy supplied by the latter being represented by its heat of combustion. This is sometimes spoken of as the total energy of the feed, but it seems, on the whole, preferable to use the term gross energy. While the gross energy of a feed is measured as a matter of convenience in the form of heat, it

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[13] *Verhandl. der Basler naturf. Ges.*, **15** (1903).

[14] Kungl. Veterinaer—og. Landbohøjskoles Laboratorium for landøkonomiske Forsøg. 94de Beretning fra Forsøgslaboratoriet, Copenhagen, 1917.

[15] *Amer. Jour. Physiol.*, **55** (1921), 53.

[16] *Experiment Station Record*, **15** (1903-4), 1037. Twenty-third Annual Report, Bur. of Animal Industry (1906), 263. The Respiration Calorimeter, Pennsylvania Agr. Expt. Station, Bul. 104 (1910).

[17] Kungl. Veterinaer—og. Landohøjskoles Laboratorium for landokønomiske Forsøg. 111te Beretning fra Forsøgslaboratoriet, Copenhagen, 1923.

[18] "A Respiration Chamber for Large Domestic Animals," New Hampshire Agr. Expt. Station, Technical Bul. 16 (1920). "Undernutrition in Steers," Publication 324, Carnegie Institution of Washington, Washington, 1923.

should be clear that it is not heat but chemical energy which is actually utilized by the animal. The animal body is not a heat engine.

Heats of combustion are ordinarily determined by burning in highly compressed oxygen in a steel bomb in the manner devised by Berthelot[19] and subsequently modified by various investigators.

The Outgo of Chemical Energy. By no means all the gross energy of the feed is capable of conversion in the body. While pure carbohydrates and fats may, under favorable conditions, be completely oxidized, ordinarily more or less of the feed materials consumed escapes from the body as unoxidized or only partially oxidized substances which still carry more or less chemical energy. This is particularly the case with the herbivora, which consume large amounts of coarse bulky feed. This outgo of chemical energy is chiefly in the feces, urine, and combustible gases. Minor amounts are found in the perspiration and in the epithelial dejecta (scurf, shed hair, growth of hair and other epithelial tissue).

As stated in Chapter 3, the feces consist of undigested feed residues together with certain so-called metabolic products. The heat of combustion of the former obviously represents unassimilated chemical energy of the feed. That of the metabolic products, although derived immediately from the body, nevertheless, from the point of view of the balance experiment, represents a loss which must be made good by the feed. The heat of combustion of the feces as a whole must, therefore, be deducted from that of the feed. This amount must be determined directly, no data being available for computing it.

Certain substances absorbed from the feed, notably the proteins, are not completely oxidized but yield partially oxidized products, of which urea is a familiar example, which are excreted in the urine. The chemical energy carried off in this way may be estimated with some degree of accuracy from the nitrogen content, or better, from the carbon content of the urine. But the ratios of energy to nitrogen and carbon are more or less variable, and in exact investigations the heat of combustion of the urine, after suitable preparation, should be determined directly.

A third channel through which chemical energy escapes is the combustible gases given off by herbivora and especially by ruminants (Chapter 3). This energy is evidently not accessible to direct determination, but since these gases have been shown to consist substantially of methane the corresponding amount of energy may be readily computed. For this purpose the heat of combustion at constant pressure should of course be used.

Metabolizable Energy. Manifestly the difference between the gross

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[19] Compare Atwater: U. S. Dept. Agr., Office Expt. Stas., Bul. 21 (1895), 121.

energy of the feed and the chemical energy of the excreta shows the amount transformed or capable of transformation into other forms of energy in the organism. This has sometimes been called available energy. As will appear subsequently (Chapter 6), however, only a part of it is ordinarily available for the general physiological purposes of the body. It seems better, therefore, to call it metabolizable energy, since this term carries no implication as to the use to which it is, or may be, put in the body. Metabolizable energy may be defined as the chemical energy of the feed minus the chemical energy of the feces, urine, and combustible gases.

The difference between the calories in the food and the sum of those in the feces, urine, and combustible gases is an exact measure of the metabolizable energy only in case a condition of maintenance is obtained. If the animal gains protein and fat, as shown by the nitrogen and carbon balances, the amount of energy actually converted into the kinetic form is less than the difference obtained above. This storage of fat, however, represents an amount of potential energy readily transformed into the kinetic form and so may be properly considered a part of the metabolizable energy of the feed.. This is partly true of the protein stored with the exception of that portion of this stored protein which is incapable of being converted into energy by the animal and is lost in the urine. According to Rubner's results each gram of urinary nitrogen derived from the metabolism of the protein of lean meat corresponds to 7.45 large calories. Armsby[20] considers this result applicable to the forms of protein consumed by herbivora. In the case under discussion it is necessary to subtract this amount multiplied by the grams of nitrogen stored from the apparent metabolizable energy gotten by difference between that ingested and the amount excreted. In other words it should be added to the amount excreted. The result is the true metabolizable energy.

This correction to nitrogen equilibrium must also be applied in case the animal is losing body substance including protein. In this case the correction for the loss of body nitrogen will be applied in the opposite direction for the urine would then contain an amount of energy loss not derived from the food fed.

The Output of Mechanical Energy. The prime physiological purpose of the feed in the mature animal is to supply energy for the various forms of work, internal and external, performed by the animal. So far as concerns the internal work, such as circulation, respiration, peristalsis, muscular tonus, and the like, or the minor movements of the animal such as change of posture and the like, it is evident that, since no permanent

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[20] "Principles of Animal Nutrition," New York, 1910, 285.

effect is produced on the surroundings of the animals, the energy thus expended is finally converted into heat and forms part of the heat outgo of the body.

When mechanical work is done upon the environment of the animal, however, this amount must be measured if a complete balance of energy is desired.

In experiments on man various forms of mechanical work, such as climbing a staircase, lifting a weight, or riding a bicycle, have been investigated. With animals substantially only two methods have been used. One of these is to have the animal perform work with a sweep power which also serves as a dynamometer. This form was used by Wolff [21] and by Grandeau and Le Clerc [22] in studying the feed requirements of the work horse.

The second form of apparatus is the tread power, in which the animal does work by lifting its own weight. This is the form used by Zuntz, in connection with the Zuntz-Geppert form of respiration apparatus, in his extensive investigations upon the metabolism of the working horse while Benedict and Murschhauser [23] and others have also applied it to man.

Work performed in the chamber of a respiration calorimeter is, of course, converted into heat and measured along with that arising from other physiological processes unless part of the work performed is done in raising a body, permitting part of the energy to remain in the potential form.

The Outgo of Heat. (a) Direct Calorimetry. The actual determination of the heat produced by an animal requires, of course, the use of some form of calorimeter. Moreover, since provision must be made for ventilation and for the determination for the gaseous products given off, the apparatus must also be a respiration apparatus, either of the closed- or open-circuit type.

For a general classification of respiration calorimeters and a description of some common forms compare "The Nutrition of Farm Animals," pages 235-240. A very complete description of all but the latest forms is given by Lefevre.[24]

The type of instrument most readily adaptable for use with large animals is the flow calorimeter in which the heat emitted is removed by a current of water. The best known and most successful form of flow calorimeter for experiments upon animals is that devised by Atwater and

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[21] *Landw. Vers. Stat.*, 21 (1878), 19; *Landw. Jahrb.*, 24 (1895), 190-193.

[22] *Amer. Sci. Agron.*, 1 (1881), 464.

[23] "Energy Transformations During Horizontal Walking," Carnegie Institution of Washington, Publication No. 231, Washington, 1915.

[24] "Chaleur Animale et Bioenergetique," Paris, 1911, 77-228.

Rosa [25] and modified by Atwater and Benedict [26] for experiments on man. This type has been adapted by Armsby and Fries [27] and by Hagemann [28] for experiments on the larger farm animals and by Capstick [29] for use with medium sized animals such as swine. This latter instrument at Cambridge, England, is designed to determine the heat output under widely different conditions of temperature. It is not used for determining the exchange of matter.

The most familiar form of emission calorimeter, which compares the rate of heat production by different sources rather than measures directly the quantity of heat produced, is that of Rubner.[30] In this the changes in volume of the air enclosed between the double walls of the animal chamber constitutes the indicator. A very similar apparatus has been devised by Rosenthal [31] in which the pressure of the confined air at constant volume serves as the indicator. Another form of emission calorimeter is the so-called compensation calorimeter. In this instrument the heat produced by the subject is balanced against that produced, for example, by burning hydrogen or by an electrical resistance in an exactly similar chamber. Haldane, [32] Bohr,[33] and, more recently, Tangl [34] have described calorimeters of this type.

Direct calorimetry in the flow type of water calorimeter is considered to be an accurate method of experimentation but the observed results obtained must be corrected for a number of factors in order to get the true heat production.

By rendering the walls of the instrument adiabatic and by keeping the temperature of the ingoing and outcoming air currents the same, the heat produced is removed by the evaporation of the water vapor produced and by the current of water used in the heat absorbers. Two corrections must be applied to this latter, however. One is caused by a difference in the pressure exerted by the water upon the thermometers in the pipes carrying the ingoing and outcoming water. The pressure is greater upon the thermometer measuring the ingoing water temperature and so the difference in temperature is too small. A second correction is necessitated by the friction of the water in the absorbers.

[25] U. S. Department Agr., Office Expt. Stas., Bul. 63 (1899); Bul. 136 (1903).

[26] Carnegie Institution of Washington, Publication No. 42, Washington, 1905.

[27] U. S. Dept. Agr., Bur. Animal Industry, Bul. 51 (1903), and *Expt. Sta. Record,* 15 (1903-04), 1037.

[28] *Landw. Jahrb.,* 41 (1911), Erganzbd. I.

[29] *Jour. Agr. Science,* 11 (1921), 408.

[30] *Ztschr. Biol.,* 30 (1894), 91.

[31] *Arch. Physiol.,* 55 (1894), 223.

[32] *Jour. Physiol.,* 16 (1894), 123.

[33] *Skand. Arch. Physiol.,* 14 (1903), 398.

[34] *Biochem. Ztschr.,* 53 (1913), 21.

Corrections must also be made for the heat introduced into or removed from the apparatus by the feed, drink, excreta, and vessels containing them. In case the animal is a dairy cow producing milk, corrections must be made for the heat removed by the milk as well as for the heat produced by the milker during the milking of the animal.

The temperature of the walls of the chamber may vary and a correction should be applied for any differences noted. Again there is a lag due to the fact that while the thermometers in the water system are read simultaneously it really takes some time for the water to circulate through the system. Also the temperature of the absorber system may differ at the start and close of an experimental period and so a capacity correction is necessary.

It is generally assumed, at least in the use of the large respiration calorimeters for the large domestic animals, that the volumes of ingoing and outcoming air are the same, temperature, pressure and other conditions being equal. But this is not strictly true for the respiratory quotient of the animal is seldom unity and any deviation in this quotient will affect the total ventilation with a corresponding affect on the incoming gases. This is strikingly illustrated in the case of the ethyl alcohol used for check runs with the respiration calorimeter. Here the respiratory quotient is two-thirds and the neglect of this factor will lead to not inconsiderable errors.

Armsby[35] has summed up the whole matter of the accuracy of the respiration calorimeter with the statement that the results of a single experiment may be regarded as accurate to within approximately the following percentages of the total amounts determined.

Carbon dioxid	0.5 per cent
Water (in aspirator samples)	6.0 per cent
Heat	1.0 per cent

The Outgo of Heat. (b) Indirect Calorimetry. For many purposes the heat production may be computed with accuracy from the results of respiration experiments. When the carbon dioxide excreted and the oxygen consumed are determined, the respiratory quotient in carnivora or omnivora, together with a determination of the urinary nitrogen, affords pretty definite information as to the proportions of fats, carbohydrates and proteins catabolized, the quotient for fat being 0.7, for carbohydrates 1.0, and for protein about 0.8. From this it is easy to compute the calorific equivalent of a unit of carbon dioxide or of oxygen. As Fries[36] has

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[35] Pennsylvania State College, Agr. Expt. Station Bul. 104 (1910). For a fuller discussion of this question see U. S. Dept. of Agriculture, Bureau of Animal Industry, Bulletin 128 (1911), 297.

[36] *Amer. Jour. Physiol.,* **55** (1921), 53.

recently shown, this method is not directly applicable to herbivora, but Andersen[37] has devised an ingenious modification of the method by which it is possible to compute the heat production from the urinary nitrogen and the amounts of carbon dioxide and methane excreted and oxygen consumed while Armsby, Fries and Braman[38] have reported data on the calorific equivalent of the total carbon dioxide excretion of cattle which promise to be useful. Additional experiments have since been reported by Braman[39] who has derived a new set of equations from the combined data.

A second method of indirect calorimetry is based on the determination of the complete balance of matter and of energy contained in feed, feces, urine, and combustible gases. This is the method used by Kellner[40] in his early investigations upon the energy metabolism of cattle and numerous subsequent ones.

Armsby and his co-workers also have made much use of this method. A fuller discussion of this method is given earlier in this chapter under the section on metabolizable energy. This second method of indirect calorimetry is very accurate and certainly equals the accuracy of direct calorimetry.

The Conservation of Energy in the Body. The methods of indirect calorimetry assume that the law of the conservation of energy obtains in the animal body. If such is the case, the results of direct and indirect calorimetry should agree. Otherwise expressed, this means that the sole source of the "animal heat" is to be found in the catabolism of

TABLE 37

THE CONSERVATION OF ENERGY IN THE BODY

Experimenter	Total Number of Days	Total Computed Heat Production, Cals.	Total Observed Heat Production, Cals.	Percentage Difference
Rubner	45	17,406	17,350	−0.32
Laulanie	7	1,865	1,859	−0.31
Atwater and Benedict	93	249,063	248,930	−0.05
Benedict and Milner	24	95,075	95,689	+0.65
Benedict	53	102,078	101,336	−0.73
Armsby and Fries	114	976,204	980,234	+0.41
	336	1,441,691	1,445,398	+0.26

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[37] Kgl. Veterinaer—og Landbohøjskoles Laboratorium for landøkonomiske Forsøg, Copenhagen, Aarsskrift, 1920.

[38] *Proc. Nat'l. Acad. of Sci.*, 6 (1920), 263.

[39] *J. Biol. Chem.*, 60 (1924), 79.

[40] *Landw. Vers. Stat.*, 47 (1896), 275.

feed or of body substances. Lavoisier's classic experiment in 1780 on a guinea pig furnished an approximate proof of this, but Rubner[41] was the first to furnish a satisfactory demonstration of this fact by modern methods.

Subsequent investigators have abundantly confirmed Rubner's results. Table 37, compiled by Armsby in 1913, gives a summary of the results reported up to that date. Many additional experiments since that time have served to confirm further the conclusions then reached.

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[41] *Ztschr. Biol.,* 30 (1894), 73.

Chapter 6.

The Measurement of Nutritive Values.

Dual Function of Food. In discussing, in the concluding section of Chapter 4, the functions of the nutrients, it was pointed out that food serves a two-fold purpose. On the one hand it supplies energy for the maintenance of the vital activities and for the performance of work. On the other hand it furnishes the necessary materials for building up and maintaining the tissues and organs of the body and for the production of the various secretions required for its normal functioning. The nutritive value of any substance depends upon the amounts of energy and of the various forms of matter which it can supply for the service of the organism.

Energy Values.

Method of Determination. The value of any substance as a source of energy to the body is measured by its effect in producing a gain or preventing a loss of energy balance, either by means of direct or indirect calorimetry, by the methods outlined in Chapter 5. In case of animals the comparative slaughter test may also be used, but practically all the recorded results were obtained by calorimetric methods. With carnivora and omnivora, a comparison may be made with the fasting (or post-resorptive) state. With herbivora it is usually more convenient to make the comparison with a basal period on a minimum ration, to which, in a second period, the substance to be tested is added.

Influence of Food on Metabolism. It has already been seen that more or less of the energy of the food escapes from the body as chemical energy in the various excreta, leaving only the metabolizable energy as a possible source of supply to the body.

In addition a further loss of energy results from the fact that the consumption of the food stimulates metabolism, resulting in a greater output of gaseous products, a greater intake of oxygen and a corresponding increase in the output of energy in the form of heat. The fact has been known since the time of Lavoisier, having been fully established by the results of numerous subsequent investigations, notably those of

Magnus-Levy[1] in Zuntz's laboratory on dogs and on men, and those of Zuntz, Lehmann and Hagemann[2] on the horse, and its significance for the energy values of feeds has been clearly pointed out by Zuntz.

Rubner,[3] it is true, in his studies of the replacement values of nutrients and in the formulation of his law of "isodynamic replacement," assumed that with small amounts of food (maintenance or less) the stimulating effect upon the metabolism was negligible and this opinion gained general acceptance. Later, however, it was shown almost simultaneously by Rubner[4] himself and by Armsby and Fries[5] that unless the surrounding temperature is so low as to stimulate directly the animal's production of heat the effect of feed consumption is as manifest with small as with large amounts. The following was the average result of two experiments by Rubner in which lean meat was fed to a dog.

	Meat Fed per Day	Daily Heat Production per Kilogram Live Weight, Cals.
Fasting	0	51.50
Fed	274	70.55

The Specific Dynamic Action. Rubner designated this effect of feed consumption on heat production as the specific dynamic action of the feed. The effect is very marked in the case of the proteins, but much less with the carbohydrates and fats. It is by no means confined to carnivorous animals, but has been observed in various species including the herbivora and man. With the dog Lusk and his associates[6] have

TABLE 38

Percentage of Metabolizable Energy Available

Average Results for Dogs

	Rubner		Lusk	
	Increment of Heat Production %	Available for Maintenance %	Increment of Heat Production %	Available for Maintenance %
Body protein	31.9	68.1	...	...
Meat protein	30.9	69.1	36.0	64.0
Gelatin	28.0	72.0	...	...
Fat	12.7	87.3	1.2	98.9
Cane sugar	5.8	94.2	...	...
Dextrose	...	...	4.9	95.1

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[1] *Arch. Physiol.*, **55** (1894), 1.

[2] *Landw. Jahrb.*, **18** (1889), 1; **23** (1894), 125; **27** (1898), Erganzb. III.

[3] *Ztschr. Biol.*, **19** (1883), 313; **22** (1886), 45.

[4] "Die Gesetze des Energieverbrauchs bei der Ernährung," 1902.

[5] U. S. Dept. Agr., Bur. Animal Indus., Bul. 51 (1903), 60-62.

[6] *J. Biol. Chem.*, **12** (1912), 349; **13** (1912), 27, 155, 185; **20** (1915), 555. *Proc. Internat. Cong. Hygiene*, 1913; *Arch Inter. Medicine*, **12** (1913), 485. *Jour. Amer. Med. Assn.*, **63** (1914), 824. *J. Biol. Chem.*, **22** (1915), 15; **36** (1918), 415.

obtained results agreeing substantially with those of Rubner except as regards fat, when computed in the same way, although they regard his method of computation as erroneous. Rubner's and Lusk's averages are contained in Table 38. It should be clearly understood that these figures are not applicable to the "digestible nutrients" of the feed of herbivora.

The investigations of Kellner and of Armsby and Fries have demonstrated that the feed of cattle produces this effect in a very marked degree; thus the heat production of a steer consuming three different amounts of alfalfa hay was as shown in Table 39.

TABLE 39

HEAT PRODUCTION BY A STEER

Standard Day of 12 Hours Standing and 12 Hours Lying

	Dry Matter of Feed per Day Kgs.	Heat Produced per Day[1] Cals.
Period 1	6.638	11134
Period 3	5.320	9843
Period 5	3.052	7394

[1] All figures for energy values in the work of Armsby and his associates which appear in this monograph are, unless otherwise noted, revised figures calculated according to an improved method of computation reported by Max Kriss and shown in detail later in this chapter.

This increase in heat production seems to result from a variety of causes. One factor is the mechanical work involved in the mastication of the feed and in moving it through the alimentary canal. With animals consuming comparatively concentrated forms of food, this factor is apparently a small one. With herbivora supported on bulky feeds it is doubtless much more considerable. In these animals, especially in ruminants, the fermentations in the first stomach and in the lower intestines are the source of a very considerable heat production, estimated by von der Heide, Klein and Zuntz[7] from rather unsatisfactory data at 7.07 cals. per gram of methane. A third factor is the direct stimulation of metabolism by the absorbed digestive products. This is particularly true of the proteins as has been shown by Lusk and his associates, the hydroxy-acids resulting from the catabolism of the proteins (Chapter 4) acting as direct stimuli to the catabolism of non-nitrogenous matter in the body cells. The much smaller effect produced by carbohydrates and fats is, according to the same authority, virtually a case of mass action, the greater supply displacing the point of equilibrium of the reactions in the direction of a greater oxidation.

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[7] *Landw. Jahrb.*, 44 (1913), 795.

Net Energy Values. Obviously that portion of the gross energy of the feed remaining after deducting the losses of unused chemical energy in the feces, urine, and combustible gases, and also the heat resulting from the specific dynamic action of the feed, is the measure of its value as a source of energy to the animal. If the feed has been added to a ration already sufficient to maintain the animal, this energy is retained in the increase of body tissue or in the organic matter of the milk produced. If the feed is given to a fasting or insufficiently fed animal, the loss of body tissue which would otherwise occur is reduced by an equivalent amount and a corresponding food value is conserved, *i.e.,* the animal is prevented, to that extent, from consuming a portion of its own flesh and fat.

This residue of feed energy after deducting the two classes of losses just indicated is called the net energy value because it shows the net result as to the storage or conservation of food energy which may be obtained by its use. The conception of the net energy value has been chiefly used in connection with the feeding of livestock and the methods by which it is determined are illustrated in the following paragraphs.

Summary of the Net Energy Conception. Before discussing the details that follow in this chapter it will be necessary to present a concise and clear statement of what is understood by gross, metabolizable, and net energy.

The gross energy of a feed is measured by the heat of combustion.

When feeds are fed to animals part of this gross energy is lost via the feces in undigested food residues, metabolic products and similar material. Part is lost via the urine in incompletely oxidized organic matter. Part is lost in the excreta of the skin or epidermis and part is lost as combustible gases such as methane.

The metabolizable energy of a feed is the gross energy minus the losses in the various excreta.

When an animal consumes feed it performs some mechanical work in prehension, mastication, peristalsis, regurgitation, and evacuation. Glandular activities are set in motion which may consume energy. Fermentations are set up in the digestive tract which cause a loss of energy. There is a direct stimulus to metabolism due to the presence of nutrients in the fluids of the animal body. There may be losses of energy during the intermediary metabolism although most of the processes here are isothermic involving no energy exchange. All of these factors result in an increased production of heat or a heat increment. The chief factor is the direct stimulus to metabolism. Rubner's "specific dynamic action," Kellner's "thermal energy," and Armsby's "heat increment" all refer to the sum of the losses detailed in this paragraph.

The net energy of a feed is the metabolizable energy minus the heat increament or energy expenditure due to the consumption of food. Or, the net energy of a feed is the gross energy minus the energy losses in the various excreta as well as the losses in energy in the form of heat incident to and resulting from the consumption of feed.

This conception of metabolizable and net energy measures the energy resulting from fermentation of feed in the digestive tract as part of the heat increment or energy expenditure due to the consumption of food. Fries, Braman and Cochrane[8] point out that this energy loss of fermentation is an excretion and consequently should be added to the energy of the excreta in determining the metabolizable energy. This decreases the absolute value of the metabolizable energy and decreases its percentage of the gross energy. Since the metabolizable energy is smaller the net energy becomes a relatively larger percentage of the metabolizable. This change simply alters the line of demarcation between metabolizable and net energy and does not affect the absolute value of the net energy. Its relation to the gross energy is unaltered.

The following figures will serve to show the extent of the change brought about by this altered method of computation. The ration was alfalfa hay and mixed grain.

METABOLIZABLE ENERGY IN PER CENT OF GROSS ENERGY

	Usual Method %	New Method %
Cow 631	53.43	43.18
Cow 615	54.85	45.29
Cow 579	56.38	46.36

NET ENERGY IN PER CENT OF METABOLIZABLE ENERGY

	Usual Method %	New Method %
Cow 631	69.87[1]	89.99[1]
Cow 615	67.72	81.77
Cow 579	69.31	83.78

[1] Owing to methods of calculation employed with the data for this cow these figures may not be used in determining the net energy in per cent of the gross.

In order to show that the ratio of net energy to gross energy is unaffected by the new method of calculation it can be seen that

$$54.85 \times 67.72 = 37.04 \text{ old method}$$

$$\text{and } 45.29 \times 81.77 = 37.03 \text{ new method.}$$

In either case the net energy is 37.04 per cent of the gross energy.

This new method of treating the heat of fermentation involves the validity of the statement that the energy loss of fermentation should be

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[8] U. S. Dept. of Agriculture, Bul. 1281 (1924).

counted as belonging to the excreta. This seems logical and the new method may come into common use. However, the figures following in this monograph are based upon the older method of computation. In either case, as has been pointed out just above, the value of the net energy is not affected and its relation to the gross energy does not change.

The Method of Computation.

Before entering into a discussion of the net energy values of stock feeds it is necessary to deal with the method of computation to be employed in deriving the results of Armsby and his co-workers. Three methods of computation have been used. All are based upon the same fundamental conception and represent successively improvements in conception and understanding of detail.

The oldest method, reported by Armsby and Fries,[9] involves the comparison of two periods in which different amounts of the feeding stuff under investigation are fed. The gain of energy is determined for each period by subtracting the heat production from the metabolizable energy. The difference in gain between the two periods divided by the difference in feed eaten represents the net energy per unit of feed. If, however, the metabolizable energy per kilogram of dry matter of the feed should be different in the two periods compared the end result would be greatly affected by this fact. It would also be affected by the direction of this difference, *i.e.*, by whether the determined metabolizable energy value is greater in the heavier or the lighter of the two rations. Small differences in metabolizable energy make large differences in the net energy depending upon the relative direction of the difference. It is possible, as Kriss[10] has recently shown, to get absurd results by this method. In publications following Bulletin 128, Armsby and Fries[11] used an improved method which involved averaging the metabolizable energy values from several periods and subtracting from this average the average heat increment of the feed. This latter was usually determined by a comparison of the greatest and least amounts of feed eaten. The average value thus obtained sometimes is derived from quite discordant results and there is no way of detecting and discarding those discordant results.

The new modification reported by Kriss[12] makes possible the compu-

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[9] U. S. Dept. of Agri., Bur. Animal Industry, Bul. 128 (1911). Also Buls. 51, 74, and 101.

[10] "An Improved Method of Computation of the Net Energy Values of Feeding Stuffs," *Jour. Agr. Research,* 1925 (in press).

[11] *Jour. Agr. Research,* **3** (1915), 435-491; **7** (1916), 379-387; **10** (1917), 599-613; **15** (1918), 269-286.

[12] *Loc. cit.*

tation of a net energy value of the feed for each period separately, the computation of the net energy required for maintenance, and in addition makes it possible to detect some abnormal periods which may with propriety be omitted from the final average. As a result certain magnifications of experimental errors are prevented.

A complete computation by the new method is given in Tables 40a to 40f inclusive. Table 40a gives the general data and Table 40b shows the calculation of the heat increment of the hay. In a somewhat similar manner the heat increment of the grain mixture is calculated correcting for the slight differences in hay consumption between the periods compared. Table 40c gives the results for the hay and the grain.

From the weights of hay and grain given in Table 40a and the heat increments of Table 40c the heat increments of Table 40d are derived. Thus: in Period II 2.7743 kilograms of timothy and 2.6769 kilograms of grain mixture were consumed. Multiplying 2.7743 by 848 gives 2353 Calories, heat increment due to the hay. Multiplying 2.6769 by 1361 gives 3643 Calories, heat increment due to the grain. The sum is 5996 Calories total heat increment. In this same period the total heat production was 11532 Calories. The difference in heat production between the total heat increment of the food and the total heat produced plainly came from the animal. It therefore represents the maintenance cost of the animal. This difference is 5536 Calories. Similarly the calculations are carried out for the other periods yielding but one figure for the hay since the results of both periods have been used in obtaining the heat increment to be applied. The average maintenance cost of the steer was, then, 5457 Calories.

Table 40e gives the computation of the net energy in the hay. In Period III the dry matter eaten and the metabolizable energy of the feed are brought forward from Table 40a. The maintenance value is the average just derived. On this ration the animal lost 2238 Calories. The difference between this 2238 Calories and the net energy for maintenance, or 3219 Calories, is the net energy supplied from the feed. In other words the net energy for maintenance was supplied by the body (2238 net Calories) and from the feed (3219 net Calories) the total being 5457 net Calories. This 3219 net Calories was supplied by 2.7983 kilograms of dry matter in the hay. The net energy per kilogram of dry matter is then 1150 Calories or 1.150 therms. The net energy of the hay consumed in this period (3219 Calories) is 56.60 per cent of the metabolizable energy (5687 Calories).

The computation of the net energy of the grain is shown in Table 40f and follows the same general principal.

TABLE 40-A

Data for Computation of Net Energy Values of Timothy Hay and of Grain Mixture No. 1

(Experiment 207, Steer B)

Period	Animal	Average Live Weight Kgs.	Dry Matter Eaten		Metabolizable Energy			Heat Production[1] Cals.	Gain Cals.
			Timothy Hay Kgs.	Grain Mixture No. 1 Kgs.	Hay Cals.	Grain Cals.	Total Cals.		
I	B		2.7608	1.3978	5621	3822	9443	9527	— 84
II	"		2.7743	2.6769	5648	8373	14021	11532	+ 2489
III	"	380	2.7983		5687		5687	7925	— 2238
IV	"		4.6299		9446		9446	9478	— 32

[1] The heat production in this example has been corrected to a standard day of 12 hours standing and 12 hours lying according to the method of Fries and Kriss. See "Metabolism of Cattle During Standing and Lying," *Amer. J. of Physiol.*, 71 (1924-5), 60.

Other experiments recalculated by Kriss according to this new method bear evidence to its greater accuracy and usefulness. Unless otherwise noted all figures in this monograph for the net energy of feeds reported by Armsby and his associates are those recalculated by Kriss employing the new method.

TABLE 40-B

Computation of Heat Increment per Kilogram of Timothy Hay

	Quantity of Dry Matter Eaten Kgs.	Heat Production Cals.
Period IV	4.6299	9478
Period III	2.7983	7925
Difference	1.8316	1553
Difference per kg. of dry matter..		848

TABLE 40-C

Heat Increment per Kilogram of Dry Matter

Feeding Stuff	Periods Compared	Heat Increment per Kg. of Dry Matter Cals.
Timothy hay	III and IV	848
Grain mixture No. 1 computed[3]	I and III	1169[1]
	II and I	1559
	II and III	1355[2]
	Average for grain	1361

[1] The same value will be obtained by comparing periods I and IV.
[2] The same value will be obtained by comparing periods II and IV.
[3] Some few details employed in deriving the heat increment of the grain mixture are omitted. For a full presentation of these details see the longer publication of Kriss.

TABLE 40-D

Computation of Maintenance Requirement

(Experiment 207, Steer B)

Period No.	Heat Increment Due to Hay Cals.	Heat Increment Due to Grain Cals.	Total Cals.	Total Heat Production Cals	Net Energy for Maintenance Cals.
I	2341	1902	4243	9527	5284
II	2353	3643	5996	11532	5536
III	2373		2373	7925	5552
IV	3926		3926	9478	
Average					5457

TABLE 40-E

COMPUTATION OF NET ENERGY VALUES OF TIMOTHY HAY

Period No.	Dry Matter of Hay Eaten, Kgs.	Metabolizable Energy of Hay, Cals.	Net Energy for Maintenance, Cals.	Gain, Cals.	Total Net Energy of Ration, Cals.	Net Energy per Kg. of Dry Matter, Cals.	Percentage Utilization of Metabolizable, Per Cent
III	2.7983	5687	5457	—2238	3219	1150	56.60
IV	4.6299	9446	5457	— 32	5425	1172	57.43
Average						1161	57.02

TABLE 40-F

COMPUTATION OF NET ENERGY VALUES OF GRAIN MIXTURE NO. 1

Period No.	Dry Matter of Hay Eaten Kgs.	Metabolizable Energy of Grain, Cals.	Total Net Energy of Ration, Cals.	Net Energy Equivalent of Hay, Cals.	Net Energy of Grain, Cals.	Net Energy per Kg. of Dry Matter of Grain, Cals.	Percentage Utilization of Metabolizable, Per Cent
I	1.3978	3822	5373	3205	2168	1551	56.72
II	2.6769	8373	7946	3221	4725	1765	56.43
Average						1658	56.58

Net Energy Values of Stock Feeds.

Determination. In one of an extensive series of experiments on fattening cattle reported by Kellner,[13] meadow hay was added to a basal ration which sufficed to produce a small gain by an ox. The results of the two periods, computed in a slightly different manner than that used by the author, are shown in Table 41, the heat produced being determined by indirect calorimetry:

TABLE 41

NET ENERGY VALUE OF MEADOW HAY FOR FATTENING CATTLE

	Dry Matter of Added Hay, Kgs.	Metabolizable Energy of Ration, Therms.[1]	Heat Production, Therms.	Energy Retained by Animal Therms.
Augmented ration	3.071	23.14	18.90	4.24
Basal ration		17.64	15.62	2.02
Difference	3.071	5.50	3.28	2.22
Difference per kg. dry matter..		1.791	1.068	0.723

[1] A therm. is 1000 large calories.

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[13] *Landw. Vers. Stat.,* **53** (1900), 1-474.

The net energy of one kilogram of dry matter of the hay was, in this case, 0.723 T., this being its net effect in producing increase.

A similar trial by Armsby and Fries[14] with a steer receiving a submaintenance ration of timothy hay gave the results in Table 40e, the heat being determined directly. The net energy per kilogram of dry matter in this timothy hay was 1.161 therms.

The results recorded in the two preceding tables may also be expressed, like those of Rubner and Lusk on the dog, in terms of the percentage of metabolizable energy of the feed which was available for the maintenance or increase of the animal, as shown in Table 42.

TABLE 42

PERCENTAGE UTILIZATION OF METABOLIZABLE ENERGY

	Metabolizable Energy of Added Feed, Therms.	Energy Utilized by Animal, Therms.	Percentage Utilization, Per Cent
Meadow hay—fattening.......	5.500	2.220	40.4
Timothy hay—maintenance....	5.687	3.219	56.6
	9.446	5.425	57.4

Net Energy Values for Different Purposes. Not only do the losses of energy in the excreta, especially the feces, differ in different species of animals, but the increased metabolism consequent on feed consumption—the so-called specific dynamic action—is evidently the result of numerous factors each of which may be expected to vary in amount as between different feeds, different species of animals and different forms of production. While the evaluation of these separate factors is a matter of much physiological interest, from the economic point of view it is their aggregate effect, as expressed by the net energy value, which is of prime importance. This, it should be clear, is not a constant for each feeding stuff but must differ according to the species of animal by which the substance is eaten and perhaps according to the sort of production which it supports.

Values for Fattening. Beef. Somewhat numerous determinations of the net energy values of feeding stuffs for mature or nearly mature beef cattle have been made by Kellner and his associates[15] and by Armsby and Fries.[16] Kellner's experiments were exclusively on mature fattening cattle, the one on meadow hay cited on p. 143 being typical. Armsby and

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[14] U. S. Dept. of Agr., Bur. Anim. Indus., Bul. 128 (1911), 177, 184.

[15] *Loc. cit.* and "Ernährung landw. Nutztiere," 6th Ed., pp. 159-169.

[16] *Jour. Agr. Res.*, 3 (1915), 435; 7 (1916), 379; 10 (1917), 599; 11 (1917), 451; 13 (1918), 43; 15 (1918), 269.

Fries' experiments included both determinations on fattening cattle, substantially like Kellner's, and also trials with submaintenance rations, as illustrated by the experiment on timothy hay cited on p. 144. Kellner employed the methods of indirect calorimetry while Armsby and Fries determined the heat production of their animals directly. The results of the two series of investigations have been summarized by Armsby.[17]

TABLE 43

NET ENERGY VALUES OF FEEDING STUFFS FOR CATTLE
CALORIES PER KILOGRAM OF DRY MATTER

Roughage	Experimenters	Gross Energy, Cals.	Losses of Chemical Energy in Excreta, Cals.	Metabolizable Energy, Cals.	Energy Expended Feed in Consumption, Cals.	Net Energy Values, Cals.
Timothy hay	A & F	4536	2529	2007	788	1218
Red clover hay	A & F	4403	2457	1946	978	968
Red clover hay	K & K	....	....	1743[1]	932	811
Mixed hay	A & F	4393	2479	1914	970	944
Alfalfa hay[2]	A & F	4354	2400	1954	1039	915
"Grass hay"	K & K	....	....	1848[1]	1045	803
Meadow hay	K & K	4433	2260	2173	1254	919
Rowen	K & K	....	....	1705[1]	958	747
Corn stover	A & F	4332	2380	1952	1295	657
Barley straw	K & K	....	....	1624[1]	877	747
Oat straw	K & K	4436	2848	1588	1014	574
Wheat straw	K & K	4444	3062	1382	1138	244
Straw pulp	K & K	4147	1013	3134	1160	1974
Concentrates						
Corn meal	A & F	4485	1211	3274	1223	2049
Hominy chop	A & F	4709	1190	3519	1046	2473
Grain mixture No. 1[3]	A & F	4673	1707	2966	1272	1694
Grain mixture No. 2[4]	A & F	4613	1594	3019	1082	1937
Cottonseed meal	K & K	....	....	2847[1]	978	1869
Linseed meal	K & K	....	....	3036[1]	1208	1828
Palmnut meal	K & K	....	....	2746[1]	1007	1739
Peanut meal	K & K	....	....	2957[1]	1159	1798
Beet molasses	K & K	3743	945	2798	988	1810
Starch	K & K	4152	1101	3051	1248	1803
Peanut oil	K & K	9458	4166	5292	1727	3565
Wheat gluten	K & K	5580	1975	3605	2096	1509

[1] Estimated from digestible organic matter.

[2] Includes alfalfa meal.

[3] No. 1 wheat bran, 14.28 per cent; corn meal, 42.86 per cent; old process linseed meal, 42.86 per cent.

[4] No. 2 corn meal, 60 per cent; crushed oats, 30 per cent; old process linseed meal, 10 per cent.

Table 43 summarizes these results. The letters A and F signify Armsby and Fries while K and K indicate that the results are those of Kellner and Köhler.

The animals used were more or less mature and consequently the net

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[17] **Penn. Agr. Expt. Sta., Bul. 142 (1916), 10-13.**

energy values found represent those for the fattening process accompanied by some gains in protoplasmic tissue. These latter may be small and in some cases are negligible.

There is a striking difference between the proportion of total energy in roughage available to the animal and that in concentrates. With the former a much larger proportion is rejected unused in the excreta. The energy expenditure in digestion and as a result of the specific dynamic action of the nutrients is much alike in both classes of feeds. The result is that the concentrates furnish a larger proportion of net energy as well as a greater quantity of net energy per unit of dry weight.

Pork. A few determinations by means of indirect calorimetry of the net energy of feeding stuffs and of single nutrients for swine have also been reported by Meissl, Strohmer and Lorenz,[18] Kornauth and Arche,[19] von der Heide and Klein,[20] Fingerling, Köhler and Reinhardt [21] and

TABLE 44

NET ENERGY VALUES OF FEEDING STUFFS FOR SWINE

Calories per Kilogram Dry Matter

	Experimenters	Gross Energy	Loss of Chemical Energy in Excreta	Metabolizable Energy	Increment of Heat Production	Net Energy Values
Grains		Cals.	Cals.	Cals.	Cals.	Cals.
Rice	Meissl, *et al.*	....	....	4308	809	3499
Barley	Meissl, *et al.*	....	....	3340	653	2687
Barley	Fingerling, *et al.*	4561	906	3655	998	2657
Dried potatoes	V. d. Heide and Klein	....	....	3331	1098	2233
Flesh meal	Fingerling, *et al.*	6230	981	5249	1056	4193
Mixed Rations						
Rice, flesh meal and whey	Meissl, *et al.*	....	....	4204	906	3298
Cockle, barley and maize	Kornauth and Arche	....	....	3587	538	3049
Rape cake, barley and maize	Kornauth and Arche	....	....	3684	615	3069
Skim milk and flour [1]	Wellmann	....	....	4318	1342	2976
Single Nutrients						
Starch	Fingerling, *et al.*	4063	29	4034	703	3331
Cane sugar	Fingerling, *et al.*	3776	112	3664	1041	2623
Straw pulp	Fingerling, *et al.*	3843	479	3364	1336	2028
Wheat gluten	Fingerling, *et al.*	5503	1006	4497	1139	3358
Peanut oil	Fingerling, *et al.*	9105	— 88	9193	668	8525
Palm oil	V. d. Heide and Klein	....	....	9273	2335	6938

[1] Omitting one very restless animal.

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[18] *Ztschr. Biol.*, 22 (1886), 63.

[19] *Landw. Vers. Stat.*, 40 (1892), 177.

[20] *Biochem. Ztschr.*, 55 (1913), 195.

[21] *Landw. Vers. Stat.*, 84 (1914), 149.

Wellman.[22] The results as compiled by Armsby [23] show rather wide variations and further investigations upon the efficiency of this economically important meat producing animal are greatly to be desired. The data now available make it clear that the hog can secure a larger proportion of the metabolizable energy of concentrates in the form of net energy than can the ruminant. Table 44 gives the values for swine.

Mutton. No determination of net energy values of feeding stuffs for sheep have yet been reported. From the results of some early respiration experiments reported by Henneberg [24] values for certain protein feeds may be computed by a somewhat questionable method, the results being notably lower than some of Kellner's. For the present, therefore, it seems advisable to use, in the case of sheep, the values computed from the results on cattle.

The results obtained in experiments on the working horse lie outside the scope of this work.

Net Energy Values for Growth. Recorded Experiments Relating Chiefly to Fattening. In the production of meat, fattening is substantially a finishing process by which the quality of the product is improved and its market value increased. The actual production of meat, however, is accomplished by the processes of growth and it therefore becomes important to inquire as to the relative efficiency of these processes in the recovery of feed energy.

The relatively rapid increase of the young animal is a matter of common knowledge. In part it is explained by the watery nature of the increase and the small proportion of fat which it contains. Nevertheless determinations of the actual gain of dry matter show that in proportion to the live weight the rate of storage of protein and of energy is high in the young animal and decreases, at first rapidly and later more slowly, as it grows older. This has led to the belief that the young animal is more efficient than the older ones as a converter of energy in the sense here under discussion, but such scanty experimental evidence as is available fails to confirm that impression. That the young animal may be a more efficient converter of gross energy is shown in Chapter 10.

Age of Animal Important Factor. Experiments on suckling calves and pigs by Soxhlet [25] and by Wilson [26] and on infants by Rubner and Heubner [27] indicate a rather lower utilization of the energy of milk by

[22] *Landw. Jahrb.*, 46 (1914), 499.
[23] "Nutrition of Farm Animals," 662.
[24] *Jour. Landw.*, 38 (1890), 15.
[25] *Erster Ber. Versuchs. Station, Wien.* 101-155.
[26] *American Jour. Physiol.*, 8 (1903), 187.
[27] *Ztschr. Biol.*, 36 (1898), 1; 38 (1899), 315.

young than by mature animals. An explanation that may be of equal value is that the younger animals had a much greater maintenance cost than was assumed in the calculations. Numerous investigations on embryonic growth, especially those of Tangl and his associates[28] and of Bohr and Hasselbach,[29] of Murlin[30] and of Carpenter and Murlin[31] show a lower recovery of energy by the embryo than that from milk by suckling animals and lower in the earlier than in the later stages of incubation. A fuller discussion of this point is given by Armsby[32] elsewhere but it should be borne in mind that the maintenance cost of the embryos was not considered. Comparative slaughter tests by Kern and Wattenberg[33] on lambs and by Tschirwinsky[34] on pigs, and calorimetric experiments by Armsby and Fries[35] on young cattle likewise indicated a somewhat decreased efficiency of recovery by the younger animals.

All these results indicating a lower efficiency of recovery of energy during growth are not very satisfactory. It appears that the young growing animal may show a smaller net energy recovery than a more mature animal and that the embryo may show still less. If this is true it may be plausible to ascribe this lower recovery of energy to the expenditure of energy in the organization of new tissue out of the materials of the egg or of the feed. As the animal grows older this expenditure constitutes a diminishing proportion of the total energy expended by the organism. Probably by the time an animal has been weaned and is consuming the normal feed of its species the percentage recovery of energy may be estimated to be not much less than that in a mature animal. The calorimeter experiments with cattle noted above confirm this latter conclusion, namely, that the percentage recovery of energy after weaning is the same as that found with mature animals. The results of Moulton with growing and fattening beef cattle (Chapter 10) gives additional evidence that this is true.

Net Energy Values for Milk Production. The second great branch of animal husbandry is milk production, dairy products contributing to the average American dietary according to Pearl[36] 70 per cent as much energy and 77 per cent as much protein as meats. Nevertheless, exact

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[28] *Arch. ges. Physiol.,* 93 (1903), 327; 98 (1903), 490; 104 (1904), 624; 121 (1908), 423 and 427.

[29] *Skand. Arch. Physiol.,* 10 (1900), 149, 153 and 413; 14 (1903), 398; 15 (1904), 23.

[30] *Amer. Jour. Physiol.,* 26 (1910), 134.

[31] *Arch. Inter. Med.,* 7 (1911), 184.

[32] "Nutrition of Farm Animals," New York, 1917, p. 393.

[33] *Jour. Landw.,* 28 (1880), 289.

[34] *Landw. Vers. Stat.,* 29 (1883), 317.

[35] U. S. Dept. Agr., Bur. Anim. Indus., Bul. 128 (1911), 51.

[36] "The Nation's Food," Philadelphia and London, 1920.

scientific data regarding the efficiency of the dairy cow as a converter of energy are scanty. While it is a relatively simple matter to compare the energy of milk with that of the feed, the dairy cow may carry on two forms of production simultaneously, *i.e.*, while producing milk she may also be laying on body tissue either on her own body or that of her calf if she is pregnant, while, on the other hand, she may be drawing on her protein, fat, and mineral reserves to help support her milk production. Only by the use of a respiration apparatus or calorimeter, however, is it possible to follow such body changes, and even then the interpretation of the results is not always easy, while the susceptibility of the good dairy cow to external conditions, as well as the natural shrinkage of milk yield with advancing lactation, add difficulties of their own.

The earliest results of respiration experiments on dairy cows recorded are those contained in a brief preliminary paper by Kellner [37] giving the nitrogen, carbon, and energy balances (determined by indirect calorimetry) of three cows receiving mixed rations and differing considerably in milk yield. After deducting from the metabolizable energy of the rations the estimated maintenance requirements of the animals and also the estimated amounts required to produce the small gains of body fat and proteins which were observed, it was computed that of the remaining metabolizable energy the following percentgaes were recovered in the milk as compared with the percentages recoverable in meat production.

TABLE 45

PERCENTAGE RECOVERY OF METABOLIZABLE ENERGY IN MILK AND MEAT PRODUCTION

	Cow A	Cow C	Cow E
Recovery in Milk	68.4%	72.8%	66.9%
Recovery in Meat	48.0%	46.0%	43.8%

Experiments by Jordan [38] and by Eckles,[39] which included partial energy balances but in which the heat production was not determined, afford similar high figures for the percentage utilization in milk production on the assumption that the slight variations in live weight which were observed did not represent any significant gain of body fat or proteins. Haecker [40] from the somewhat less complete data of his extensive experiments on the dairy herd of the Minnesota Station has computed somewhat lower values for the percentage utilization. The average results of these investigations were as shown in Table 46.

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[37] 5ter Internat. Kongress für Milchwirtschaft, 1911.

[38] N. Y. (Geneva) Agr. Expt. Sta., Bul. 197 (1901), 24-32 and 20th Rpt. (1901), 29.

[39] Mo. Agr. Expt. Sta., Research Bul. 7 (1913).

[40] Minn. Agr. Expt. Sta., Bul. 140 (1914), 45.

TABLE 46

ESTIMATED PERCENTAGE RECOVERY OF METABOLIZABLE ENERGY IN MILK PRODUCTION

	Maximum	Minimum	Mean
Jordan Cow 10	...	...	49.2
Jordan Cow 12	64.0	56.9	60.7
Eckles	72.8	50.4	61.9
Haecker	66.2	50.3	54.7

Eckles also calls attention to the fact that, with one exception, the actual energy content of the milk in his experiment was greater than the amount available in the ration for meat production as computed by the use of Kellner's factors.

However, one of the two cows used by Jordan failed to give a high recovery, and the value of the other evidence may be vitiated by false assumptions concerning maintenance costs. The maintenance cost of the nervous dairy type of animal may well be considerably above that usually assumed, largely from work on beef cattle.

The average availability of the metabolizable energy of mixed rations for steers is about 55 per cent. Haecker's results, the most extensive on milk production of all those cited, are essentially the same. The average of the results with Jordan's two cows is likewise about 55 per cent. Kellner's data are based on assumptions concerning the maintenance cost which may well be wrong.

The net energy value of feeds may be greater for milk production than it is for fattening or for flesh production. That any such difference cannot be explained on the basis of a greater loss in producing fat from non-fatty ingredients of the feed than in producing protein is indicated by the results of Moulton [41] on beef cattle. If the production of fat under such circumstances involved a loss of energy one would expect a greater loss in cattle highly fattened than in those moderately fattened. On the contrary the results on beef cattle have shown that the moderately fattened ox recovered in its gains 53.4 per cent of the metabolizable energy in its feed while the highly fattened ox recovered 52.5 per cent. The same ration was shown to have 55 per cent of its metabolizable energy in the form of net energy by the respiration calorimeter method where the animal was not producing any appreciable flesh.

The direct determination of net energy for milk production by means of the respiration calorimeter has been attempted by the Institute of Animal Nutrition. Møllgaard has pointed out that this direct determination is not possible of accomplishment and has devised and used a method of determining the ratio of net energy for milk production to that for

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[41] *J. Biol. Chemistry,* 31 (1917), 389.

body increase. This work is given in some detail in Chapter 9 to which the reader may turn for reference.

Maintenance and Production Values. When the feed consumed is used solely to prevent loss of body tissue, *i.e.,* for maintenance, it may be supposed that the substances absorbed from the digestive tract, notably the carbohydrates and the organic acids, are oxidized somewhat directly to supply the necessary energy. In the producing animal, on the contrary, a portion of the absorbed substances is synthesized to more complex compounds, especially fat. It is natural to suppose that such a synthesis may be accompanied by a dissipation of energy. If this be true, the net energy values for fattening would necessarily be less than those for maintenance.

No decisive results on this point are on record. Kellner's experiments were all made on mature fattening animals and he specifically calls his results production values. Armsby and Fries' experiments afford comparisons of sub-maintenance and super-maintenance rations of the same feeding stuffs. The individual results are, however, unfortunately quite variable but a consideration of them as a whole [42] fails to indicate any greater evolution of heat per unit of feed on supermaintenance than on submaintenance rations. This would tend to indicate that the formation of fat in the body is nearly or quite an isothermic reaction and that the net energy values of feeding stuffs are approximately the same for maintenance and for fattening. The work of Moulton just cited confirms this statement. No comparisons for other species or for other forms of production are available.

Influence of Amount of Feed. The method of determining the net energy value either above or below maintenance which has been illustrated on preceding pages assumes it to be constant per unit of feed consumed, or, in other words, that the loss of energy in the excreta and in the increased heat production is a linear function of the amount of feed consumed. This seems not to accord with the general belief that heavy rations are relatively less effective than lighter ones and that the fat animal utilizes its feed less efficiently than the thin one. A variety of factors may take part in producing the result attested to by this experience. The animal may digest less of the food, especially the grain, when heavily fed due to a mechanical removal of part of this grain from the scene of digestion before the digestive processes have had time to function. A second factor may be that the full-fed animals may have a greater maintenance cost both actually per unit of surface area and relatively in proportion to the consumption of food.

On the other hand fermentation on lighter rations is proportionally

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[42] *Jour. Agr. Research,* 3 (1915), 472-476.

greater and a greater loss of heat resulting here may counter-balance the loss due to lack of digestion. Again, there seems to be little if any convincing evidence that a unit of metabolizable energy yields less product at one time than at another or in fat production than in the production of normal growth. Armsby has discussed this in greater detail elsewhere[43] and it seems unnecessary to take it up in detail here. The conclusion reached was as follows:

> "On the whole the probabilities seem to be that the limit to the most efficient use of feed energy, in herbivora at least, is set by the capacity of the alimentary canal to digest and assimilate feed rather than by the capacity of the organism to utilize the material transmitted to it by the organs of resorption. If this proves to be the case, the net energy values may be regarded as being, if not strictly constant, at least nearly so over a wide range of feeding."

This method of computation has been questioned by Benedict and Ritzman,[44] who have reported some very interesting results of a study of undernutrition on metabolism. A calculation of the heat production from the carbon dioxide output gave a value for the "standard metabolism" some 33 per cent above the basal metabolism of Armsby. This standard metabolism is the heat production observed with cattle 24 hours after the last feed and computed for 24 hours' standing. Therefore part of this 33 per cent increase may be due to the after effects of digestion since the digestive tract of cattle will be far from empty 24 hours after the last feed. More prolonged fasting (53 hours) reduced this "standard metabolism" about 10 per cent and in only one case was a greater reduction obtained (20 per cent).

These authors report unpublished work by Armsby showing that after the first 72 hours of fasting the amount of methane produced is very small and remains constant until 144 hours, beyond which his experiments did not extend. From the carbon dioxide and heat production of the cows used by Armsby and similar results with Benedict's steers, the latter shows that his figure for "standard metabolism" can be but 12 per cent too high.

This method of computing the basal metabolism may be defective, but further evidence on this point is desirable. Experiments now in progress at Durham, New Hampshire, and unpublished results at the Institute of Animal Nutrition at State Collage, Pennsylvania, will throw further light on this question. In the meantime, it should be borne in mind that the assumption of a linear relation between feed consumption

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[43] "The Nutrition of Farm Animals," 664.

[44] "Undernutrition in Steers," Publication 324, Carnegie Institution of Washington, Washington, 1923, 253.

and energy production seems logical and yields results for the basal metabolism of cattle which compare well per unit of surface area with that of other species.

Breeding and Individuality. The existence of striking differences between individuals of the same species in regard to the economic utilization of feed is a commonplace of live stock husbandry. In the various important breeds of farm animals this capacity has been developed by skillful breeding and selection and the heredity thus more or less firmly established is a most significant factor in profitable production, often making the difference between profit and loss.

Numerous factors go to make up this difference but, contrary to a somewhat general belief, there is no good evidence that the efficiency of conversion in the restricted sense here considered is one of them. While individual differences in digestive power have been frequently observed, they are usually too small to be of significance while there is no evidence that the improved breeds have any special superiority in this respect as regards the percentage utilization of metabolizable energy. Experiments with the respiration calorimeter by Armsby and Fries[45] on a pure bred and a scrub steer, extending over three years, seemed to show a slight superiority for the former, especially in the first two years, but with a considerable range of possible error. However, the experiments of the first two years are not satisfactory. The third year experiment hardly shows any superiority of the pure bred over the scrub steer in utilizing feed energy, the latter showing a slightly better utilization of timothy hay and the former showing a somewhat better utilization of the grain mixture employed.

Similarly Kellner's extensive respiration experiments already referred to include a number of different animals and the results show a generally good agreement as regards the utilization of the energy of the feed although it does not appear whether or not the animals differed materially in type.

A considerable number of breed tests of cattle, sheep and swine made by the American Experiment Stations and summarized by Henry and Morrison[46] failed to indicate any marked superiority of one breed over another as regards the quantity of feed consumed per unit of gain.

Condition. It is a well-established fact that fattening animals make an increasingly expensive gain as their weight increases. This, however, according to a single comparison by Armsby and Fries[47] on a steer in good condition and on the same animal after being well fattened does not

[45] U. S. Dept. Agr., Bur. Anim. Indus., Bul. 128 (1911), 39-53.

[46] "Feeds and Feeding," Madison, Wisconsin, 1917, 391, 440, 509, and 582.

[47] *Jour. Agr. Research,* 11 (1917), 451.

appear to be due to any material difference in the percentage utilization of the feed supplied in excess of the maintenance requirement but to arise largely from the greatly increased maintenance requirement of the fat animal.

Computed Net Energy Values. It is apparent from the foregoing pages that actual determinations of the net energy have as yet been made in but few of the great variety of stock feeds.

To make the results of such investigations more widely useful in practice, two methods have been devised for computing the net energy values of feeding stuffs in those numerous cases in which they have not been determined directly. Both methods are based upon the composition and digestibility of the feeding stuffs, concerning which, as appeared in Chapter 3, fairly extensive knowledge is available.

The first method is that of Kellner. In brief, he sought to determine the net energy values of the single nutrient by adding approximately pure proteins, carbohydrates, and fats to a basal ration in precisely the same manner as in the experiment in hay described on page 143. Having done this, he applied the factors thus obtained to the digestible proteins, carbohydrates, and fats of the feeding stuffs and then corrected the results in case of roughage for the additional energy estimated to be expended in the mastication and digestion of the crude fiber and in case of concentrates by a factor ("Wertigkeit") derived from respiration experiments on similar feeds. The details of his methods are described in his book [48] in the appendix of which extensive results for German feeding stuffs are tabulated. As a concession to a supposed prejudice against the use of new terms, Kellner expressed his results in terms of so-called "starch values," *i.e.,* of the weight of starch supplying the same amount of net energy as a unit of the feeding stuff in question. For example, the starch value of 100 kilograms of good meadow hay is given in his table as 31.0 kilograms, *i. e.,* 31 kilograms of starch would supply the same amount of net energy as 100 kilograms of the hay. Kellner's starch values have come into somewhat general use in European countries, but experience has shown that this attempt to express energy values in terms of matter is unfortunate and confusing, and, as the writers believe, an unnecessary concession. Starch values, however, may be readily converted into net energy values, one kilogram of starch being equal to 2360 Calories or 2.36 therms and one pound of starch to 1064 Calories or 1.064 therms.

Armsby and Fries [49] have attempted to reach the same end by a somewhat simpler method. The metabolizable energy is estimated from the

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[48] "Die Ernährung der landwirtschaftlichen Nutztiere," 6th Ed., 159-169.

[49] *Jour. Agr. Research,* 3 (1915), 486; "Nutrition of Farm Animals," 673.

total digestible organic matter of the feeding stuffs by the use of average factors and from this is subtracted the increment of heat production per unit of dry matter as estimated from actual results on similar materials. For example, alfalfa hay has per kilogram 49.29 per cent or 492.9 grams of digestible organic matter. Coarse fodders yield 3.5 calories of metabolizable energy per gram of digestible organic matter. The heat production for alfalfa hay is 1.169 (revised figure, 1.059) Calories per gram of dry substance eaten or 1.071 Calories per gram of average alfalfa hay. Thus we find

Alfalfa hay (3.5 Calories × 492.9) — 1,071 Calories = 654 net Calories per kilogram or 29.7 therms per 100 pounds.

This method has been applied to the data contained in Henry and Morrison's tables of the average composition and digestibility of American feeding stuffs for cattle and for swine with the results recorded in the appendix of "The Nutrition of Farm Animals."

Energy Values of Human Foods.

Methods of Determination. The methods for determining the energy values of human foods have developed along distinctly different lines than those for stock feeds. Those for the latter, as appears from the foregoing pages, are substantially calorimetric. For the former they are predominantly chemical, although based of course on calorimetric data.

The great bulk of the food of civilized man consists of refined products from which the coarser portions have been removed. It consists to a very large extent of the endosperm of seeds (flour and meal), sugar, meats, poultry, eggs, and dairy products. In these materials, as contrasted with those consumed by domestic animals, it is not a difficult task and does not require expensive appliances to determine with a good degree of accuracy, the amounts of true proteins, carbohydrates and fats which they contain. Investigation of the energy values of human foods and dietary has accordingly taken the course of determining factors for the energy values of the three classes of nutrients and applying these to the results of chemical analysis.

Heats of Combustion of Nutrients. The first step, of course, is the determination of the heats of combustion of the several nutrients. These have been determined for a considerable number of members of each of the three groups by modern methods and the results have been compiled by Atwater [50] and by Fries [51] while Benedict and Osborne [52] have

[50] U. S. Dept. Agr., Office Exp. Stas., Bul. 21 (1895), 127.
[51] U. S. Dept. Agr., Bur. Anim. Indus., Bul. 94 (1907), 11.
[52] *J. Biol. Chem.*, 3 (1907), 119.

determined the heats of combustion of nineteen carefully purified vegetable proteins.

Metabolizable Energy of Nutrients. While numerous earlier experimenters concerned themselves with the question of the energy values of foods and nutrients, it is to the fundamental investigations of Rubner [53] and of Atwater [54] that most of our present knowledge is due. These investigations were directed to the determination of the metabolizable energy, or so-called fuel values, of the nutrients, it being assumed that these represented their value as sources of energy to the body. In determining these there must be deducted from the gross energy values as expressed in the heats of combustion, first, the amounts of energy escaping in the feces and second, in the case of the proteins, the energy contained in the incompletely catabolized products carried off in the urine.

Rubner's investigations related especially to the proteins. Up to that time it had been customary simply to subtract from the gross energy of protein the energy of the corresponding amount of urea as computed from the nitrogen. Rubner showed, however, that the loss of energy in the urine was materially greater than this and also that the loss in the feces was not negligible. For the average human dietary he estimates the fuel values of the digested proteins, carbohydrates, and fats as follows:

	Per Gram	Per Pound
Protein (N × 6.25)	4.1 Cals.	1860 Cals.
Carbohydrates	4.1 "	1860 "
Fats	9.3 "	4220 "

These values are his so-called isodynamic values so widely cited in the literature of human nutrition.

Atwater's investigations were fundamentally similar to Rubner's but were on a broader basis. For an average dietary containing about 44 per cent of animal and 55 per cent of vegetable food he gives the following estimates of fuel value:

	Per Gram Available	Per Gram Total	Per Pound Total
Proteins (N × 6.25)	4.4 Cals.	4.0 Cals.	1820 Cals.
Carbohydrates	4.1 "	4.0 "	1820 "
Fats	9.4 "	8.9 "	4040 "

In explanation of the use of the words "available" and "total" in this table the following statement will serve: According to Atwater each gram of total protein in the diet yields 4 Calories of energy, but each gram of protein that is digestible yields 4.4 Calories.

[53] *Ztschr. Biol.*, 19 (1883), 313; 20 (1884), 250 and 337; 42 (1901), 261.
[54] Conn. (Storrs), Agr. Expt. Sta. Rpt., 1899, 73.

A somewhat more complete summary of Rubner's and of Atwater's investigations has been given elsewhere by Armsby.[55]

The Recovery of Protein.

Contrast with Energy. The agricultural animal functions not only as a converter of energy but as a converter of protein. In the mature or nearly mature animal the storage of energy resulting from the consumption of surplus feed is largely in the form of fat. In the growing or milk-producing animal, on the other hand, a considerable part of the stored energy is contained in the protein of body tissue or of milk. In herbivorous animals the proteins thus stored consist of converted vegetable proteins, and, since protein is an essential constituent of human dietaries, the study of the rôle of the animal in food production necessarily includes a consideration of its efficiency as a converter of protein.

This is far from being as simple a matter as the efficiency regarding energy. Energy is essentially a unitary conception, even though it is carried by a great variety of substances both in the feed and in the body. Protein, on the contrary, as has been already seen in previous chapters, is a collective term—a group name for a vast variety of chemical individuals which may have very different degrees of availability.

Finally, the subject is complicated by differences in the biological values of proteins. Animal proteins in particular, due to differences in structure or for other reasons, are in general distinctly more valuable either for maintaining the stock of protein in the body or supporting growth or milk production than are most vegetable proteins. Moreover the individual proteins of each of these two classes may differ among themselves quite widely as regards nutritive value. The utilization of protein in the animal body is greatly affected by the rate of supply as shown subsequently. According to our present conceptions of the storage of energy the rate of supply has little if any effect upon the utilization of energy.

For these reasons it is scarcely possible to formulate any general statements regarding the percentage recovery of protein. The following pages, therefore, relate chiefly to some of the reasons for these difficulties and are necessarily couched in rather general terms.

The Storage of Protein. In the growing animal protein is stored in the sense that the growing animal is constantly adding to its muscular tissue as well as to all other protoplasmic tissues. The total quantity of such tissues, then, increases until the animal has secured its full growth. This constitutes an increase in the quantity of such tissues as are needed

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[55] "Principles of Animal Nutrition," New York, 1910, 272-281.

for the proper functioning of the larger and mature animal. This is not stored protein in the sense that it is an auxiliary supply not needed for the daily functioning of the animal. Although this type of addition of protein virtually ceases with maturity this is only true in case the animal has enjoyed optimum or even maximum growth. Fattening mature cattle for market certainly adds to the total quantity of protein tissue. There will be not only a greater quantity of fatty tissue with a larger amount of fat, but the protein in this tissue may be increased in amount although it becomes less in proportion. Other tissues may also increase. This storage, or increase, of protein in the mature animal is rather small compared to the increase in the fat stored.

Protein may be stored in the animal body in an entirely different sense. In addition to the increase of total functioning protoplasmic tissues, protein may be stored within the cells as material apparently not necessary but reserved for some future emergency. There is a decreasing protein catabolism during fasting until a minimum is reached which is rather characteristic of the particular individual animal. When the animal is subsequently fed, protein may be retained. It is retained when carbohydrate is fed with protein in the ration much more readily than when fat is fed with the protein. Phosphoric acid may be retained at the same time thus forming, according to Lüthje,[56] forming new tissue including bone. If the retention of phosphoric acid is insufficient to build up "flesh" the protein retained must exist in the form of "deposit protein." This protein is not stored in the blood but is perhaps retained in the cellular fluids in much the same manner as glycogen is retained by the cells.

According to Rubner as quoted by Lusk,[57] "the greater the impoverishment of the protein supply in an animal fed with fat, the more powerful is the protective effect of small quantities of ingested protein over the loss of body protein. The retention, or storage, of protein depends also on the protein content of the animal as well as on the quantity of protein fed.

Lusk[57] sums up the facts as follows: "According to these laws adult cells which have been depleted of their protein may gradually improve their nutritive condition until they reach an *optimum,* at which point they lose their power to attach additional protein."

This rapid retention together with a later loss of ability to retain protein is illustrated by some work of McCollum.[58] He fed a pig a diet containing 14 grams of nitrogen per day in the form of casein and starch,

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[56] *Deut. Archiv. f. klin. Medizin,* 81 (1904), 278.
[57] "The Science of Nutrition," Philadelphia, 1921, 287.
[58] *Amer. Jour. Physiol.,* 29 (1911-12), 215.

so that the value of the diet was 100 calories per kilogram during an experimental period of thirty-six days. The animal retained 43 per cent of the nitrogen ingested, adding during the first three days 9.65 grams of nitrogen to the body daily and during the last three days but 3.69 grams daily.

That protein may be stored in the body and later drawn upon for body uses has been shown by Greene[59] in a study of Columbia river salmon. These fish lose large quantities of muscular tissue and fat during the fast of spawning migration while developing the sex tissues. In addition to this loss, the muscular tissue that is left has its protein level, *i.e.*, the percentage of protein remaining in the fat-free tissue, reduced by 10 to 30 per cent. Greene argues that, since the fish retains muscular vigor until the end of the migration as shown by its ability to leap and climb rapids and falls, this latter loss of protein represents stored protein which may be removed without attacking the vital structure of the muscle cell.

Moulton[60] has shown that beef animals may experience similar losses of protein from the muscular tissues. A fat eleven months old beef steer was fed so as to lose about one-half pound a day for approximately eleven months. At the end of this time the total protoplasmic tissue, especially the muscular tissue, had decreased in amount but in addition the protein level in the remaining muscular tissue had decreased about 10 per cent. The particular protein fraction lost in this animal was the globulin-albumin fraction.

Single Proteins. It has already appeared that there are marked differences in the constitution of the individual proteins as indicated by differences in the proportions of the amino acids obtained by hydrolysis. With the concurrent development of the technique of nutrition experiments with small animals by Hopkins, Osborne and Mendel, McCollum and others, equally marked differences in the biological values of single proteins have been revealed. An extreme example is offered by the zein of maize. This is an incomplete protein, lacking lysin, glycin and tryptophan, all of which are present in the proteins of animal tissue. Experiments by Willcock and Hopkins,[61] Henriques,[62] and Osborne and Mendel[63] have demonstrated what would be inferred from this fact, *viz.*, that zein alone is incapable of supporting either maintenance or growth. In other words the efficiency of the animal in converting zein alone is zero. A less extreme example is afforded by the glutenin of wheat,

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[59] *J. Biol. Chem.*, 39 (1919), 435.

[60] *Ibid.*, 43 (1920), 67.

[61] *Jour. Physiol.*, 35 (1906), 88.

[62] *Ztschr. physiol. Chem.*, 60 (1909), 108.

[63] Carnegie Institution of Washington, Publication, 156 (1911); *J. Biol. Chem.*, 13 (1912), 233; 17 (1914), 325.

which as compared with proteins of ox muscle contains a considerable excess of glutamic acid, alanin and tyrosin but is relatively deficient in phenylalanin, aspartic acid, arginin, and lysin. It is to be presumed that the value of such a protein for building up animal tissue would be limited by the amino acid present in relatively minimal amounts and that its biological value, and therefore its percentage recovery, would be low as compared with a protein supplying a more suitable amino-acid mixture.

Mixture of Proteins. As would be anticipated from the differences in constitution just mentioned, experiment has shown that the deficiencies and excesses of two or more proteins may mutually supplement each other so that a mixture of proteins may have a higher biological value, and therefore show a greater percentage recovery, than the mean of the individual proteins composing it. This supplementary effect has been so fully established by the investigations of Osborne and Mendel, McCollum and others as scarcely to require citation. As regards the protein recovery in the sense here being considered, however, it is evident that since practically all feeding stuffs contain a mixture of several proteins, only direct experiments on a particular feeding stuff can determine the availability of its protein.

Proteins of Mixed Rations. Still further, the rations of agricultural animals rarely consist of a single feeding stuff. Ordinarily a considerable variety is used, including, in the case of herbivora, the vegetative organs as well as the seeds of plants. Just as the single proteins in a mixture can supplement each other, we must suppose that the mixtures of protein in the several feeds making up the rations may likewise supplement each other. In the present state of our knowledge, however, it appears hopeless to endeavor to make estimates along this line.

Influence of Protein Supply. In so far as the recovery of feed proteins in the body tissue or in milk is dependent upon their biological values and the corresponding extent to which they supplement each other, the difficulty in the way of any exact estimate is substantially a lack of experimental data.

As already intimated, however, the percentage recovery of any particular protein or mixture of proteins by the animal is largely dependent upon the amount consumed. As regards energy, the animal body has a large reserve storage capacity. It would appear that within quite a large range of supply, the organism disposes of surplus feed energy substantially in the same way and approximately to the same quantitative extent. With protein the case is radically different. The animal can use protein only to build up body tissue (or to a certain extent, to increase the cytoplasm of existing cells) or for the production of milk proteins in the cells of the udder. Its capacity to store protein is therefore limited by its capacity for growth or for milk secretion. Protein supplied in excess of this capacity is deaminized, as described in Chapter 4, and its non-nitrogenous residue utilized as a source of energy. As a mathematical consequence the percentage recovery is diminished. This relation may be illustrated by an imaginary case. Let it be assumed that a calf five months old can store daily 100 grams of protein and that a balance experiment shows a gain by the body of 90 grams of protein, a maintenance cost of 70 grams and a total consumption of 160 grams. Obviously, 100 per cent of the particular protein mixture supplied in excess of the maintenance requirement has been recovered. Suppose now the protein supplied be increased to 200 grams, *i.e.,* to 130 grams above the maintenance requirement. Since the animal can store up only 100 grams of this, the remaining 30 grams will be deaminized and its nitrogen excreted and the percentage utilization in this case will be not 100 per cent but $100 \div 130 = 77$ per cent. This is the case, not because the protein is of poorer quality but simply because the supply exceeds the capacity of the converter. The following hypothetical table shows clearly how the apparent percentage recovery would decrease as the amount of protein consumed was increased.

TABLE 47

Apparent Recovery of Protein

Protein Consumed	Required for Maintenance	Left for Production	Actual Production	Percentage Recovery
150	70	80	80	100
160	70	90	90	100
170	70	100	100	100
180	70	110	100	91
190	70	120	100	83
200	70	130	100	77

This aspect of the question has been discussed especially by Fingerling[64] in connection with experiments on calf feeding and the following selection from his actual results illustrates how an increase of feed protein above that necessary to support maintenance and insure the maximum gain by the animal cuts down the percentage recovery.

TABLE 48

Influence of Protein Supply on Percentage Retention of Nitrogen

	Digested Nitrogen of Feed Grams	Urinary Nitrogen Grams	Gain by Calf Grams	Per Cent of Feed Protein Retained
June 2-5	42.49	7.91	34.58	81.4
June 25-30	62.97	28.77	34.20	54.3

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[64] *Landw. Vers. Stat.,* 74 (1910), 1.

Recent co-operative experiments on the growth of cattle[65] likewise afford illustrations of the effect of high protein rations in reducing the percentage recovery of protein. For example two comparable groups of calves at the Massachusetts Experiment Station gave the following results per thousand pounds live weight:

TABLE 49

INFLUENCE OF HIGH PROTEIN RATIONS ON RECOVERY OF PROTEIN

	High Protein	Low Protein
Protein Digested, pounds	1.76	0.84
Maintenance, pounds	0.50	0.50
Available for growth, pounds	1.26	0.34
Observed gain, pounds	0.46	0.32
Percentage recovery	37	94

Although the high-protein rations resulted in a greater total growth, the percentage recovery is only a little more than one-third that observed on the low protein rations.

Conclusions. In the light of the foregoing paragraphs it is clear that no general value exists for the percentage recovery even of the same protein by the same species and still less any value for protein in the general sense in which the term is frequently used. The maximum percentage recovery can be obtained only when the available protein supply is limited to the minimum of the particular protein in question which is necessary to support normal growth and the same is doubtless true in the case of milk production.

On the other hand, there are not lacking indications like that of the experiments just cited that a surplus of protein may stimulate the total storage by the animal though at the expense of a reduced percentage recovery and the experience of practical feeders points in the same direction. Whether the efforts of the feeder should be directed to secure the greatest possible efficiency of his feed proteins or the greatest practicable production of meat or milk proteins depends substantially on economic conditions.

Vitamins.

Recovery. It appears to be generally admitted that the so-called vitamins originate in the plant and that animals acquire them from their feed. Up to the present time, however, no satisfactory method for the quantitative determination of vitamins has been devised, and consequently it is impossible to estimate their percentage recovery.

[65] Bulletin of the National Research Council, 2, No. 12 (1921), 279-280.

Relations to Nutrition. It has been fully established that, at least for certain species of animals, notably for the rat, and presumably for all birds and mammals, an adequate ration must include minimum amounts of both the water-soluble and fat-soluble vitamins.

This brief statement pretty nearly covers our present knowledge of the relations of the vitamins to nutrition. As was natural in a new field, investigation has thus far been almost exclusively qualitative. Much has been learned by biological tests regarding the occurrence of vitamins and as to their relative abundance in different food materials. Their behavior in the various processes of cooking and preserving human foods is being studied. But aside from the facts of their indispensability and that very minute amounts of them suffice to render rations adequate, almost nothing is yet known regarding their physiological functions, although it is clear that they cannot supply any significant amounts of either ash, protein or energy.

Influence on Availability of Food. In particular, as regards the special subject of the present work it is not clear how or to what extent they affect the efficiency of the animal as a transformer in the sense discussed in Chapter 9. In the vast majority of experiments it has simply been determined whether the animal did or did not maintain themselves or make normal growth when offered certain rations *ad libitum*, even the total feed consumption frequently remaining undetermined. Now a noteworthy feature of such experiments is that the nutritive failure usually coincides in time and degree with a diminished food intake. While it is scarcely possible to distinguish between cause and consequence in such a case, Karr's[66] recent experiments on dogs strongly suggest that the failure of appetite may be an important factor. If lack of vitamins is a cause of disease, then an animal receiving food deficient in them is presumably in a state of incipient illness. If we may judge from our own experience, the appetite would be affected, less food would be consumed, thus still further decreasing the vitamin supply, nutrition would be slowed down and a vicious circle might be established leading to nutritive failure.

At any rate, whether through diminished food demand or inadequate food supply, it seems clear that the assimilative processes become less active and the animal mechanism is unable to work up to its capacity as a converter. Such an animal would evidently be less efficient economically than a normal one because it would yield less product from a unit of total food. No evidence has come to the notice of the writers, however, showing whether or not such an animal performs such an amount of chemical transformation as it is able to bring about any less efficiently—whether,

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[66] *J. Biol. Chem.*, 44 (1920), 255.

e.g., a unit of surplus carbohydrates would yield any less fat, or in general a unit of surplus food energy would result in any smaller gain.

Past investigations upon the vitamins have been of immense significance to the science of nutrition. They have enabled us to detect qualities and deficiencies in food substance quite undiscoverable by the earlier, chemical methods and have made possible a new qualitative classification of human foods and stock feeds. When more profound investigations upon the chemical nature and physiological functions of the vitamins shall have been made, and when their influence upon the quantitative relations between food and product shall have been further studied, it may be possible to discuss their influence upon the efficiency of the animal as a converter. Until then, it will be necessary to use the qualitative knowledge which we now have of the vitamin content of different feeding stuffs to assure ourselves that our experimental determinations upon various rations are not vitiated by neglect of this factor.

Chapter 7.

Composition of the Increase.

When an animal consumes feed in excess of the supply required for maintenance, a production of body substance, milk, eggs, or work results. One or more may result at the same time in an animal. For example the work horse may gain in body substance, a beef steer, or ox, may perform some work while gaining flesh, or the dairy cow may produce milk while gaining in body materials. The performance of work lies outside of the purposely limited scope of this monograph. The composition of milk has been dealt with in Chapter 2. The maintenance cost will be considered in the following chapter. Therefore the composition of the increase and its energy value will be presented here.

The increase may be growth of vital body tissues, or muscle, or it may be largely due to fat deposition. Growth and fattening would then be two forms of increase which might be treated under separate headings. Since, however, this division is arbitrary and the two kinds of increase occur together in many cases, both will be considered together here.

Slaughter Experiments.

Either the comparative slaughter test or the respiration experiment may serve as a means of investigation. Of the former there are on record studies of the composition of the increase in young pigs by Wilson[1] and Wellman[2] and in older pigs by Lawes and Gilbert[3] and Soxhlet.[4] Kern and Wattenberg[5] have presented data on the composition of young sheep and Lawes and Gilbert,[6] Henneberg, Kern and Wattenberg,[7] Friske[8] and Pfeiffer and Friske[9] have published data on the composition of the increase of older sheep.

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[1] *Amer. Jour. Physiol.*, 8 (1903), 197.
[2] *Landw. Jahrb.*, 46 (1914), 499.
[3] *Phil. Trans.*, II, 1859, 493.
[4] *Centbl. Agr. Chem.*, 10 (1881), 674.
[5] *Jour. Landw.*, 28 (1880), 289.
[6] *Phil. Trans.*, II, 1859, 493.
[7] *Jour. Landw.*, 26 (1878), 545 and *Ztschr. Biol.*, 17 (1881), 295.
[8] *Landw. Vers. Stat.*, 71 (1909), 441.
[9] *Ibid.*, 74 (1911), 409.

TABLE 50

Composition of the Gains in Swine During Growth and Fattening

		From	To	Water %	Fat %	Protein %	Ash %	Calories per Kilogram
		Days						
Wilson	Skim	0	16	80.52	0.98	18.11	0.39[1]	1120.95
	Lactose	0	16	79.20	1.37	17.70	1.73[1]	1134.72
	Dextrose	0	16	79.87	1.13	17.02	1.98[1]	1073.33
Wellman	VIII	21	49	74.88	7.66	15.99	2.09	1595.24
	IX	21	59	76.21	6.38	15.51	2.09	1454.79
	VII	42	96	65.82	15.86	15.26	2.80	2402.00
		Months						
Lawes and Gilbert	Average			22.00	71.50	6.44	0.06	7155.30
Soxhlet	2		16½	58.96	24.45	13.42	3.17	3083.51
	3		16½	35.99	53.59	6.80	3.62	5474.96

[1] By Difference.

The work of Lawes and Gilbert[6] was the first showing the composition of the increase of mature cattle when fattening. Jordan[10] presented data on the composition of fairly mature cattle when fattened moderately and Trowbridge, Moulton, and Haigh[11] have calculated from data presented by them the composition of the increase from a thin to a half-fat condition and from half fat to very fat. Respiration experiments by Soxhlet[12] on three young calves included determinations of the gain or loss of ash, while the live weights of the calves were also recorded. A calculation of the composition of the increase based upon the live weights seems justified since the feed was exclusively milk and variations in the contents of the digestive and excretory tract were probably slight.

Short fattening experiments on geese by Schulze[13] and by Chaniewski[14] make possible the calculation of the composition of the increase in fattening geese. The results of all of this work are presented in Tables 50, 51, and 52. Unjustified assumptions by Tschirwinsky[15] render a calculation of the composition of the increase made by his pigs undesirable. Data regarding dogs and cats are also on record in the investigations of Thomas[16] and Gerhartz.[17]

A study of the tables presented shows that in very young animals

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[10] Maine Agr. Expt. Sta., Rpt. 1895, Vol. 2, 36-77.
[11] Mo. Agr. Expt. Sta., Research Bul., **30** (1919).
[12] I^{er} Ber. Versuchs. Stat., Wien, 101-155.
[13] *Landw. Jahrb.*, **11** (1882), 57.
[14] *Ztschr. Biol.*, **20** (1884), 179.
[15] *Landw. Vers. Stat.*, **29** (1883), 317.
[16] *Arch. Anat. u. Physiol., Physiol Abth.*, **194** (1911), 9.
[17] *Arch. ges. Physiol.*, **135** (1910), 163.

TABLE 51

COMPOSITION OF THE GAINS IN SHEEP DURING GROWTH AND FATTENING

		Periods	Water %	Fat %	Protein %	Ash %	Calories per Kilogram
Kern and Wattenberg ...	Lot I	I & II	43.84[2]	44.85	11.31[1]	....	4887.95
		III & IV	27.27	65.70	7.03[1]	....	6622.46
		V	22.18	72.10	5.72[1]	....	7155.09
	Lot II	I & II	38.41	51.68	9.91[1]	....	5456.26
		III	16.03	79.84	4.13[1]	....	7798.92
		Years					
Lawes and Gilbert		1¼	20.13	70.40	7.13	2.34	7073.50
Henneberg	Fat	2¾	25.80[2]	67.56	6.64	....	6776.73
Kern and Wattenberg ...	Very fat	......	20.30[2]	74.47	5.23	....	7352.05
	Last stage of fattening	......	6.45[2]	91.87	1.68	....	8800.79
Friske		4	12.03[2]	72.90	15.07	....	7758.12
Pfeiffer and Friske		3½	64.33[2]	28.56	7.11	....	3107.40

[1] By Difference.
[2] Includes ash.

TABLE 52

Composition of the Gains in Cattle and Geese During Growth and Fattening

		Age or Condition		Composition				
	Cattle	From Days	To Days	Water %	Fat %	Protein %	Ash %	Calories per Kilogram
Jordan[1]	Protein rich	28	1053.5	35.32	44.64	14.11	5.90	5035.34
	Protein poor	671	983.5	40.92	37.51	15.58	5.97	4442.08
Trowbridge, Moulton and Haigh	Mature Steer	Thin to Half fat		39.76	46.11	11.75	1.97	5041.12
	Mature Steer	Half fat to Very fat		22.29	67.66	6.63	1.87	6795.86
Soxhlet	Calf C	......		62.55	14.86	19.24	3.35	2500.23
	B 1	......		61.28	15.94	19.15	3.63	2597.61
	B 2	......		62.13	17.22	17.15	3.50	2605.74
Lawes and Gilbert	Cattle 4 yrs.	Half fat to Fat		24.64	66.20	7.69	1.47	6717.38
	Geese							
Schulze		9 months		37.06	58.39	3.34	1.21	5645.60
Chaniewski		......		24.15	61.46	3.02	1.37	5914.38

[1] The figures differ somewhat from the original on account of calculations of the composition of the skin. See Chapter 2.

(Wilson's pigs) the increase is practically all protoplasmic tissue, *i.e.*, water and protein. With somewhat older animals the increase contains from 10 to 25 per cent fat, older and fatter animals show 45 to 65 per cent fat in the increase and Henneberg, Kern and Wattenberg's very fat sheep shows about 92 per cent fat in the increase. It will be noted that the energy value of a kilogram of increase runs from about 1100 large Calories in Wilson's pigs to 8800 large Calories in the sheep just cited.

Respiration Experiments.

Respiration experiments on both young and mature animals have confirmed the results of the slaughter experiment as regards the changing relation of protein to fat as growth changes to fattening. The work of Soxhlet just quoted furnishes the data on young calves, and the extensive work of Kühn and Kellner [18] at the Moeckern Experiment Station gives results for mature cattle. Only those experiments showing between 70 and 95 per cent of fat in the organic matter gained are quoted. The number of individual experiments total 55. The results of Henneberg, Fleischer and Müller [19] on sheep and Meissl [20] on swine are also presented.

TABLE 53

PROPORTIONS OF PROTEIN AND FAT IN FATTENING INCREASE

Investigator	Animal	Range of Percentage of Fat in Organic Matter Gained %	Average Composition of Organic Matter of Gain	
			Total Protein %	Fat %
Soxhlet	Calf C		56.42	43.58
	Calf B 1		54.57	45.43
	Calf B 2		49.90	50.10
Kellner	Cattle Group I	70-74.99	26.25	73.75
	Group II	75-79.99	23.30	76.70
	Group III	80-84.99	17.17	82.83
	Group IV	85-89.99	12.55	87.45
	Group V	90-94.99	8.06	91.94
Henneberg, Fleischer and Müller	Sheep	......	4.26	95.74
Meissl, Strohmer and Lorenz	Swine 1	......	9.75	90.25
	2	......	10.67	89.33
	3	......	16.39	83.61
	4	......	15.16	84.84

Since the gains of ash and of water were not determined in these experiments they cannot serve as a means of computing the composition of the increase. Table 53 gives the results.

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[18] *Landw. Vers. Stat.*, 44 (1894), 370; 53 (1900), 1.

[19] *Jahresber. Agr. Chem.*, 16-17 (1876), II, 145.

[20] *Ztschr. Biol.*, 22 (1886), 63.

The Minnesota Experiments on Cattle.

The recent extensive slaughter experiments by Haecker [21] furnish data for calculating the composition of the increase in cattle by one hundred pound stages. The cattle were kept in what was termed "normal con-

TABLE 54

Composition of Gain in Empty Weight of Cattle

(Haecker)

From To Lbs. Lbs.	Water %	Fat %	Protein %	Ash %	Calories per Kilogram
103- 207	68.78	8.31	18.31	4.61	1826.01
96- 301	62.71	14.86	18.16	4.28	2439.03
99- 416	63.78	12.73	19.12	4.37	2291.32
94- 504	60.76	16.03	19.00	4.21	2597.65
104- 600	59.11	17.24	19.29	4.37	2728.90
95- 708	58.47	18.62	18.39	4.51	2808.84
95- 815	56.68	20.44	18.66	4.23	2996.84
89- 912	50.75	28.23	17.08	3.94	3646.51
101-1008	49.87	29.41	16.79	3.92	3742.04
126-1109	45.02	35.21	16.01	3.76	4248.20
98-1204	45.97	34.67	15.70	3.65	4179.39
99-1304	48.02	31.95	16.35	3.67	3958.12
105-1413	45.90	34.80	15.86	3.45	4200.80
115-1508	41.28	40.21	15.39	3.12	4687.52

TABLE 55

Composition of Successive Gains in Empty Weight of Cattle

(Haecker)

Increase From To Lbs. Lbs.	Water %	Fat %	Protein %	Ash %	Calories per Kilogram
100- 200	68.83	18.29	8.27	4.61	1821.08
200- 300	57.18	18.04	20.75	4.03	2991.13
300- 400	65.94	20.99	8.59	4.48	2004.44
400- 500	52.05	18.61	25.58	3.76	3481.74
500- 600	51.65	20.78	22.44	5.13	3306.75
600- 700	55.89	14.41	24.54	5.16	3145.08
700- 800	47.12	20.04	30.02	2.82	3984.08
800- 900	21.66	9.04	65.70	3.60	6746.43
900-1000	36.48	12.88	48.21	2.42	5304.41
1000-1100	8.84	9.90	78.69	2.57	8027.77
1100-1200	49.39	12.98	34.99	2.64	4055.64
1200-1300	47.86	11.86	35.05	5.23	3997.87
1300-1400	45.16	21.68	33.78	—0.61	4433.78
1400-1500	0.08	11.37	88.41	0.14	9033.39
Steers from Pasture					
600- 700	48.26	18.40	31.03	2.31	3986.99
700- 800	14.23	10.77	74.55	0.31	7684.22
800-1000	67.49	22.00	4.43	6.09	1666.92
1000-1200	31.15	8.33	59.81	0.70	6147.30

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[21] Minnesota Agr. Expt. Sta., Bul. 193 (1920).

dition." The protein, it must be remembered, was determined by difference in this work. The composition of the increase in empty weight from the start to each hundred pound stage and between successive one hundred pound stages has been calculated and recorded in Tables 54 and 55. The gains at first are largely protein and water with an energy content of 1800 large Calories per kilogram. The final gains contain about 88 per cent fat and have an energy content of 9000 large Calories per kilogram.

The Missouri Experiments on Cattle.

The reported results on cattle by Moulton, Trowbridge, and Haigh[22] present the composition of the increase in the empty weight of cattle from birth to various ages and on three different planes of nutrition. The

TABLE 56

Composition of Gains of Cattle from Birth

(Moulton, Trowbridge, Haigh)

	Water %	Fat %	Protein %	Ash %	Phosphorus %	Calories per Kilogram
		Full Fed from Birth				
Birth to 3 mo.	61.87	12.76	20.94	4.97	0.865	2397.28
5.5 mo.	50.51	28.53	15.75	3.65	0.669	3599.61
8.5 mo.	57.61	19.41	18.25	3.70	0.650	2875.88
11 mo.	54.22	24.38	17.06	3.49	0.553	3280.04
18 mo.	50.00	29.98	16.06	3.48	0.624	3754.76
21 mo.	48.06	32.27	15.56	3.80	0.688	3943.73
34 mo.	44.61	38.02	13.13	3.59	0.563	4351.65
39.5 mo.	36.98	48.33	11.63	2.79	0.464	5244.97
44.5 mo.	39.43	44.19	12.44	3.03	0.569	4898.02
47 mo.	38.03	45.75	11.94	3.20	0.563	5017.71
		Fed for Full Growth without Appreciable Fattening				
Birth to 3 mo.	62.71	10.21	21.50	5.30	0.882	2187.05
5.5 mo.	55.19	18.29	18.63	5.23	0.919	2791.13
8.5 mo.	55.57	22.72	16.56	3.84	0.725	3094.20
11 mo.	58.61	17.89	17.94	4.56	0.736	2714.08
26 mo.	60.15	16.32	18.31	5.15	0.867	2586.07
34 mo.	56.41	20.36	18.06	4.88	0.751	2955.26
40 mo.	54.22	22.20	18.19	4.79	0.856	3137.22
44.5 mo.	55.89	18.04	20.13	5.00	0.870	2852.41
48 mo.	49.93	26.69	17.69	5.05	0.898	3534.94
		Fed for Scanty Growth				
Birth to 3 mo.	69.53	5.06	22.13	4.20	0.644	1734.07
5.5 mo.	61.82	10.56	20.81	4.95	0.905	2181.17
8.5 mo.	60.18	13.18	19.25	5.24	0.979	2341.38
11 mo.	60.40	16.45	17.00	4.36	0.777	2524.17
18.5 mo.	64.53	11.51	17.81	5.07	0.896	2101.32
26 mo.	62.25	13.29	19.06	4.89	0.788	2341.05
40.5 mo.	61.89	11.40	20.50	5.84	1.013	2243.30
45 mo.	56.50	17.58	20.00	4.97	0.879	2801.39
48 mo.	56.22	18.61	19.63	5.01	0.871	2878.16

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[22] Mo. Agr. Expt. Sta., Research Bul. 55 (1922).

TABLE 57

Composition of Successive Gains of Cattle

(Moulton, Trowbridge, Haigh)

	Water %	Fat %	Protein %	Ash %	Phosphorus %	Calories per Kilogram
			Full Fed from Birth			
Birth to 3 mo.	63.30	12.76	20.94	4.97	0.865	2397.28
3 to 5.5 mo.	46.30	34.75	13.63	3.05	0.569	4069.69
5.5 to 8.5 mo.	71.40	2.65	21.69	3.68	0.641	1480.46
8.5 to 11 mo.	47.66	33.36	15.63	3.30	0.369	4051.13
11 to 18 mo.	45.68	35.06	15.25	3.63	0.745	4190.91
18 to 21 mo.	27.55	59.14	9.56	6.35	1.225	6153.43
21 to 34 mo.	35.50	53.08	7.00	3.03	0.261	5433.34
34 to 39.5 mo.	16.09	64.25	16.19	0.82	0.905	7013.98
39.5 to 44.5 mo.	8.47	93.79	−2.81	−0.96	0.104	8740.42
44.5 to 47 mo.	2.30	86.00	−0.94	6.82	0.381	8107.19
			Fed for Full Growth without Appreciable Fattening			
Birth to 3 mo.	62.71	10.21	21.50	5.30	0.882	2187.05
3 to 5.5 mo.	53.23	21.33	17.56	5.09	0.929	3018.96
5.5 to 8.5 mo.	59.36	22.95	15.31	2.58	0.545	3045.20
8.5 to 11 mo.	62.85	11.81	19.44	5.59	0.730	2222.15
11 to 26 mo.	60.57	15.93	18.63	5.69	0.981	2567.19
26 to 34 mo.	20.22	60.52	13.81	2.68	−0.230	6525.18
34 to 40 mo.	34.38	33.82	23.88	3.87	2.302	4562.24
40 to 44.5 mo.	43.63	34.73	5.25	−3.30	−0.524	3592.97
			Fed for Scanty Growth			
Birth to 3 mo.	69.53	5.06	22.13	4.20	0.644	1734.07
3 to 5.5 mo.	55.75	14.38	20.63	6.47	1.273	2533.44
5.5 to 8.5 mo.	55.73	23.02	11.88	5.87	1.234	2857.48
8.5 to 11 mo.	56.84	25.84	13.38	2.67	0.365	3210.07
11 to 18.5 mo.	66.92	6.08	20.44	6.07	1.063	1735.10
18.5 to 26 mo.	58.95	16.89	21.06	4.43	0.490	2795.98
26 to 40.5 mo.	45.08	28.25	18.50	4.12	1.028	3728.86
40.5 to 45 mo.	34.09	31.11	31.44	8.32	1.219	4733.45
45 to 48 mo.	55.40	26.97	15.81	5.51	0.775	3454.99

composition of the gains between the successive ages are also given. Tables 56 and 57 give the results. The composition of the total increase from birth may contain but 5 per cent of fat in the young thin calf and have an energy content of only 1734 large Calories per kilogram. For the old very fat steer the increase will contain 45 to 48 per cent fat and have an energy content of 5000 to 5245 large Calories per kilogram. The successive gains show more strikingly the increasing fat content of the final gains. For old fat cattle the last increase may contain about 94 per cent fat and have an energy content of 8900 large Calories per kilogram.

Calculation of the Energy Content of the Gain.

All of the energy equivalents presented in the foregoing tables have been calculated from factors excepting those of Wellman which were directly determined in the bomb-calorimeter. The factors used were selected in the following manner. For protein of cattle the average of the figures for the heat of combustion determined by Rubner, Stohmann and Langbein, and Köhler as reported in Chapter 2 (page 59) was used. For the protein of sheep and of swine the value reported by Köhler was used and for the protein of geese the average of the figures for cattle, sheep and swine. For fat the average of values reported for each animal by Fries [23] have been used. Table 58 gives the energy values used.

TABLE 58

Energy Equivalent of Protein and Fat

	Calories per Gram	
	Protein	Fat
Cattle	5.6662	9.4889
Sheep	5.6387	9.4765
Swine	5.6758	9.4962
Geese	.....	9.3450
Average	5.6602	

By the method of simultaneous equations the large Calories per gram for the protein and fat in the gains of Wellman's young pigs have been calculated. The results follow:

	Calories per Gram	
	Protein	Fat
1. Pigs VII and VIIa	5.4740	9.8922
2. Pigs VIII and VIIIa	5.6334	9.0695
3. Pigs IX and IXa	5.6214	9.0869
4. Average of VIII and IX	5.6274	9.0782
Average of lines 1 and 4	5.5507	9.4852

The average figures are not far from those shown in the table just preceding. Another method of comparison is that employing the factors for swine given in Table 58 for the protein and fat gained by Wellman's pigs. The results appear in the following table:

	Calories per Kilogram Gain		
	Computed	Observed	Difference—Calories
Pig VIII	1634.97	1595.24	+ 39.27
Pig IX	1486.18	1454.79	+ 31.39
Pig VII	2372.23	2402.00	— 29.77

These figures are very close together and appear to verify the average figures for the protein and fat gained by swine used in the computations. The energy content of the other animals reported in the tables was not

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[23] U. S. Dept. Agric., Bur. An. Industry, Bul. 94 (1907), 113.

determined by the bomb calorimeter. Therefore no comparison of observed and calculated energy values of the gains can be made.

Estimating the Composition of the Increase.

The early gains of young animals are largely water, protein, and ash. This is especially true if the needs of the body for growth approximate the supply received in the food. Thereafter the proportion of fat in the increase may grow progressively larger until the gains are almost exclusively fat. There are several factors which will affect the composition of the increase among which are age, kind of animal, and plane of nutrition. An estimation of the composition of the gains from data concerning the food fed, the digestibility and net energy of the ration, and the maintenance cost of the animal would hardly be justified in the present state of our knowledge. Either the comparative slaughter test or the balance experiment conducted in the respiration chamber should be employed where the composition of the increase is desired.

Chapter 8.

The Overhead Feed Cost—Maintenance

Basal Catabolism and Maintenance. The amount of matter and energy used by a fasting animal while in a state of perfect rest—preferably reclining and asleep—is known as the basal catabolism. These needs arise from a variety of internal activities, both mechanical and chemical. The most important mechanical activity is that of the muscular work of circulation and respiration together with the maintenance of muscular tonus. The secretory and excretory activities of the various glands are typical of the chemical activity. The animal must depend upon metabolism of body tissues for its source of matter and energy for these purposes. Ultimately all this activity assumes the form of heat and can be measured in a calorimeter.

The above ideal condition is rarely attained in animal experimentation and is difficult and, perhaps, even impossible with the herbivorous animal. Benedict and Ritzman[1] have succeeded in obtaining experimental results with the beef steer after twenty-four hours of fasting. The animals must still have had food residues in part of their complicated digestive tracts, especially the omasum, and so the value for the heat output calculated from the carbon dioxide production does not represent basal catabolism but a "standard" metabolism, as the authors point out. They also report longer fasts with the dairy cow carried out by Armsby.

To this demand for basal catabolism, then, there must be added for maintenance those additional quantities of matter and energy demanded by the usual additional activity of the animal during a body weight maintenance trial and while consuming food. These additional quantities are needed for the following purposes: First, the general increased metabolism due to an awakened activity of the body and increased muscular tonus. Second, the work of standing, walking, lying down and getting up, which activities are a part of the cost of the usual body weight maintenance. Third, the additional work performed by the animal in seizing, masticating, swallowing, digesting, and voiding food and food residues. Fourth, the increased metabolism of all cells due to the presence of an

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[1] "Undernutrition in Steers," Publication 324, Carnegie Institution of Washington, Washington, 1923.

extra supply of food in the blood and lymph. Fifth, allowance must be made for the incomplete digestibility of the rations and the excretion of incompletely catabolized products.

The metabolizable energy is the gross energy of the food or ration minus the losses incurred under the fifth heading. Manifestly a food or ration with a high percentage of metabolizable energy is a better one than that with a low percentage. Again the animal should not be charged with differences due to the ration. Since different foods cause different losses under headings three and four it is still better to compare them on the basis of net energy, which basis allows for the losses dealt with under headings three and four above. Variability in the net values of a ration for different purposes has been briefly treated in Chapter 6.

Determination of the Basal Catabolism. An indirect method of estimating the basal catabolism of cattle has been employed by Armsby and the results have been summarized by Armsby, Fries and Braman.[2] The animals employed were awake and more or less active and were standing during part of the time. By employing only those periods during which the animal was lying quietly they have been able to estimate the twenty-four-hour fasting catabolism from a comparison of the total metabolism on two different amounts of the same feed. For example, a steer receiving two different amounts of the same mixed ration gave the following results:

	Dry Matter Eaten Daily Kgm.	Daily Heat Production Calories
Period 1	9.146	16,511
Period 2	4.463	10,905
Difference	4.683	5,606
Heat increment per kilogram of dry matter	....	1,197

Of the total metabolism of 10,905 calories in period 2, therefore, 1197 × 4.463 or 5342 Calories may be regarded as the heat production caused by the 4.463 kilograms of dry matter eaten. The remainder (10,905 — 5342) or 5563 Calories is the calculated heat production without food or, in other words, the basal catabolism. This assumes that the heat production is a linear function of the amount of feed, which cannot be regarded as proved. No distinct indications to the contrary have appeared within the range of these experiments, as the authors point out, and the calculations of Wood and Yule[3] from Kellner's respiration experiments on fattening cattle seem to confirm the assumption since they show that the gains of

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[2] *Jour. Agr. Research*, 13 (1918), 43.
[3] *Jour. Agr. Science*, 6 (1914), 239.

energy are proportional to the metabolizable energy consumed above maintenance.

In this study of Armsby, Fries and Braman just referred to some twenty-eight experiments with different steers and different feeds are reported. The basal catabolism per square meter of body surface for twenty-four hours lying varied from 605 to 1401 Calories with a mean value of 964 Calories. For twelve hours' standing the mean value is 1173 Calories and 1365 Calories for twenty-four hours' standing. From these results the maintenance cost of a thousand pound unfattened beef steer standing twelve hours has been calculated to be 5918 Calories or almost 6 therms, which is the value generally used by Armsby.

For swine Armsby, Fries and Braman [4] have calculated an average twenty-four-hour heat production of 1078 Calories per square meter of body surface. In arriving at this figure the basal catabolism determinations of Meissl, Strohmer and Lorenz [5] and of Tangl [6] as well as the calculations of Fingerling, Köhler and Reinhardt [7] were used. In Tangl's and Fingerling's experiments the animals spent most of the time in the lying position while Meissl makes no statement on this point.

Zuntz and Hagemann [8] have computed the basal catabolism of the horse from the results of numerous determinations of the respiratory exchange while standing quietly. Their method of computation is based on much the same principle as that employed by Armsby for cattle. The average figure is 948 Calories per square meter of body surface per twenty-four hours.

The Standard Metabolism of Benedict and Ritzman. The work of Benedict and Ritzman on "Undernutrition in Steers" [9] gives a value for the metabolism of cattle between the basal catabolism dealt with above and the maintenance cost which will be discussed in the following sections of this chapter. These investigators, using the respiration chamber at Durham, New Hampshire, have determined the carbon dioxide production and from that the energy production with twelve steers on low planes of nutrition. Group I consisting of three steers was fed for body weight maintenance. Group II consisting of five animals was fed a ration representing one-half of the maintenance requirement. Group III had four animals fed two-thirds to two-fifths of the maintenance cost. A

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[4] *Loc. cit.*
[5] *Ztschr. Biol.*, 22 (1886), 63.
[6] *Biochem. Ztschr.*, 44 (1912), 252.
[7] *Landw. Vers. Stat.*, 84 (1914), 149.
[8] *Landw. Jahrb.*, 27 (1898), Ergänzungsbd., 3, 284.
[9] Publication 324, Carnegie Institution of Washington, Washington, 1923.

fourth group was later added in order to study digestion on low planes of nutrition.

The Group I cattle after being adjusted to maintenance on a hay ration gave a calculated heat output of 1820 Calories per square meter of body surface per twenty-four hours standing. This figure is the result of measurements taken twenty-four hours after the last feeding and represents what the authors designate as the "normal standard" metabolism. The basal metabolism of cattle under somewhat similar circumstances has been given above as 1365 Calories. This difference may be due to the fact that these Group I animals of Benedict and Ritzman were above the basal state. These animals must have had feed residues in the digestive tract. Another explanation is that the heat production of cattle on feed is not a linear function of the feed consumed.

In a private communication to Benedict a number of fasting experiments on cows at the Pennsylvania Institute of Animal Nutrition have been quoted by Armsby. He shows that the methane production of these cows became constant after 72 hours. It is therefore argued that the digestive activity had ceased by the end of this time. The carbon dioxide production of these cows for the first twelve hours after the twenty-four hours of fasting was but 12 per cent above the carbon dioxide production for the second 24 hours after the 24-hour fast. Benedict concludes that, therefore, the heat production of his steers cannot be more than 12 per cent above the basal state. It is, however, about 33 per cent too high.

Evidently further experimentation is necessary to determine where the cause of the difference may lie. It would appear probable that methane production should disappear before it can be concluded that all digestive changes have ceased. (See the discussion in Chapter 6, p. 152, on this point.)

The Condition of Maintenance. The exact condition existing during maintenance trials may vary greatly according to the type of the experiment. With the live weight-small open lot experiment the second item in the second paragraph just preceding, namely the activity of the animal, may be considerable and may vary much between individuals. It is desirable to reduce it to a minimum. On the other hand the respiration calorimeter imposes restrictions on the activity of the animal and may materially reduce the maintenance cost. This must be borne in mind in comparing lot experiments with calorimeter experiments. The conception of maintenance must involve the idea of conserving the existing status of the animal while doing no work and producing no product. There should be an exact balance between income and outgo of ash, nitrogen, carbon, hydrogen, and energy, showing that there was neither a loss nor a gain of protein fat, carbohydrate, or mineral matter. Strictly, there should be no translocation of material within the animal itself. These statements imply that maintenance involves no change in the condition or degree of fatness of the animal. For a maintenance trial of any length with animals which have not reached full growth this is, of course, impossible and would, if possible, lead to a gain of matter by the body. This would be in violation of the principle of the balance of matter formulated above.

Units of Reference. It is both convenient and necessary to have some means of comparing the maintenance costs of different species, or different individuals of the same species, varying in age, weight, or size. Large animals catabolize more matter and produce more heat than smaller ones but the difference is not proportional to size or weight in animals carefully selected for uniformity and covering a wide range of weights. Smaller animals have a proportionately larger catabolism corresponding to a proportionately larger surface and in young animals to a proportionately greater percentage of active tissue.

This surface law was first enunciated by Rubner [10] in 1883, although Bergman [11] had suggested it many years before and Müntz [12] had called attention to it a few years previously. The ratio of fasting catabolism to surface is not mathematically constant, but it does approach uniformity and has been shown by E. Voit [13] to be approximately true for animals ranging in size from man to domestic fowls and including cold-blooded animals. C. Richet [14] made similar observations to those of Rubner.

Meeh [15] in 1879 was the first to make accurate observations on the relation of surface to weight in man. His formula $S = kW^{2/3}$ has remained the standard in animal nutrition ever since but is no longer used in human nutrition. Other important observers have been Funke,[16] Fubini and Ronchi,[17] Bouchard [18] and Lissauer.[19] These investigators have all dealt with man as their material.

Miwa and Stöltzner [20] first introduced linear measurements into the formula. Howland and Dana [21] have more recently proposed another

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[10] *Ztschr. f. Biol.,* 19 (1883), 545.

[11] "Wärmeökonomie der Thiere," Göttingen, 1848, 9; "Anatomisch-physiol. Uebersicht des Thier-reichs," Stuttgart, 1852, 272.

[12] *Ann. Inst. Agron.,* 1878, III, 59.

[13] *Ztschr. f. Biol.,* 41 (1901), 113.

[14] *Arch. de Physiol.,* 17 (1885), 284.

[15] *Ztschr. f. Biol.,* 15 (1897), 425.

[16] *Moleschott's Untersuchungen z. Naturlehre,* 4 (1858), 36.

[17] *Ibid.,* 12 (1881).

[18] *Traité de Pathologie générale,* Paris, 1900, 31, 200, 384.

[19] *Jahrb. f. Kinderh.,* 58 (1902), 392.

[20] *Ztschr. f. Biol.,* 36 (1898), 314.

[21] *Amer. J. Dis. Child.,* 6 (1913), 33.

modified formula. D. and E. F. DuBois [22] have made some exact measurements on man and have devised a method and proposed a formula, both of great usefulness.

Recently, Dreyer, Ray and Walker [23] have made measurements of birds and small mammals and have included, besides weight and surface area, also the blood volume and cross sections of trachea and aorta. These were all nearly proportional to the two-thirds power of the weight.

For beef cattle Trowbridge, Moulton, and Haigh [24] have presented data on body weight, surface area, blood weight and volume, and total body nitrogen for a number of individuals. The value of *k* was shown to vary with state of development and fatness of the animal. Four different values for *k* in the Meeh formula were shown to be necessary for four different kinds of beef animal. Moulton [25] made a more critical study of these data and found that for the thirty-five beef animals studied the surface was proportional to the five-eighths power of the weight for thin and medium cattle and to the five-ninths power for fat and very fat cattle. The formulæ are respectively

$$A = 0.1186\ W^{5/8}$$

and

$$A = 0.158\ W^{5/9}$$

where *A* is the surface area in square meters and *W* is the warm empty weight in kilograms. The relation of surface to fat free empty weight and to total body nitrogen was found to be proportional to the two-thirds power of these weights. The surface area was proportional to the five-eighths power of the blood weight. It should be emphasized that in Moulton's formulæ *W* signifies the warm empty weight, in other words the live weight of the cattle minus the large quantities of food, food residues and excreta contained. In the original formula of Meeh *W* represents the gross weight of the subject. It is certain that the contents of the digestive tract should have no effect upon the surface area of an animal. The presence of much body fat has a greater effect tending to disturb what might be considered normal relations between weight, body tissues, and surface area.

In 1914 Murlin and Hoobler [26] and Benedict and Talbot [27] all concluded

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[22] *Jour. Amer. Med. Assn.*, **63** (1914), 827. *Arch. Int. Med.*, **15** (1915), 868.

[23] *Phil. Trans.*, **201** (1909-10), Ser. B., 133—*Proc. Roy. Soc.*, **86** (1912-13), Ser. B, 39 and 56.

[24] Mo. Agr. Expt. Station, Research Bul. 18 (1915).

[25] *J. Biol. Chem.*, **24** (1916), 299.

[26] *Proc. Soc. Expt. Biol. and Med.*, **11** (1914), 115.

[27] *Amer. Jour. Dis. Child.*, **8** (1914), 1. Carnegie Institution of Washington, Pub. 201 (1914).

that among infants metabolism is more nearly proportional to body weight than to body surface. An extensive critique of the body surface was made in 1919 by Harris and Benedict [28] and the latter [29] devised a photographic method for measuring surface. More recently Benedict and Talbot [30] have pointed out that the accurate measurements of body surface made possible by Du Bois may legitimately be used in a manner heretofore never practicable in metabolism experiments, provided that they are considered as *physical* measurements and with no erroneous conceptions as to the existence of a causal relationship between surface-area and heat elimination. Murlin [31] has contributed a timely warning to critics of the value of the surface-area law and Lusk [32] has pointed out that the relations shown by Moulton to exist between surface and body weight, body nitrogen, and blood of beef animals renders unnecessar ythe provision stressed immediately above by Benedict and Talbot.

Armsby, Fries, and Braman [33] have compared the estimated fasting catabolism of cattle with the basal catabolism of other species per unit of weight and per unit of surface area. They found the catabolism to be equally well correlated with the estimated body surface and with the live weight. However, they did not determine the actual basal catabolism of the cattle. Moreover, it must be remembered that the cattle studied by them had live weights between approximately 200 and 650 kilograms. Within these limits the curve for the surface area-body weight relation is so nearly a straight line that it would make practically no difference whether surface or weight were used. The final proof of the greater usefulness of the surface area law lies in its greater applicability over a wide range of weights.

Factors Affecting the Maintenance Cost. In addition to the size and weight of an animal, or its body surface, there are many other factors that may affect its maintenance cost. Chief among these are: age of the animal; condition, or degree of fatness; the previous plane of nutrition; length of the maintenance trial; season of the year, or temperature and general climatic conditions such as wind or rain; type and relative activity of the animal.

It is well known that the young organism has a high rate of metabolism while the old animal is living at a much slower rate. Trowbridge, Moulton, and Haigh [34] have presented some evidence that the maintenance

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[28] Carnegie Inst. of Washington. Pub. 279 (1919), 129.
[29] *Amer. Jour. Physiol.*, 41 (1916), 275.
[30] Carnegie Inst. of Wash. Pub. 302 (1921), 159.
[31] *Science, N. S.*, 54 (1921), 196.
[32] "The Science of Nutrition," Philadelphia, 1921, 122 and 130.
[33] *Jour. Agr. Research*, 13 (1918), 43.
[34] Mo. Agr. Expt. Station, Research Bul. 18 (1915), 31.

cost may decrease with age. Tigerstedt [35] summarizes extensive data on man and shows that the metabolism per unit of surface area diminishes slowly from youth to maturity. The work of DuBois [36] and of Benedict and Talbot [37] shows that the metabolism of man per unit of surface area varies with age. The work of Armsby and Fries quoted in greater detail on page 153 showed that for one animal a decreased cost with age was noted but not with the other. If a younger age does mean a greater maintenance cost it may be due to greater muscular activity usually exhibited by young animals.

The condition, or fatness, of beef steers seemed to have no effect on the cost of maintenance according to Trowbridge, Moulton and Haigh.[34] However, their results were obtained with live weight maintenance and the fat steers might well have been losing fat and adding lean flesh and so keeping the weight constant. Armsby and Fries,[38] employing the respiration calorimeter, have shown that fattened steers have a greater cost of maintenance per unit of surface area, *i.e.,* in proportion to the two-thirds power of the weight, than do unfattened steers. The same conclusion was reached by McCandlish and Gaessler [39] working with dairy cows. The latter investigators referred the maintenance costs to live weight by direct proportion. The results would have been of greater applicability had the calculations to the thousand-pound basis been made in proportion to the two-thirds or five-eighths power of the weight. The results obtained by G. Kühn and Kellner [40] while feeding approximate maintenance rations add weight to this argument since the value of 7.95 therms of net energy necessary to maintain their fat cattle is considerably above the values for thin and medium cattle collected by Armsby.[41] Means [42] has reported the results of experiments to determine the effect of uncomplicated obesity on the basal metabolism of man. He found normal values for heat production per square meter of body surface for people as much as 160 per cent over weight.

Trowbridge, Moulton and Haigh [43] have shown that the higher the previous plane of nutrition the greater is the maintenance cost during a following maintenance trial. The cost is given per unit of surface area.

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[35] "Nagel's Handbuch der Physiologie des Menschen," I, 469.

[36] *Archives of Internal Medicine,* 17 (1916), 887.

[37] "Metabolism and Growth from Birth to Puberty," Carnegie Institution of Washington, Publication 302, 145 and 173.

[38] *Jour. Agr. Research,* 11 (1917), 461.

[39] Iowa State College, Agr. Expt. Sta., Research Bul. 60 (1920).

[40] Reported by Kellner: *Landw. Vers. Stat.,* 53 (1900), 6-16.

[41] "The Nutrition of Farm Animals," New York, 1917, 291.

[42] *Arch. of Int. Medicine,* 17 (1916), 704.

[43] *Loc. cit.*

Mumford, Hogan and Salmon,[44] employing the units of reference as given by Moulton, have reached the same conclusion as a result of their work with cattle on very low planes of nutrition.

Trowbridge, Moulton and Haigh[43] have indicated that a long maintenance trial is conducive to a decreased maintenance cost but they point out that increasing age and previous treatment (plane of nutrition) are strong contributing factors. There was a noticeable tendency for the animals to become more economical as they became accustomed to the plane of nutrition.

Lowered planes of nutrition below the state of maintenance result in a lowered metabolism, or maintenance cost, according to Benedict and Ritzman.[45] In working with steers on drastic ration curtailment they show a specific depression in metabolism due to undernutrition from 2150 Calories per square meter of body surface per 24 hours standing to 1475 Calories after a period of submaintenance feeding on hay.

The animal has well known means of controlling its body temperature in spite of changes in external temperature. These are classed as chemical and physical means of regulation. The latter works by means of controlling the vaporization of moisture from the surface and its temperature through circulation and perspiration. When these means fail chemical regulation intervenes and the metabolism is increased in the case of cold external conditions to produce the additional heat necessary to maintain body temperature. The temperature of the surroundings at which chemical regulation intervenes has been termed the "critical temperature." The critical temperature for man wearing ordinary clothing appears to be about 15° C. For the dog it is about 20° C., for the guinea pig 30° to 35° C., and for the hog about 20° to 23° C. Tangl[45a] and von der Heide and Klein[46] have determined the latter values. The value for swine has also been determined by Capstick and Wood[46a] in the animal calorimeter built at Cambridge, England. They found the critical temperature for the hog to be 21° C. This determination has not been made for cattle. Cold, moist air increases the heat losses from the animal body while warm, dry air does not necessarily reduce the losses. The energy catabolism of the ordinary animal is on the whole affected less by external temperature and other thermal conditions than has been frequently imagined. Trowbridge, Moulton and Haigh[47] have shown that for their

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[44] *Jour. Agr. Research,* 22 (1921), 115.

[45] Publication 324, Carnegie Institution of Washington, Washington, 1923.

[45a] *Biochem. Ztschr.,* 44 (1912), 252.

[46] *Ibid.,* 55 (1913), 195.

[46a] *Jour. Agr. Science,* 12 (1922), 257.

[47] *Loc. cit.*

cattle the maintenance cost was least in the spring and early summer and greatest in the winter. The warm summer months caused an increase over the minimum probably due to flies and other annoyances of the hot summer.

It seems self-evident that greater activity of an animal will increase its maintenance cost. That it increases heat production in a calorimeter is so well known that it is rather gratuitous to mention it. Trowbridge, Moulton and Haigh [48] have presented some figures for beef cattle showing that the more active animal has a greater maintenance cost. Armsby and Fries [49] made determinations of the maintenance cost of a pure-bred beef animal and a scrub steer. The latter had more or less Jersey blood and was of a decidedly more nervous disposition than the pure-bred. The difference in the requirements of the two animals can reasonably be ascribed to this difference in temperament.

TABLE 59

Type as Affecting Maintenance

Year	Pure-Bred Steer Net Therms	Scrub Steer Net Therms
1905	5.873	6.052
1906	6.272	6.305
1907	4.723	6.007
Average	5.623	6.141

The Maintenance Requirement of Swine. The older experiments on the fasting catabolism of farm animals are those of Meissl, Strohmer and Lorenz [50] and of Tangl [51] upon swine. The former were carried out at a temperature close to 20° C., while some of Tangl's were below the critical temperature. Armsby [52] has calculated these results—excluding Tangl's below the critical temperature—per 100 pounds in proportion to the two-thirds power of the live weight. Meissl's swine gave 1.266 therms and Tangl's 1.249 therms. Per square meter of body surface Armsby calculated the value to be 1.089 therms. Fingerling, Köhler and Reinhardt,[53] using an entirely different experimental method, arrived at the value of 1.045 therms per square meter. Capstick and Wood [54] using the "large white" pedigreed hog about ten months old found the catabolism about 100 hours after the last meal to be 904 Calories or 0.904 therm per square meter of body surface per day. This was a direct determination

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[48] *Loc. cit.*, p. 36.
[49] U. S. Dept. Agr., Bur. An. Ind., Bul. 128 (1911), 53.
[50] *Ztschr. f. Biol.*, 22 (1886), 63.
[51] *Biochem. Ztschr.*, 44 (1912), 252.
[52] "The Nutrition of Farm Animals," New York, 1917, 286.
[53] *Landw. Vers. Stat.*, 84 (1914), 149.
[54] *Jour. Agr. Science*, 12 (1922), 257.

in a calorimeter with the animal fasting and asleep. It is a measure of the true basal catabolism and therefore is lower than the maintenance cost.

The metabolizable energy contained in actual maintenance rations of swine can be determined fairly accurately from experiments by von der Heide and Klein,[55] Taylor,[56] Carlyle,[57] Ostertag and Zuntz,[58] and Dietrich.[59] Table 60 summarizes the results. Armsby [60] has calculated the net energy using the factor 78.14 per cent and has found the net energy requirements shown in Table 61.

TABLE 60

Metabolizable Energy for Maintenance of Swine

	Therms per 100 Pounds
Maximum	2.558
Minimum	0.897
Average of all	1.534
Average omitting lowest and two highest	1.474

TABLE 61

Net Energy for Maintenance of Swine

	Therms per 100 Pounds
Maximum	1.998
Minimum	0.701
Average of all	1.199

The fact that this last average value agrees closely with the fasting catabolism reported above should not be taken as fixing the maintenance cost. The great range in the results of the maintenance trials indicates the urgent need for more experimentation.

The Maintenance Requirements of Sheep. No fasting catabolism experiments have been made with sheep. Some respiration and digestion experiments by Henneberg, Kellner, Hagemann, Wolff and others have been used by Armsby [61] to calculate the metabolizable energy requirements and from them the net energy cost. Table 62 presents his calculations. Calculated in proportion to the surface, *i.e.*, in proportion to the two-thirds power of the experimental weights and the 1000-pound weight of reference for cattle, Armsby found the net maintenance cost of sheep to be but 3.670 therms. His results for cattle on the same basis are 6 therms.

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[55] *Biochem Ztschr.*, 55 (1913), 195.
[56] Wis. Agr. Expt. Sta., Rpt., 1901, 67.
[57] *Ibid.*, Bul. 104 (1903), 31.
[58] *Landw. Jahrb.*, 37 (1908), 226.
[59] Ill. Agr. Expt. Sta., Bul. 163 (1913).
[60] *Loc. cit.*, 288.
[61] *Loc. cit.*, 292-4.

TABLE 62

Maintenance Requirements of Sheep

	Per 100 Pound Live Weight Metabolizable Energy Therms	Net Energy Therms
Respiration Experiments:		
Henneberg and Stohmann	1.475	0.779
Henneberg, Fleischer and Müller	1.420	0.781
Kellner	1.110	0.611
Hagemann	1.282	0.705
Average	1.322	0.719
Live Weight Experiments:		
Wolff, 1871, 6 experiments	1.634	0.863
Wolff, 1892-1893, 8 experiments	1.725	0.863
Carlyle and Kleinheinz	1.513	0.832
Average	1.624	0.853
Average of all	1.368	0.791
Average of two classes	1.473	0.786

This seems to show that the metabolism of sheep is distinctly lower than that of cattle and other species of animals.

The Maintenance Requirement of Cattle. With ruminants it is apparently impracticable, if not impossible, to determine the fasting catabolism. Instead two methods may be used. The basal catabolism may be calculated from two different periods when two different amounts of the same feed have been fed, both being less than that necessary for maintenance. Armsby[62] has developed this method with his calorimeter. The revised results are shown in Table 63. Nineteen different experiments of this kind, on nine different steers, comprise the work reported. The range of the figures is wide but this range is not at all unusual.

The net energy in actual maintenance rations has been calculated by Armsby[63] from the results reported by Kühn and Kellner, Haecker, Evvard, Eckles, Armsby, and Armsby and Fries. Kühn and Kellner worked with the respiration apparatus while the others used live-weight experiments. Table 64 gives the compilation using the original figures of Armsby. Here again the range of the figures is rather wide. The average of the respiration experiments is 5.934 therms and of the live-weight experiments 6.181 therms. The average obtained by Armsby's indirect method of calculation, omitting the alfalfa meal experiment, is 5.995 therms.

A fuller discussion of these results is given by Armsby[64] elsewhere.

The extensive maintenance trials with cattle reported by Trowbridge,

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[62] *Loc. cit.,* p. 282.
[63] *Loc cit.,* p. 291.
[64] U. S. Dept. Agr., Bur. An. Ind., Bul. 143 (1912).

TABLE 63

Net Energy Requirement for Maintenance of Cattle Corrected to 12 Hours Standing

Year	Experiment	Animal	Ration		No. of Determinations		Average Net Energy for Maintenance per Day and 1,000 Lbs. Live Weight
			Roughage	Concentrates	On Roughage	On Mixed Ration	Therms
1902	174	I	Timothy hay	Linseed meal	...	4	7.374
1903	179	I	Clover hay	...	1	...	5.984
1907	207	A	Timothy hay	...	1	...	4.685
			Timothy hay	Grain mixture	...	2	
1907	207	B	Timothy hay	...	1	...	6.144
			Timothy hay	Grain mixture	...	2	
1909	209	F	Alfalfa hay	...	3	...	6.096
			Alfalfa hay	Grain mixture	...	3	
1909	210	D	Corn stover	...	3	...	4.694
1911	211	D	Mixed hay	...	3	...	6.452
			Mixed hay	Hominy chop	...	1	
1911	211	G	Mixed hay	...	3	...	6.042
			Mixed hay	Corn meal	...	1	
1912	212	H	Alfalfa hay	...	6[1]	...	4.657
1913	216	J	Alfalfa hay	...	3	...	5.605
			Alfalfa hay	Starch	...	4	
1914	217	J	Alfalfa hay	Grain mixture	...	2	5.367
1915	220	K	Clover hay	...	1	...	6.425
			Clover hay	Corn meal	...	3	
Average of all							5.794
Average, omitting corn stover[2]							5.894

[1] Including three on alfalfa meal.

[2] Corn stover experiment not altogether satisfactory.

TABLE 64

Net Energy in Daily Maintenance Rations of Cattle[3]

No. of Single Experiments	Experimenter	Character of Feed	Condition of Animal	Per 1,000 Pounds Live Weight Maximum Therms	Minimum Therms	Average Therms
	Respiration Experiments					
17	Armsby and Fries	Roughage	Medium	7.430	4.723	5.936
5	" " "	Mixed rations	"	6.474	5.960	6.194
22	" " "	Average of all[1]	"	7.430	4.723	5.995
7	Kellner	Roughage	"	6.780	4.921	5.742
29	Average[2]					5.934
	Kellner	Mixed rations	Fat	8.871	7.319	7.946
	Live Weight Experiments					
10	Armsby	Hay only	Thin	7.044	6.136	6.505
3	Armsby	Mixed rations	"	6.039	4.713	5.423
6	Haecker		Medium	5.676	4.662	5.021
3	Evvard, 1st 60 day Experiment	Mixed rations	"	7.850	6.450	7.180
1	Evvard, 362 day Experiment	" "	"	....	....	8.090
7	Eckles	" "	"	7.079	5.841	6.173
	Average[2]					6.181
3	Evvard, 2nd 60-day Experiment	Mixed rations	Partly fattened	10.620	8.150	9.070

[1] Omitting the experiment on alfalfa meal.

[2] Giving each experiment equal weight.

[3] The figures of Armsby quoted here are not revised owing to certain practical difficulties. The change in the figures would, however, be slight.

Moulton and Haigh [65] have purposely been omitted since the method of calculating the energy content of the maintenance rations gives results estimated to be about 10 per cent too high.

Mumford, Hogan and Salmon [66] have recently reported a number of live-weight trials with cattle. They calculated the energy gained or lost through changes in body weight and corrected the energy consumption accordingly. Check animals served as guides in this calculation, but the validity of the method is not as great as that of direct experiments or of indirect calculations from respiration and calorimeter experiments. The results are shown in Table 65.

TABLE 65

MAINTENANCE COST ON LOW PLANES OF NUTRITION

No. of Animals	No. of Periods	Net Therms per 1000 Pounds		
		Group I	Group II	Group III
3	12	5.777		
3	11		4.869	
4	14			4.408

The animals were on three different planes of nutrition. Group I was fed to grow rapidly but not to become fat. Group II was fed to gain about one-half pound per day and Group III to gain about one-third pound per day. The maintenance cost decreased with decreasing plane of nutrition, the larger decrease being between Groups I and II.

The Missouri Results Recalculated. A statement concerning the extensive investigations begun at the University of Missouri in the spring of the year 1907 and known collectively as the "Use of Feed" experiment may well be given at this point. To H. J. Waters, then Dean of the College of Agriculture and Director of the Agricultural Experiment Station, belongs the credit for the conception of this important project and the direction of the early years of the work. Waters designated this experiment as "A proposed inquiry into the composition of the carcasses of cattle at different ages, different stages of development and in different conditions of fatness, or an attempt to ascertain to what uses steers of different ages, on different rations, and in different conditions of fatness put their food." He stated further that "the primary object of this experiment is to ascertain the rate of growth during each period of the life of a steer, when the period of most rapid growth ends, and to measure the effect of the rate of growth upon the ability of the animal to fatten." P. F. Trowbridge took full charge of this experiment after Waters left

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[65] Mo. Agr. Expt. Sta., Research Bul. 18 (1915).
[66] *Jour. Agr. Research,* **22** (1921), 115.

the institution and the final preparation of the data for publication and the interpretation of results were largely left to C. R. Moulton.

This general experiment included extensive trials to determine the cost of maintenance of cattle, the effect of fattening mature cattle, the effect of lowered plane of nutrition upon the growth of young fat cattle, as well as the effect of three different planes of nutrition upon the growth and composition of cattle from birth to maturity. The latter cattle were known as the "Use of Feed" cattle and were divided into three groups.

Group I animals were fed all they would eat of the ration. They were not considered full fed unless at least twice in ten days some of the feed was refused.

Group II animals were fed to secure maximum growth without the storage of surplus fat. This condition was determined by the opinion of the men of the animal husbandry department. For younger animals (under 2 years) a gain of about one pound per day seemed to give this condition. These animals refused practically no feed.

Group III animals were to have the growth distinctly retarded. They were to be in a condition in which one would expect to find cattle that were not being properly cared for. An average gain of one-half pound per day was judged to keep animals in about the desired condition. Animals under 18 months required to gain a little more than this or they became extremely thin. Animals over three years old began to improve in condition if allowed to gain continuously the one-half pound per day.

The results of these Missouri experiments have been reported in the following Research Bulletins of the Missouri Agricultural Experiment Station, Bulletins Nos. 18, 28, 30, 38, 43, 54, 55, 59, 61, and 62.

The results reported in Missouri Research Bulletin 18 have been recalculated employing the following method. Four representative steers of the Missouri "Use of Feed" group had been used by Armsby in his calorimeter. The Missouri feeds were used and the determinations of the metabolizable and net energy values of the rations were determined. This experiment was possible only through the co-operation of the United States Bureau of Animal Industry, the Institute of Animal Nutrition of the Pennsylvania State College, and the Agricultural Experiment Station of the University of Missouri. The senior author of this monograph represented the first two agencies and the junior author represents the third agency.

The following factors were used in calculating the energy content of the rations. The figures are not the revised figures determined according to the accurate method of calculation reported by Kriss and explained in Chapter 6. Revised figures for these rations have not been prepared as yet excepting for one of three animals used by Armsby. The use of the older figures seems justifiable until more work has been done at the Pennsylvania Institute of Animal Nutrition.

Group	Metabolizable Energy per Pound of Digestible Matter	Heat Increment per Pound of Dry Matter
Use of Feed	1.722 therms	0.5157 therms
Regular and special maintenance	1.731 therms	0.6033 therms

The calculations to the thousand-pound basis were made in proportion to the five-ninths power of the weights for the fat cattle and to the five-eighths power for other cattle. The results are given in Table 66. The average for all the maintenance trials is 6.093 therms of net energy with variations from 4.523 to 8.114 therms. Relative differences in activity, plane of nutrition, and fatness of the animals may well account for some of the differences. It is possible that some of the animals were gaining fat and others losting fat while keeping the body weight constant.

TABLE 66

MAINTENANCE TRIALS WITH MISSOURI CATTLE

Animal Number	Length of Trial Days	Average Live Weight, Pounds	Daily Metabolizable Energy, Therms	Daily Net Energy, Therms	Net Energy per 1,000 Pounds, Therms
500	120	855.4	11.389	6.706	7.394
500	140	918.2	11.661	6.840	7.215
502	180	992.6	11.407	6.556	6.587
507	153	1015.2	11.789	6.680	6.618
509	120	847.0	11.126	6.551	7.267
512	80	1047.9	14.437	8.355	8.114
512	124	1242.2	15.557	8.950	7.816
524	180	724.5	9.084	5.332	6.522
526	90	842.8	11.586	6.702	7.458
18	284	767.3	9.637	5.210	6.148
48	150	836.6	11.463	6.185	6.915
121	160	758.9	10.286	5.545	6.589
164	760	934.1	10.029	5.091	5.312
197	737	1081.2	11.020	6.232	5.935
588	1245	1212.3	11.148	6.219	5.514
589	580	1065.3	10.518	5.907	5.678
595	362	608.8	7.269	3.646	4.972
597	188	736.3	8.667	4.351	5.268
596	60	462.8	5.364	2.854	4.619
598	60	462.2	5.255	2.792	4.523
590	60	609.0	7.533	4.011	5.468
596	240	865.2	10.415	5.529	6.053
598	290	665.1	7.990	4.241	5.472
590	280	707.4	7.997	4.244	5.268
596	110	1240.7	13.626	5.980	5.226
598	110	926.9	12.003	5.486	5.753
590	110	845.7	9.650	4.330	4.808
Average of all trials					6.093

The first nine animals—the "Use of Feed" group—gave an average net maintenance cost of 7.103 therms. In terms of metabolizable energy this is equivalent to 12.648 therms.

The average of these twenty-seven trials is very close to the 6 therms proposed by Armsby [67] as an average value.

TABLE 67

CALCULATED MAINTENANCE COST

Growth and Fattening Experiments

Animal Number	Length of Trial, Days	Average Live Weight, Pounds	Total Net Energy Consumed, Therms	Energy Recovered in Gains, Therms	Net Energy Consumed in Excess of Gains, Therms	Excess Net Energy per 1000 Pounds Per Day, Therms
Group I						
556	72	195.6	280.1	97.7	182.4	8.14
557	147	271.3	874.4	418.6	455.8	7.88
547	238	251.6	1,031.8	372.3	659.5	7.43
505	303	376.1	2,231.5	814.9	1,416.7	9.41 [1]
541	307	411.1	2,001.4	754.2	1,247.3	7.67
532	482	644.5	4,361.8	1436.8	2,925.0	8.31
504	615	640.7	5,271.4	1631.2	3,640.2	8.14
515	1006	884.3	8,879.8	2709.3	6,170.5	6.70
527	1176	1157.9	12,706.4	3759.8	8,946.6	6.85
513	1343	1145.7	13,667.5	3549.8	10,117.7	6.84
501	1422	1226.7	15,416.7	3872.2	11,544.5	7.02
Group II						
554	72	163.6	202.9	54.4	148.6	7.53
552	142	203.2	424.0	111.8	312.3	6.87
550	238	211.9	776.7	181.7	595.0	7.58
538	307	272.9	1,075.0	278.1	796.9	6.57
503	324	374.6	1,970.6	496.1	1,474.5	9.18 [1]
523	775	541.9	4,341.0	728.3	3,612.7	7.23
507	1003	701.5	6,751.8	1117.0	5,634.8	7.24
526	1176	657.8	7,199.0	1144.8	6,054.2	6.95
502	1344	802.7	9,443.3	1131.3	8,312.0	7.24
512	1426	846.6	11,481.7	1498.7	9,983.1	7.89
Group III						
555	72	163.2	177.2	10.0	167.2	8.49
548	142	184.5	369.8	52.1	317.7	7.49
558	243	185.9	557.6	96.9	460.7	6.31
540	307	255.4	898.0	197.6	700.3	6.05
531	485	331.9	1,670.5	213.6	1,456.9	6.61
525	765.5	462.6	3,626.5	470.6	3,155.9	7.16
524	1211.5	540.4	6,194.1	585.1	5,609.0	7.19
509	1348	668.6	8,534.0	965.9	7,568.1	7.49
500	1427	685.2	9,431.7	1027.1	8,404.6	7.72
Average						7.31

[1] Omitted from average.

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[67] "Nutrition of Farm Animals," 292.

The preparation of the data in Chapter 9 made it apparent that the five-eighths or five-ninths power was increasing the spread of the maintenance costs and resulting in extreme percentage recoveries of energy in the gains made. These data on the percentage recovery of energy can serve as a basis for calculating maintenance costs. Subtracting from the total net energy consumed in the feed the energy recovered in the gains leaves the the net energy available for maintenance. This was reduced to the daily net energy for maintenance and this latter value was plotted against the average live weight in pounds. The result is shown in Figure 6, which furnishes data for the derivation of the following formula:

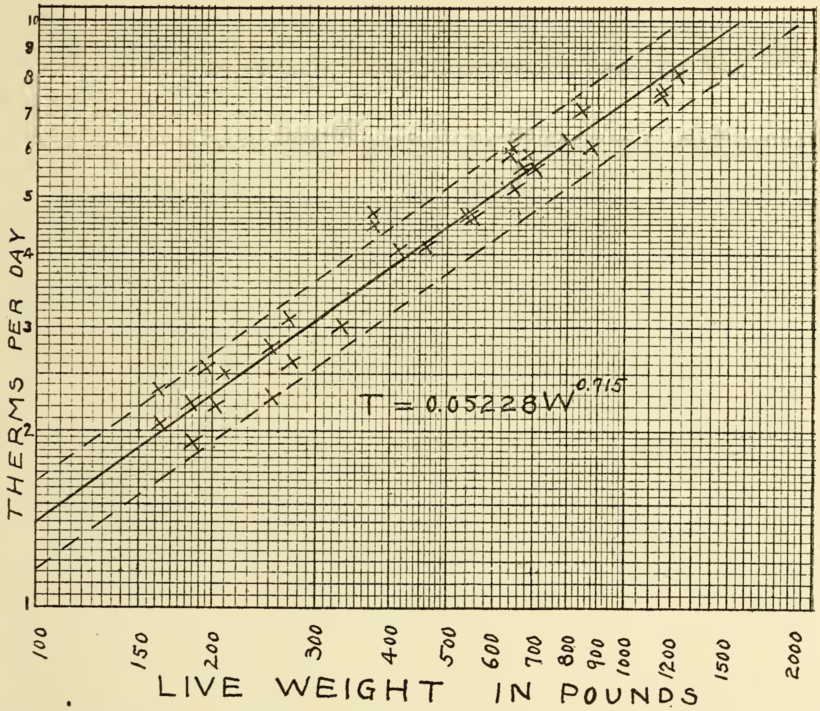

FIG. 6.—Relation between maintenance cost and live weight. Data of Missouri "Use of Feed" cattle during growth and fattening.

$$T = .05228\ W^{0.715}$$

where T is therms of net energy and W is live weight in pounds. For a thousand-pound steer, then, the maintenance cost is approximately 7.3 ± 1.2 therms for this group of animals. Very high values for two animals have been omitted in this calculation. Table 67 gives the details.

This figure indicates that the maintenance costs of these animals while gaining weight are proportional to the 0.715 power of the average live weight. Two-thirds is equivalent to 0.666, five-eighths to 0.625, and five-ninths to 0.555. The maintenance cost, then, increases more rapidly with weight than does the surface area.

The Missouri results with growing and fattening cattle having the run of small lots gives 7.3 ± 1.2 net therms per thousand pounds as the average maintenance cost. Some of these animals had been on body weight maintenance trials and gave a maintenance cost per thousand pounds of 7.10 therms when calculated in proportion to the five-eighths power of the weights. When the 0.715 power was used the cost became 7.264 therms net energy. That the higher requirement shown by the "Use of Feed" animals is not due to the fact that they were gaining in body tissue is attested by the fact that the live weight maintenance costs agree very well with those calculated by difference during growth and fattening. The average of the results from all twenty-seven cattle on body weight maintenance in the open lot gives 6.093 therms by the five-eighths power and 6.182 therms by the 0.715 power method. These figures are not much above the 6 therms of Armsby's standard.

Chapter 9.

Net Efficiency

Efficiency of Production of Body Substance

The net energy value of a feeding stuff or ration for growth or fattening, or both, is that part of its metabolizable energy which can be stored up by the animal in the increase. The ration of such an animal must supply an amount of net energy equal to the maintenance requirement plus the quantity of energy contained in the gain. There may be losses of energy in addition to the maintenance cost besides those considered when the net energy was discussed in the previous chapter. In other words, there may be losses due to the chemical changes involved in the formation of fat from proteins and carbohydrates. The available data indicate that these losses are not of great moment. This chapter deals with the utilization of energy consumed above that required for maintenance.

Calculations of the net energy values for growth and fattening have been made by a few investigators, notably Armsby.

The difference in maintenance value and production value for meadow hay is shown by Armsby.[1] Of this ration 53.7 per cent of the metabolizable energy had been available for maintenance while for fattening 40.4 per cent [2] was available. This calculation is based on an experiment by Kellner upon a mature ox, in which meadow hay was added to a basal ration already sufficient to cause some gain. The addition of 7.7 pounds of the hay to the ration increased the metabolizable energy by 5.50 therms, the heat production by 3.28 therms and the energy of the fat and protein gained by the animal by 2.22 therms. This is a recovery of 40.4 per cent of the metabolizable energy of the ration added.

The percentage utilization of the metabolizable energy of milk for the growth of young sucklings was also computed by Armsby [3] assuming the fasting catabolism to be the same as in mature animals. For infants the percentage utilization was 73.10, for little pigs it was 70.31 and for calves 73.77.

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[1] "Nutrition of Farm Animals," 360.
[2] The uncorrected value of 40.7 was originally reported.
[3] "The Nutrition of Farm Animals," 392.

The use of energy in embryonic growth has been calculated by the same author [4] from results obtained by Tangl and Mituch upon hens' eggs. In the embryos there were recovered 59.87 and 63.84 per cent of the energy used for the production of the embryos.

The Missouri Experiments on Cattle.—Very few data exist which permit of the accurate calculation of the efficiency of production of body substance by our domestic animals. The extensive work of Moulton,

TABLE 68

ENERGY STORED IN GAINS BY CATTLE

Missouri Data

Animal	Age, Months	Weight Protein Gained, Kilograms	Weight Fat Gained, Kilograms	Energy in Protein Stored, Therms	Energy in in Fat Stored, Therms	Total Energy Stored,[1] Therms
Group I. Full Fed from Birth						
556	3	7.07	6.08	40.05	57.66	97.70
557	5.5	18.30	33.18	103.72	314.88	418.60
547	8.5	23.63	25.13	133.87	238.46	372.33
505	11	35.89	64.44	203.37	611.49	814.86
541	11	39.22	56.06	222.24	531.92	754.15
532	18	61.39	114.75	347.87	1,088.89	1,436.76
504	21	64.31	133.51	364.38	1,266.82	1,631.21
515	34	81.57	236.82	462.18	2,247.11	2,709.30
527	39.5	83.42	346.42	472.66	3,287.17	3,759.83
513	44.5	90.04	320.33	510.21	3,039.60	3,549.81
501	47	91.93	353.18	520.92	3,351.26	3,872.18
Group II. Fed from Full Growth Without Appreciable Fattening						
554	3	4.60	2.98	26.05	28.31	54.36
552	5.5	7.46	7.32	42.26	69.49	111.76
550	8.5	9.72	13.34	55.06	126.59	181.66
538	11	18.36	18.34	104.05	174.04	278.09
503	11	29.95	34.39	169.71	326.37	496.08
523	26	51.61	45.93	292.46	435.82	728.28
507	34	68.28	76.94	386.88	730.08	1,116.96
526	40	66.44	80.97	376.47	768.33	1,144.80
502	44.5	79.81	71.57	452.21	679.08	1,131.28
512	48	74.92	113.20	424.51	1,074.15	1,498.66
Group III. Fed for Scanty Growth						
555	3	1.92	0.09[2]	10.85	0.85[2]	10.00
548	5.5	4.97	2.52	28.16	23.93	52.10
558	8.5	7.96	5.45	45.13	51.76	96.89
540	11	13.30	12.89	75.37	122.27	197.64
531	18.5	18.12	11.69	102.68	110.95	213.63
525	26	38.35	26.70	217.28	253.33	470.62
524	40.5	53.44	29.75	302.77	282.28	585.05
509	45	68.98	60.60	390.86	575.00	965.86
500	48	70.02	66.44	396.74	630.41	1,027.15

[1] Calculated from the factors for beef cattle given in Chapter 7.
[2] Loss.

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[4] "The Nutrition of Farm Animals," 394.

Trowbridge and Haigh[5] furnishes accurate data for the composition of the increase and of the ration fed to give this increase. The metabolizable and net energy of the rations can be calculated fairly accurately as a result of the co-operative work discussed in Chapter 8.

The weights of protein and fat gained by thirty different beef cattle and the energy content of the gain is given in Table 68. The energy in the gains varies from ten thousand to nearly four million large Calories. The gains covered from three to forty-eight months of growth and fattening.

Table 69 gives the complete data for the energy consumption and the recovery in the gains. The average maintenance requirement of the "Use of Feed" steers was used for all animals excepting those for which an individual maintenance cost had been determined. The maintenance requirements have been calculated from the average figure of 12.648 metabolizable therms using the five-eighths and five-ninths powers and also using the 0.715 power.

On the first basis the Group I cattle show recoveries ranging from 136.24 per cent to 46.03 per cent, but 8 out of 11 animals give an average of 55.17 per cent recovery of metabolizable energy consumed above maintenance. The Group II and Group III cattle show many instances where the calculated maintenance cost appeared to exceed the metabolizable calories consumed in the food. In other cases the recovery in the gains greatly exceeded the metabolizable energy consumed above maintenance. Of the thirty results but twelve can be used in calculating the average which is 55.72 per cent.

When calculated on the basis of the 0.715 power for maintenance the extreme cases of energy recovery are greatly reduced. Ten out of eleven Group I animals give an average of 56.34 per cent recovery of the metabolizable therms and eighteen out of the total of thirty give an average of 56.50 per cent recovery.

In calculating the above averages it has been necessary to omit those animals for which the maintenance cost appeared to exceed the metabolizable energy of the ration as well as those which showed gains greatly in excess of the metabolizable energy consumed above maintenance. The former would give a negative percentage recovery, if such a conception is possible, and the latter a percentage in excess of 100. The results from five other animals were arbitrarily omitted in calculating the averages because the recovery exceeded 78 per cent.

Some differences in the maintenance cost when computed to cover long feeding trials or where the margin of food consumption over main-

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[5] Missouri Agr. Expt. Station, Research Buls. 28, 30, 38 and 55.

TABLE 69

Availability of Energy for Growth and Fattening of Cattle

Missouri Data

				Using ⅝ and ⅚ Power of Weight				Using 0.715 Power of Weight		
Animal Number	Length of Trial, Days	Average Live Weight, Pounds	Metabolizable Energy Consumed, Therms	Calculated Maintenance Cost, Therms	Energy above Maintenance, Therms	Energy in Gains Made, Therms	ity—Per- Availabil- Percentage Recovery, Per Cent	Calculated Maintenance Cost, Therms	Energy above Maintenance, Therms	Availabil- ity—Per- centage Recovery, Per Cent
Group I										
556	72	195.6	400.1	328.4	71.7	97.7	[2]	283.6	116.6	83.82[3]
557	147	271.3	1,353.9	822.7	531.2	418.6	78.81[3]	731.6	622.3	67.27
547	238	251.6	1,712.3	1,270.7	441.6	372.3	84.32[3]	1,122.3	590.0	63.11
505	303	376.1	3,655.6	2,073.8	1,581.8	814.9	51.51	1,904.6	1,751.0	46.54
541	307	411.1	3.459.7	2,227.8	1,231.9	754.2	61.22	2,056.6	1,403.2	53.75
532	482	644.5	7,754.2	4,632.7	3,121.5	1,436.8	46.03	4,453.1	3,301.0	43.53
504	615	640.7	9,404.8	5,889.2	3,515.6	1,631.2	46.40	5,658.0	3,746.9	43.54
515	1006	884.3	15,965.0	11,884.0	4,081.0	2,709.3	66.39	11,653.0	4,312.0	62.83
527	1176	1157.9	22,427.0	16,136.0	6,291.0	3,759.8	59.77	16,518.0	5,909.0	63.63
513	1343	1145.7	24,529.7	18,323.7	6,206.0	3,549.8	57.20	18,721.0	5,808.7	61.11
501	1422	1226.7	27,478.4	20,152.4	7,326.0	3,872.2	52.85	20,814.7	6,663.7	58.11
Group II										
554	72	163.6	287.1	293.7	[1]	54.4	[1]	249.6	37.5	[2]
552	142	203.2	607.5	663.4	[1]	111.8	[1]	574.7	32.8	[2]
550	238	211.9	1,260.0	1,141.4	118.6	181.7	[2]	992.6	267.4	67.94
538	307	272.9	1,775.4	1,724.4	51.0	278.1	[2]	1,534.3	241.1	[2]
503	324	374.6	3,186.2	2,218.5	967.8	496.8	51.26	2,030.8	1,155.4	43.19
523	775	541.9	7,290.0	6,683.7	606.2	728.3	[2]	6,325.2	964.8	75.49
507	1003	701.5	11,468.2	9,470.2	1,997.9	1,117.0	55.91	9,172.9	2,295.3	48.67
526	1176	657.8	12,307.4	12,020.4	287.0	1,144.8	[2]	11,576.0	731.4	[2]
502	1344	802.7	16,135.2	13,740.3	2,394.9	1,131.3	47.24	13,411.4	2,663.8	42.47
512	1426	846.6	19,688.9	18,225.5	1,463.4	1,498.7	[2]	17,954.8	1,734.1	86.42[3]

TABLE 69—*Concluded*

				Using 5/8and 5/9 Power of Weight				Using 0.715 Power of Weight		
Animal Number	Length of Trial, Days	Average Live Weight, Pounds	Metabolizable Energy Consumed, Therms	Calculated Maintenance Cost, Therms	Energy above Maintenance, Therms	Energy in Gains Made, Therms	Availability—Per-Percentage Recovery, Per Cent	Calculated Maintenance Cost, Therms	Energy above Maintenance, Therms	Availability—Percentage Recovery, Per Cent
Group III										
555	72	163.2	252.1	293.3	[1]	10.0	[1]	249.1	3.0	[2]
548	142	184.5	536.0	625.5	[1]	52.1	[1]	536.4	[1]	[1]
558	243	185.9	885.0	1,073.8	[1]	96.9	[1]	922.9	[1]	[1]
540	307	255.4	1,467.5	1,654.5	[1]	197.6	[1]	1,463.3	4.2	[2]
531	485	331.9	2,790.3	3,078.9	[1]	213.6	[1]	2,788.0	2.3	[2]
525	765.5	462.6	6,002.0	5,980.4	21.7	470.6	[2]	5,579.5	422.5	[2]
524	1211.5	540.4	10,379.9	9,576.7	803.2	585.1	72.84	9,060.5	1,319.4	44.34
509	1348	668.6	14,395.7	13,563.0	832.7	965.9	[2]	13,080.3	1,315.4	73.43
500	1427	685.2	15,951.3	14,655.0	1,296.3	1,027.1	79.24 [3]	14,165.0	1,786.3	58.06

[1] Calculated maintenance cost is in excess of metabolizable energy consumed.

[2] Energy recovered in gains exceeds the calculated energy consumed above maintenance.

[3] These results as well as those marked [1] and [2] were omitted in calculating the average.

tenance needs was small gave rise to impossible recoveries. These idiosyncrasies may be smoothed out by comparing the energy consumption above maintenance of the total thirty cattle to the total recovery, counting the two cases where the maintenance cost exceeded the food consumption as negative values. Thus, the thirty cattle consumed above maintenance 49,162.772 therms of metabolizable energy and recovered in the gains of body substance 29,667.587 therms. This gives an average recovery of 60.37 per cent.

For the same ration fed some of these animals in the calorimeter, Armsby obtained the results shown in Table 70, to which have been added the average results shown above.

TABLE 70

Percentage of Net Energy and Percentage Recovery in Gains

Missouri Use of Feed Ration

	Per Kg. of Dry Matter			
	Average Metabolizable Energy Cals.	Heat Increment Cals.	Net Energy Cals.	Net as Per Cent of Metabolizable Energy
Steer 520 (C)	2517	1139	1378	54.75
Steer 506 (E)	2625	1166	1459	55.58
Steer 508 (F)	2625	1105	1520	57.90
Average of all	2598	1137	1459	56.16

	Consumed Above Maintenance, Therms	Recovered in Gains, Therms	Recovery of Metabolizable Energy in Gains, Per Cent
Average of 12 animals by ⅝ths and 5⁄9ths powers			55.72
Average of 18 animals by 0.715 power			56.50
Total of 30 animals	49,162.772	29,667.587	60.37

The figures for the metabolizable and net energy and for the heat increment of the ration used by the Missouri cattle are the unrevised figures. Revised data have been prepared for Steer 508 only, the other data being withheld temporarily from publication due to certain problems that are presented in the determination of the net energy by growing animals (Steers 520 and 506). The continued use of the older figures seems justifiable until these problems are cleared up. Also the Missouri cattle used in obtaining the data of Tables 68, 69, and 70 had to face these same problems, and so the composite figure may be the more justifiable.

These percentages of net energy in the ration and of recovery in the gains serve as a measure of the relative values of feeds for animal production and of the efficiency of the animal as a converter. Comparisons in the last respect must always be made on the same ration and under similar, if not identical, conditions. The average percentage availability of the energy of this ration by the calorimeter method is 56.16 per cent and by the comparative slaughter method 55.72, 56.50, and 60.37 per cent according to three modifications in the calculations. Perhaps the second figure is the most reliable. At any rate these latter figures are an excellent experimental verification in practice of the figures of the calorimeter.

With other Missouri cattle on a somewhat similar ration, Moulton[6] has shown a recovery in the gains in the case of two steers of 53.39 and 52.49 per cent of the metabolizable energy consumed above maintenance. The availability of this same ration calculated by the method of Armsby was shown to be 55 per cent.

The Möckern Experiments on Cattle. The Möckern experiments upon cattle by G. Kühn and Kellner[7] in the respiration chamber serve as an excellent source of knowledge regarding the net utilization of feed by cattle. Maintenance requirements were calculated in proportion to the two-thirds power of the weights. Armsby[8] has recalculated the results making corrections for differences in weights of the animals and differences in the amount of the basal ration consumed in the trial and in the basal ration periods. For the details reference must be made to the original work.

The results on eight different varieties of feed show recoveries varying from 17.4 per cent for extracted wheat straw to 66.8 per cent for beet molasses and 67.3 per cent for peanut oil.

The Göttingen-Weende Experiments on Sheep. A series of respiration experiments on sheep was made by Kern and Wattenberg at the Göttingen-Weende Experiment Station in 1879. The results were reported after Kern's death by Henneberg and Pfeiffer.[9] In these experiments varying quantities of nearly pure proteins were added to a basal ration of hay and barley meal. The experiments suffered some defects in technique and the original calculations contained errors of method which Armsby corrected in his calculations. Differences in methane production and gain of fat having been properly accounted for, Armsby[10] arrives at the figures shown in Table 72.

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[6] *J. Biol. Chem.*, 31 (1917), 389.

[7] *Landw. Vers. Stat.*, 44 (1894), 257; 47 (1896), 275; 50 (1898), 245; 53 (1900), 1.

[8] "Principles of Animal Nutrition," New York, 1910, 455.

[9] *Journ. f. Landw.*, 38 (1890), 215.

[10] "Principles of Animal Nutrition," 465.

TABLE 71

Percentage of Metabolizable Energy Recovered in the Gains

Feed Used	Sample	Ox	Percentage Recovery
Meadow Hay	V	F	40.0
	V	G	36.2
	Average		38.3
	VI	H 2	50.4
	VI	H 7	48.4
	VI	J	34.8
	Average		44.5
	Average V and VI..................		41.4
Oat straw		F	38.8
		G	33.4
		Average	36.1
Wheat straw		H	10.8
		J	24.0
		Average	17.4
Extracted Rye Straw		H	67.3
		J	58.6
		Average	63.0
Beet molasses	I	F	58.5
	II	H	83.4
	II	J	50.2
		Average	66.8
Starch Kühn's Experiments	I	III	50.0
	I	IV	49.2
		Average	49.6
	II	V 2a	53.2
	II	V 2b	53.7
	II	V 3	59.7
	II	VI 2b	48.1
	II	VI 3	46.6
		Average	50.4
		Average I and II.	50.0
Starch Kellner's Experiments	I and II	B	65.4
	I and II	C	57.6
		Average	61.5
	III	D	53.7
	III	F	64.8
	III	G	65.8
		Average	61.4
	IV	H	56.0
	IV	J	54.8
		Average	55.4
		Average III and IV	58.4

TABLE 71—*Concluded*

Feed Used	Sample	Ox	Percentage Recovery
Wheat Gluten Kühn's experiments		III 3	45.3
		III 4	48.0
		Average	46.7
		IV	58.2
Wheat Gluten Kellner's Experiments	I	B 1	36.9
	I	B 3	49.7
	I	C	43.2
		Average	43.3
	II	D	37.3
		Average I and II.	40.3
Peanut oil	I	D	51.6
	II	F	65.1
	II	G	69.4
		Average	67.3

With the exception of Period II, for which there is no obvious explanation, the results are fairly uniform and do not seem to indicate any considerable differences in the utilization of different quantities. These figures are considerably higher than in the Möckern experiments, but in view of the uncertainties attaching to them much stress should not be laid on this fact.

TABLE 72

PERCENTAGE OF METABOLIZABLE ENERGY RECOVERED IN GAINS OF SHEEP

Feed	Period	Energy of Added Food, Cals.	Energy of Resulting Gain, Cals.	Per Cent Utilized, Cals.
Conglutin	II	715.4	605.7	84.68
	III	1245.8	842.4	67.63
	IV	1902.3	3288.8	67.76
Flesh meal	V	1288.2	780.7	60.59
	VI	582.1	403.6	69.35

Experiments on Swine. Six respiration experiments on swine by Meissl, Strohmer and Lorenz[11] and similar experiments on a swine by Kornauth and Arche[12] have served Armsby[13] as a basis of calculating the percentage recovery of the excess food in the gains made by swine. The metabolizable energy was computed by the means of factors and no corrections for methane or determinations of the amounts were made. The maintenance requirements were calculated from the fasting catabolism assuming 91 per cent net availability of the ration for maintenance. Too much value should not be attached to such computation, but it is con-

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[11] *Zeit. f. Biol.,* 22 (1886), 63.
[12] *Landw. Vers. Stat.,* 40 (1892), 177.
[13] "Principles of Animal Nutrition," 452.

sidered worth while to reproduce the figures which appear in Table 73. Where the proportion of protein in the food was similar, the percentage recovery is much the same in the two sets of experiments.

TABLE 73

PERCENTAGE OF METABOLIZABLE ENERGY RECOVERED IN THE GAINS OF SWINE

Food	Excess Above Maintenance, Cals.	Recovered in Gain, Cals.	Percentage Recovery	Nutritive Ratio 1:
Meissl, Strohmer and Lorenz:				
Rice	4292	3464	80.7	15.4
Rice	5386	4048	75.2	14.1
Barley	2503	1774	70.9	9.3
Rice, flesh meal, and whey	3809	2556	67.1	2.4
Kornauth and Arche:				
Cockle, barley and maize	1633	1170	71.1	6.7
Rape-cake, barley and maize	1677	1095	65.3	6.2

Comparative Efficiency of the Production of Milk and Body Substance.

The results on net energy for milk production reported in Chapter 6 hardly lend themselves to a computation of the relative efficiency of production of milk and body substance. Certain feeding standards exist which are expressed in different terms and which are derived from different kinds of production. Thus the feeding units of Kellner and Armsby have been worked out from fattening trials with oxen. The former is expressed as starch values and the latter in terms of Calories or therms. The Scandinavian, or Nordic, feeding unit on the other hand has been worked out with feeding trials with milk cows. This unit is expressed in terms of kilograms of barley or of dry solids in roots or other feeding stuffs. This unit will produce 3 kilograms of milk containing 3.5 per cent fat and having an energy equivalent of 700 Calories. This Nordic feeding unit then represents 2100 Calories in milk production according to Nils Hansson.[14] He further calculates that the Kellner starch value, equivalent to the effect of 1 kilogram of starch in fattening of ruminants, gives rise to a production of 248 grams of body fat. This body fat contains 9.5 Calories per gram and the energy equivalent is then 2356 Calories. The fodder mixtures used in the Swedish practice are such that one Nordic food unit corresponds to 0.7 kilograms of starch value. Multiplying 2356

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[14] "Die Nettoenergie der Futtermittel bei der Futterung von Milchkühen," Internationaal Congres Voor Rundveeteelt, The Hague, 1923.

Calories by 0.7 gives 1650 Calories which a Nordic feed unit would have yielded in producing body fat. The same food that yields 2100 Calories in milk production yields only 1650 Calories in body fat production, which is 78.6 per cent of the former or a decrease during production of body fat of 21.4 per cent. Another way to express the results is to state that a food which will yield 1000 Calories in milk production will yield 786 calories in producing body fat.

Experiments of Mollgaard. Holger Møllgaard[15] has recently discussed this whole question at some length. He points out that milk production depends primarily, as far as quantity is concerned, on the productiveness of the milk gland and, secondarily, on the quantity and composition of the feed. Therefore, the energy content of the milk produced under given experimental conditions is no reliable measure of the net energy of the feeding stuffs supplied. This means that the direct determination of the net energy of any feeding stuff in milk production is impossible. The only other way that can be employed is to determine the ratio of net energy in milk production to the net energy in fat production. Møllgaard presents experimental evidence to show that this ratio is independent of the quantity and composition of the milk as well as of the composition of the food. The latter is true as long as changing composition does not induce any change in the chemical processes by which the milk is made. This means practically that proteins and fats of the feed must not be converted into milk sugar. A food composition making such a process necsesary will never occur in practical feeding. Hence the ratio will not be changed by any composition of food occurring in practice.

The first method used by Møllgaard to determine the ratio of net energy in milk production to the net energy in body fat production is an indirect one based upon the following principles: Using the directly measured digestion quotients the starch value of the feed is determined according to Kellner's method. The starch value is converted into net energy. The balance of energy is determined by means of respiration experiments. The average net energy required for maintenance is computed proportionally to the two-thirds power of the live weight using Armsby's figures per 1000 pounds. Subtracting this from the net energy in the feed gives the net energy available for production. When this is corrected by the energy balance as determined there is left the net energy which is available for milk production. This is compared with the energy content of the milk produced. To determine this ratio is the

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[15] "New Views Regarding the Scientific Feeding of Dairy Cattle," International Congress of Cattle Breeding," The Hague, 1923.

same as determining the energy equivalent of the milk itself for fattening. This energy equivalent per 1000 Calories in the milk is called the production equivalent of the milk. A simpler expression, perhaps, is the following: The *production equivalent* is the energy content of body gains which would be produced by the feed that results in the production of 1000 Calories in milk.

From six experiments on dairy cows Møllgaard calculates that feed which produced 1000 Calories in milk would produce 822 Calories in body fat gained. From the records of Danish cow-testing associations he has computed in a similar manner that feed which produced 1000 Calories in milk would produce only 818 Calories in body fat gained. From similar Swedish statistics of Nils Hansson he showed that feeds which produced 1000 Calories in milk would produce 802 Calories in body fat. These figures are really only good approximations of the true value for various assumptions must be made in following the above method of computation not the least of which is assumptions concerning the maintenance cost of the cows in the tests.

A new and very exact method of determining this ratio has been devised and used by Møllgaard. A cow yielding at least 15 kilograms of milk daily is fed on a food sufficient to give a slight gain of energy by the animal. The balance of energy is determined exactly by means of a complete metabolism experiment covering 28 days and comprising 6 respiration experiments of 24 hours each. When this is done the yield of milk is artificially diminished by reducing the quantity taken out of the milk gland 500 grams every day for 6 to 10 days without any change in quantity or composition of the food. When the yield has dropped a certain amount (3-5 kilograms) and the new quantity is constant the animal has, in comparison with the preceding position, a surplus of food, *and this surplus has the quantity and composition which is just necessary for the production of the amount of milk lost. This surplus will induce a gain of energy corresponding to its net energy in fat production.* Under these circumstances it is clear that the food which produces a gain of energy by the body is the same food that produced the milk yield which was lost. This method of direct measurement of the relative energy equivalent of food for milk production and for fattening is very ingenious.

Using this method one experiment is reported with one cow yielding 15.4 kilograms of milk containing 2.8 per cent of fat in the period of high production against 9.9 kilograms milk containing 3.1 per cent of fat in the period of low production. Table 74 shows the results.

The energy gain by the body is corrected for the extra energy consumed in the feed. Then it is found that the feed which had supported

TABLE 74

Energy Content of Milk and Body Gains of a Cow

Experiment	Kg. Milk Produced	Fat Per Cent	Metabolizable Energy of Feed, Cals.	Energy Content of Milk, Cals.	Energy in Body Gains, Cals.
28	15.4	2.8	29,996	9446	1647
29	9.9	3.1	30,150	6381	4438
Difference	5.5		154	3065	2791

a production of 3065 Calories in the form of milk causes a production of 2637 Calories in the form of body gains. The ratio, then, or the production equivalent is 860 net Calories. Stated more clearly: the feed which produced 1000 Calories in milk produced only 860 Calories in body gains. This figure is not far from the values calculated by the preceding method.

From this preliminary work Møllgaard feels justified in reporting the following conclusions:

(1) The net energy of the feeding stuffs is greater in milk production than in fat production.

(2) The value of the production equivalent is probably independent of the composition of the milk.

(3) The numerical value of the production equivalent probably lies between 800 and 850 net Calories.

Experiments of the Institute of Animal Nutrition. Recently Fries, Braman and Cochrane[16] have reported on "The Relative Utilization of Energy in Milk Production and in Body Increase." The work was done in Armsby's calorimeter with three different dairy cows and it covered eight experimental periods. Alfalfa hay and mixed grain was fed. The grain was made up of: wheat bran, 3 parts; ground oats, 3 parts; corn meal, 3 parts; old process linseed meal, 1 part. During one period one cow (Cow 631) was dry and gained 3863.5 Calories in the form of body substance. From the average live weight the cost of maintenance was estimated. This, in terms of metabolizable energy, was subtracted from the total metabolizable energy consumed leaving 7755.7 Calories of metabolizable energy available for production. The recovery in body substance, therefore the net energy, was 49.815 per cent of the amount available. In producing body substance the dry matter of the ration consumed above maintenance yielded 1.2121 therms of net energy per kilogram.

In another period this same cow produced milk and recovered in the milk 64.832 per cent of the metabolizable energy available for milk pro-

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[16] U. S. Dept. of Agr. Bul. 1281.

duction. One kilogram of dry matter of the feed consumed above that needed for producing body substance and for maintenance yielded 1.5604 therms of net energy. The net energy value for body increase was, then, 22.32 per cent less than for milk production. Stated in another manner, feed which would produce 1000 Calories in the form of milk produced only 776.8 Calories in the form of body increase.

Assuming that the net energy value for body increase applied to all three cows these investigators obtained the values for milk production shown in Table 75.

TABLE 75

Net Energy Values for Milk Production
(Results of Fries, Braman and Cochrane)

Cow	Period	Net Energy in Terms of Metabolizable Energy, Per Cent	Net Energy per Kilogram Dry Substance, Therms
631	I	64.83	1.560
	II	97.76	2.322
615	I	75.76	1.776
	II	67.26	1.670
	III	60.13	1.487
579	I	68.92	1.739
	II	69.69	1.780

During period II Cow 631 gave only 0.8 kilograms of milk daily. While dry in period III she was with calf. The calculated maintenance cost was therefore probably too low. The authors have recalculated period II allowing for errors that might be due to the facts just set forth. They found the corrected figures to be as follows:

Cow	Period	Net Energy in Terms of Metabolizable Energy, Per Cent	Net Energy per Kilogram Dry Substance, Therms
631	II	74.91	1.780

Using the corrected value for Cow 631 period II, the average net energy value for milk production is 1.685 therms per kilogram of dry substance in the feed. The 1.2121 therms net enery for production of body substance shown by Cow 631 in period III is but 71.94 per cent of the average net energy for milk production. Expressed another way this means that feed which will yield 1000 Calories in the form of milk will yield but 719.4 Calories in the form of body gains. This value would have more validity if the net energy for producing body substance had been determined for all seven periods for the three cows rather than for one period for one cow.

All of these results reported have not been corrected for differences in time spent standing and lying. Furthermore, the maintenance cost was calculated from Armsby's average and the live weights of the cows. Differences in the cost of maintenance might well have had an effect upon the results reported. This effect could have been in amount only and not in the direction of the difference. In other words feed will yield less energy in body substance gained than in milk produced. The exact value of this ratio cannot well be determined by these experiments although the indications are that it is below 0.8 to 1.0. Stated in the terms employed by Møllgaard, feed which produces 1000 Calories in the form of milk will produce less than 800 Calories in the form of body substance.

Comparative Net Efficiency. All of the experiments quoted in this section show that the dairy cow can return more of the metabolizable energy consumed above its needs for maintenance and body gain in the form of milk than can be returned in the form of body substance. According to Hansson and Fries, Braman and Cochrane the latter is less than 80 per cent of the former. However, the work of Møllgaard, which is not open to the criticism that must be met by the other experiments, shows that the recoveries in body gains may be 86 per cent of the recoveries in milk produced. According to Fries, Braman and Cochrane[17] milk production takes place normally and principally not by transformation of body tissue but by a more direct and less expensive process. The milk gland must then produce milk directly from the absorbed nutrients of the feed. This activity of the milk gland must be more efficient than the activity of other body cells in producing fat and protein, *i.e.,* body substance, from the same nutrients of the feed.

The Effect of the Protein Level upon the Utilization of Net Energy. In connection with his study of the ratio of net energy for milk production to net energy for body increase, Møllgaard[18] investigated the protein requirement for milk production and its effect upon the "production equivalent." He points out that several researches and much practical experience suggest a connection between the protein in the food and the percentage of fat in the milk. This is strikingly shown by an experiment covering eight periods in which different amounts of digestible nitrogen were fed to the same cow. The work was done at a time in the period of lactation when the fat percentage was expected to be constant. The fat varied directly with the nitrogen intake but was constant for those periods having a like consumption of nitrogen.

If this is true then the protein requirement is not determined by the

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[17] *Loc. cit.*

[18] International Congress of Cattle Breeding, The Hague, 1923.

extent of the synthesis of milk protein only, but other factors are involved also. The important thing is that a certain part of the food be made up of proteins and that the proteins are of maximum biological value such as are secured by using mixed concentrates. The proportion of protein net energy to total net energy of the food available for milk production is called by Møllgaard "the quotient of production." The problem of the protein requirement becomes, then, a question of the value of the "quotient of production."

An increase in the protein supply for the adult animal above the amount necessary for maintenance will not induce a gain of protein but will merely augment the heat production (specific dynamic action). This means that an increase in the "quotient of production" (proportion of protein) above a certain limit must involve an increase in the value of the production equivalent. Hence the problem of the protein requirement for milk production may be expressed most clearly as a question of the value of the "quotient of production" where the production equivalent is at its minimum.

The ratio of protein net energy to total net energy in the total feed fed a producing cow may be an entirely different thing from the "quotient of production" which expresses that ratio in the food which is available for milk production. When this ratio in the feed has a value of about 0.18 for crude protein or 0.16 for true protein Møllgaard showed with two cows that practically the same ratio exists in the quotient of production. The corresponding production equivalent was 831 for one cow and 807 for the other. Both cows were gaining some protein and more energy.

Two other cows did not receive enough energy for their needs but were almost in nitrogen equilibrium. The absolute amount of protein in the ration was not high but the small amount of energy supplied made the ratio of protein energy to total energy in the feed larger (0.22 and 0.27) than in the two preceding experiments. The production equivalent in one case was 769 and in the other 824. The quotient of production observed in the animal was 0.18 and 0.21. The difference between the value 769 and the average production equivalent is no larger than the probable error. If the maintenance requirement of this animal is corrected by the probable error the production equivalent becomes 821. The conclusion follows that whether a cow is fed on a plane of nutrition which induces a gain of energy or on a plane which causes a loss of energy by the animal the final results in the organism are about the same when milk production is kept at a constant level during the experiment.

In a fifth experiment the loss of energy by the animal was very much greater while the amount of protein available for milk production was greater. The quotient of production in the feed was 0.27 for crude protein. Since the animal lost 2823 Calories from its body while showing a slight gain of protein, the quotient of production for crude protein in the animal becomes 0.19. The production equivalent is 1049. If the oxidation of protein is corrected to the level observed in the first two experiments it is found that 419 more grams of protein is oxidized. This corresponds to a heat production of 1860 Calories. When the balance of energy of this experiment is corrected by this quantity the production equivalent is reduced to 852 net Calories.

The average of these five experiments gives a value of 0.19 for crude protein and 0.16 for true protein for the quotient of production observed in the animal. Using experiments of Haecker and Woll to determine the utilization of protein in milk production, Møllgaard calculates a quotient of production for crude protein of 0.18. The standards of Haecker and Woll, then, give practically the same result as found by Møllgaard.

If these results are confirmed by further experiments a new fundamental principle will be introduced into the nutrition of farm animals. Expressing the average value of the quotient of production found in the animal by "K," this principle is stated as follows:

"When the quotient of production in the food added to the maintenance ration of a milking cow is equal to K, then the production equivalent is equal to its minimum and the quotient of production is unaltered in the organism except in the case of a deficit in energy."

This means that the utilization of energy and protein reaches its maximum when the quotient of production in the feed is equal to K.

Setting the value of K at 0.2 for convenience and calculating the quotients of production for a number of feeding stuffs Møllgaard next shows that these feeds can be divided into two groups, one having values of K above 0.2 (some even above 0.5) and the other values of K below 0.2 (as low as 0.03 in the case of wheat straw). To obtain a mixed feed having a quotient of production of K it is necessary to mix a feed from one group with a feed from the other group. A convenient table to aid in the calculations is given.

Utilization of Total Energy Consumed Above Maintenance

The preceding sections of this chapter have dealt with the efficiency of the animal in using the metabolizable energy of the ration consumed above maintenance. Of equally practical significance is the efficiency

TABLE 76

Net Efficiency of Animal as a Converter

		Percentage of Gross Energy			
Feed Used *Ruminants*	Experimenters	Rejected Unused in Excreta Per Cent	Lost in Heat Production Per Cent	Net Energy Used Per Cent	Net Energy in Terms of Metabolizable Per Cent
Roughage:					
Timothy hay	Armsby and Fries	56	17	27	60.82
Red clover hay	“ “ “	56	22	22	49.62
Red clover hay	Kellner and Köhler				46.53[1]
Mixed hay	Armsby and Fries	56	23	21	49.37
Alfalfa hay	“ “ “	55	24	21	47.74
“Grass hay”	Kellner and Köhler				43.46[1]
Meadow hay	“ “ “	51	28	21	42.30
Rowen	“ “ “				43.81[1]
Maize stover	Armsby and Fries	55	30	15	33.64
Barley straw	Kellner and Köhler				46.00[1]
Oat straw	“ “ “	64	23	13	36.14
Wheat straw	“ “ “	69	26	5	17.66
Straw pulp	“ “ “	24	28	48	62.99
Concentrates:					
Maize meal	Armsby and Fries	27	27	46	62.55
Hominy feed	“ “ “	25	22	53	70.27
Grain mixture No. 1	“ “ “	37	27	36	57.12
Grain mixture No. 2	“ “ “	35	23	42	64.20
Cottonseed meal	Kellner and Köhler				65.65[1]
Linseed meal	“ “ “				60.22[1]
Palmnut meal	“ “ “				63.33[1]
Peanut meal	“ “ “				60.81[1]
Beet molasses	“ “ “	25	26	49	64.69
Starch	“ “ “	27	30	43	59.17
Peanut oil	“ “ “	44	18	38	67.37
Wheat gluten	“ “ “	35	38	27	41.86

TABLE 76—*Concluded*

Feed Used	Experimenters	Percentage of Gross Energy: Rejected Unused in Excreta Per Cent	Percentage of Gross Energy: Lost in Heat Production Per Cent	Percentage of Gross Energy: Net Energy Used Per Cent	Net Energy in Terms of Metabolizable Per Cent
Ruminants					
Mixed Ration:					
Alfalfa hay and grain mixture No. 2	Armsby and Fries	43[3]	25[3]	32[3]	56.16[3]
Swine					
Concentrates:					
Rice	Meissl, *et al.*				81.21
Barley	" " "				80.46
Barley	Fingerling, *et al.*	20	22	58	72.68
Dried potatoes	v. d. Heide and Klein				67.04
Flesh meal	Fingerling, *et al.*	16	17	67	79.88
Mixed Rations:					
Rice, flesh meal, and whey	Meissl, *et al.*				78.45
Cockle, barley, and maize	Kornauth and Arche				85.00
Rape cake, barley, and maize	" " "				83.30
Skim milk and flour[2]	Wellman				68.91
Single Nutrients:					
Starch	Fingerling, *et al.*	1	17	82	82.57
Cane sugar	" " "	3	28	69	71.60
Straw pulp	" " "	12	35	53	60.29
Wheat gluten	" " "	18	21	61	74.66
Peanut oil	" " "	—1	7	94	92.73
Palm oil	v. d. Heide and Klein				74.82

[1] Metabolizable energy estimated from digestible organic matter.

[2] Omitting one very restless animal.

[3] For this ration the unrevised data are given.

of utilization of the gross energy. The percentage losses in the excreta and heat production together with the percentage of net energy in the gross and the metabolizable energy are given in Table 76. The material is from respiration calorimeter experiments most of which have been discussed before. Greater details are given elsewhere.[19]

It is seen that ruminants use but 5 per cent of the gross energy of wheat straw, at least above the critical temperature of the animal. Of the hays from 17 to 27 per cent is utilized. The protein concentrates are somewhat less than 30 per cent utilizable while the grains and carbohydrate materials are 36 to 49 per cent utilizable. The Missouri ration of alfalfa hay and grain mixture No. 2 is 32 per cent utilized. Extracted straw pulp is as well utilized as the low protein concentrates.

For swine the utilization is greater but this is partly on account of the feeds used being single nutrients and these single nutrients are highly digestible. Straw pulp is 53 per cent utilized, sugar 69 per cent, starch 82 per cent and peanut oil 94 per cent.

Direct comparison of the two types of animal can be made with straw pulp, wheat gluten, and peanut oil. With these three feeds swine show 5, 34, and 56 per cent greater utilization. Swine handle the high concentrates in a more efficient manner.

The efficiency of the animal as a converter during growth and fattening can be shown by the comparative slaughter tests reported by Moulton and discussed in the fore part of this chapter. The Missouri ration of alfalfa hay and mixed grain No. 2 was 57.34 per cent metabolizable. Multiplying the percentage recovery found by this factor gives the results shown in Table 77, in which the percentage utilization found by the calorimeter is given for comparison.

TABLE 77

GROSS ENERGY UTILIZED BY CATTLE

Missouri Comparative Slaughter Trials

Method	Percentage of Gross Energy Utilized
Respiration Calorimeter	32.20
Average of 12 Animals:	
⅝ths and 5/9ths power	31.95
Average of 18 Animals:	
0.715 power	32.40
Average of 30 Animals:	
Total Recovery	34.62

The efficiency of utilization of the gross energy of the ration consumed above the needs for maintenance is 32.20 per cent by the respiration calorimeter method and 31.95, 32.40, or 34.62 per cent by the comparative slaughter method. The agreement is good throughout and especially close in the case of all but the last figure.

[19] Armsby, "The Nutrition of Farm Animals," 634-667.

Chapter 10.

Gross Efficiency

The efficiency of the animal as a converter is best measured, as far as the animal is primarily concerned, in terms of the utilization of the metabolizable energy consumed above maintenance; or, if the lack of ability of the animal to metabolize all of the energy furnished it be properly considered as a charge against the animal, in terms of the utilization of the gross energy consumed above maintenance. The efficiency of utilization of the total gross energy consumed may depend quite as much upon the method of handling the animal, *i.e.,* upon the feed allowed above the maintenance requirements, as upon the limitations inherent in the animal. However, if the animal is being fed efficiently the percentage utilization of the total gross energy consumed is of vital practical importance to the feeder and to the consumer.

All items such as losses during digestion, the heat increment, and the energy requirements for the necessary physical work done in the feed lot, are properly chargeable to the animal under this latter concept.

The Gross Efficiency of Cattle.

Jordan's Experiment. Among the earliest investigations which yield results that may servie to determine the gross efficiency of cattle as converters in the production of body substance is the slaughter experiment by Jordan[1] cited in Chapter 2. The latter part of his feeding trial furnishes the data presented in Table 78. The gains of the two steers over the check animals have been recalculated using the revised data of Chapter 2. The gains of protein and fat are multiplied by the following factors: protein, 2.570 therms per pound; and fat, 4.304 therms per pound.

TABLE 78

GROSS EFFICIENCY OF CATTLE—JORDAN'S STEERS

Animal	Dry Matter Consumed, Pounds	Gross Energy Consumed, Therms	Protein Stored, Pounds	Fat Stored, Pounds	Energy Stored, Therms	Gross Efficiency, Per Cent
Steer 2	5632.8	11,490.9	33.15	104.86	536.52	4.7
Steer 3	5106.1	10,416.4	43.25	104.14	559.37	5.4

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[1] Annual Report Maine State College, 1895, Pt. II, 36-77.

These factors are derived from those used in Chapter 7 by the proper use of the relations of pounds to grams and therms to large calories. The dry matter of the ration consumed serves for calculating the gross energy consumption by using the factor, 2.04 therms per pound of dry matter. This is derived from the factor 4.5 therms per kilogram of dry matter, which is an approximate average of the values given by Armsby[2] for the feeds used by Jordan, *i.e.,* 4.518 therms for timothy

TABLE 79

GROSS EFFICIENCY OF CATTLE AS CONVERTERS

Missouri Data

Animal Number	Days on Experiment	Average Live Weight, Pounds	Metabolizable Energy Consumed, Therms	Gross Energy Consumed, Therms	Energy Recovered in Gains Therms	Percentage Gross Efficiency	Percentage Metabolizable Energy Above Maintenance to Gross
Group I.	Full Fed.						
556	72	195.6	400.1	697.9	97.7	14.0	16.7
557	147	271.3	1,353.9	2,361.2	418.6	17.7	26.4
547	238	251.6	1,712.3	2,986.2	372.3	12.5	19.8
505	303	376.1	3,655.6	6,375.4	814.9	12.8	27.5
541	307	411.1	3,459.7	6,033.8	754.2	12.5	23.3
532	482	644.5	7,754.2	13,523.3	1,436.8	10.6	24.4
504	615	640.7	9,404.8	16,402.0	1,631.2	9.9	20.8
515	1006	884.3	15,965.0	27,843.0	2,709.3	9.7	15.5
527	1176	1157.9	22,427.0	39,112.7	3,759.8	9.6	15.1
513	1343	1145.7	24,529.7	42,779.9	3,549.8	8.3	13.6
501	1422	1226.7	27,478.4	47,922.4	3,872.2	8.1	13.9
Group II.	Medium Fed.						
554	72	163.6	287.1	500.7	54.4	10.9	7.5
552	142	203.2	607.5	1,059.6	111.8	10.6	3.1
550	238	211.9	1,260.0	2,197.5	181.7	8.3	12.2
538	307	272.9	1,775.4	3,096.3	278.1	9.0	7.8
503	324	374.6	3,186.2	5,556.8	496.1	8.9	20.8
523	775	541.9	7,290.0	12,713.7	728.3	5.7	7.6
507	1003	701.5	11,468.2	20,000.5	1,117.0	5.6	11.5
526	1176	657.8	12,307.4	21,464.2	1,114.8	5.3	3.4
502	1344	802.7	16,135.2	28,139.9	1,131.3	4.0	9.5
512	1426	846.6	19,668.9	34,337.5	1,498.7	4.4	5.1
Group III.	Scant Fed.						
555	72	163.2	252.1	439.7	10.0	2.3	0.70
548	142	184.5	536.0	934.8	52.1	5.6	
558	243	185.9	885.0	1,543.4	96.9	6.3	
540	307	255.4	1,467.5	2,559.3	197.6	7.7	0.16
531	485	331.9	2,790.3	4,866.3	213.6	4.4	0.05
525	765.5	462.6	6,002.0	10.467.6	470.6	4.5	4.0
524	1211.5	540.4	10,379.9	18,102.6	585.1	3.2	7.3
509	1348	668.6	14,395.7	25,106.2	965.9	3.8	5.2
500	1427	685.2	15,951.3	27,819.0	1,027.1	3.7	6.4

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[2] *Jour. Agr. Research,* 3 (1915), 444.

TABLE 80

Gross Efficiency of Cattle as Converters

Minnesota Data

No. of Indi-viduals	Gain		Average Dry Matter Consumed, Lbs.	Average Storage		Energy Stored		Total Energy Stored Therms	Gross Energy Consumed, Therms	Percentage Gross Efficiency
	From Lbs.	To Lbs.		Protein, Lbs.	Fat, Lbs.	In Protein, Therms	In Fat, Therms			
4	100	200	305.5	13.9	6.3	35.7	27.1	62.8	623.3	9.9
4	100	300	850.8	29.9	24.5	76.8	105.3	182.1	1,735.6	10.6
5	100	400	1,491.7	48.9	32.5	125.6	139.9	265.5	3,043.1	8.8
5	100	500	2,144.0	64.3	54.2	165.2	233.6	398.8	4,373.8	9.0
2	100	600	2,841.9	80.4	71.8	206.5	309.2	515.7	5,797.6	8.8
4	100	700	3,886.0	93.2	94.4	239.5	406.2	645.7	7,927.5	8.1
3	100	800	4,767.1	114.2	125.0	293.4	538.0	831.4	9,724.9	8.6
4	100	900	5,760.9	121.2	200.4	311.6	862.6	1,174.2	11,752.3	9.9
4	100	1000	6,643.8	133.5	233.9	343.1	1,006.5	1,349.6	13,553.3	9.9
3	100	1100	7,473.0	139.8	307.5	359.2	1,323.6	1,682.8	15,244.9	11.0
3	100	1200	9,506.8	157.9	348.7	405.8	1,501.0	1,906.8	19,393.9	9.9
2	100	1300	8,714.5	172.2	336.5	442.7	1,448.2	1,890.8	17,777.6	10.6
1	100	1400	10,091.4	181.8	398.9	467.3	1,716.7	2,184.0	20,586.5	10.6
1	100	1500	12,995.2	193.2	504.4	496.4	2,170.9	2,667.3	26,501.1	10.1

hay, 4.442 therms for corn meal, and 4.532 therms for wheat bran. Jordan fed timothy hay and grain mixtures made up of linseed oil meal, corn meal and wheat bran. The factor used is sufficiently accurate, although a direct determination from the feeds actually consumed would be better.

The animals were on a moderate ration and were fairly mature at the start of the experiment. The gains made were from 1023 pounds to 1300 pounds for Steer 2 and from 913 to 1280 pounds for Steer 3. The first steer made its gains in 325.5 days while the second took only 312.5 days. The gains were, therefore, not very rapid. Steer 2 showed a gross recovery of 4.7 per cent and Steer 2 of 5.4 per cent of the total energy consumed in the ration.

The Missouri Experiments. The gross efficiency of cattle as converters can be calculated from the Missouri data from comparative slaughter trials previously discussed. The respiration calorimeter had shown the ration used to be 57.34 per cent metabolizable. Using this as a factor the gross energy intake has been calculated. The energy recovered in the gains and the percentage of the gross energy consumed are shown in Table 79. The animals were put on the experiment at the age of a few days and were slaughtered after the number of days given in the table. The greatest efficiency on this mixed ration was 17.7 per cent in the case of the 5.5 months old Group I calf and the last efficiency by the three months old Group III calf. In general the efficiency decreases as the length of the experiment or the age of the cattle increases. The cause of this decrease may be better stated as follows: The greater the consumption of food above the maintenance cost the more efficient is the gross recovery, or the smaller the proportion of the total food needed for maintenance the greater the efficiency of the animal. Both increasing age and lowered plane of nutrition are accompanied in this experiment by a greater proportion of food required for maintenance.

The young Group II cattle are but little more efficient than the old Group I steers and the young Group III animals but little more efficient than the old Group II cattle.

The Minnesota Experiments. Calculations of the efficiency of the cattle fed at Minnesota for "normal" growth on a mixed ration can be made from the data given.[3] By the use of the factors used in computing the efficiency of Jordan's steers the results shown in Table 80 were obtained. The gross efficiency of these cattle was very uniform, running from 8.1 to 11.0 per cent and averaging 9.7 per cent. This is about the efficiency of the Missouri Group II cattle under one year old.

[3] Minnesota Agr. Expt. Station, Bul. 193 (1920).

The Gross Efficiency of Swine.

The Experiments of Washburn and Jones. The gross efficiency of swine in the production of body substance is shown by the young pigs of Washburn and Jones.[4] Their figures show the retention of physiologically available calories assuming the ration to be 95 per cent digestible and calculating the energy intake from this and an assumed energy equivalent of the nutrients. The rations were based on milk or modified milk and in a few cases included grain. A direct determination of the

TABLE 81

Retention of Physiologically Available Calories by Young Pigs

(Washburn and Jones)

Number of Individuals	Diet	Percentage of Calories Above Maintenance	Percentage of Total Calories
16	Skim Milk	30	24.6
27	2.5% Milk	38	32.2
15	5% Milk	45	39.0
6	Standard	44	35.7
6	Holstein Skim Milk	30	23.9
6	Jersey Skim Milk	33	27.1
5	Holstein 2.5% Milk	40	33.7
7	Jersey 2.5% Milk	41	36.2
6	Holstein 5% Milk	47	41.5
6	Jersey 5% Milk	45	39.4
1	Normal 2.5% Milk	42	34.8
2	Homogenized 2.5% Milk	54	44.0
2	Homogenized 2.5% Corn Oil and Skim Milk	52	42.0
	Homogenized at 85 Degrees F.		
1	Normal 5% Milk	41	35.4
2	Homogenized 5% Milk	43	36.3
2	Homogenized 5% Corn Oil	46	39.2
2	Normal 8% Milk	44	39.0
3	Homogenized 8% Milk	51	44.3
3	Homogenized 8% Corn Oil	40	34.1
	Homogenized at 185 Degrees F.		
4	Normal	23	20.3
3	Homogenized	24	19.8
3	Homogenized Corn Oil	22	18.4
	Mineral Supplement		
3	Normal Plain	34	26.3
3	Normal—Calcium Phosphate	33	25.9
3	Evaporated plain	50	37.7
3	Evaporated—Calcium Phosphate	40	31.0
3	Sweetened Condensed Plain	46	35.9
3	Sweetened Condensed—Calcium Phosphate	40	32.2
	Dilution		
3	2.5% Milk	33	26.2
3	2.5% Milk Diluted	31	23.1
2	Skim Milk	20	14.4
3	Standard Skim Milk and Grain	40	31.9
3	Standard 2.5% Milk and Grain	48	38.8

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[4] Vermont Agr. Expt. Station, Bul. 195 (1916).

energy intake would have been preferable but the figures reported are nevertheless valuable. Table 81 gives the results. The gross efficiency varied from 14.4 per cent for 2 pigs on a skim milk diet to 44.3 per cent for 3 pigs on homogenized milk containing 8 per cent of fat. The rations containing a higher fat content showed greater efficiency than those having a low fat content.

The Kansas Experiments. Swanson [5] reports data from the Kansas State Agricultural College on swine which furnish figures for the gross efficiency of these animals as producers of body substance when fed rations of corn with or without supplements. The energy of the food consumed and of the body substance gained was calculated by the author from the nutrients in the feed and from the protein and fat stored by the use of factors, which give results that are too low. However, the ratios are not seriously affected. Table 82 gives the results recalculated employing the factors 2.04 therms per pound of dry matter consumed in the ration and 2.574 therms and 4.304 therms per pound respectively for the protein and fat stored. The dry matter used does not include the ash supplement in the ration since this manifestly adds no energy to the food. The latter two figures are derived from the energy values per gram of protein and fat of swine given in Chapter 2. The energy equivalent of the dry matter is the one used previously in this chapter.

The percentage of the total gross energy stored, or the gross efficiency, for 24 of the pigs runs from 20.9 per cent to 38.7 per cent. Two animals show 3.3 and 7.5 per cent and three—not included in the table—lost in body substance. The higher values are obtained with those pigs which received protein supplements in the ration. The average for the ten animals receiving corn without protein supplement is 20.2 per cent, while the sixteen receiving protein supplement show a gross efficiency of 35.0 per cent. The average of all but the two low individuals is 31.3 per cent.

The Gross Efficiency of the Dairy Cow.

But few data exist which permit of the accurate calculation of the gross efficiency of the dairy cow. The early brief work of Kellner and Jordan cited in Chapter 7 and the less complete data of Haecker are not considered to be extensive or complete enough to warrant calculating the gross efficiency. However, the work of Eckles [6] at Missouri furnishes fairly complete data for such calculations and it has the added advantage of being more comparable with the Missouri slaughter experiments on cattle.

[5] *Jour. Agr. Research,* 21 (1921), 325.

[6] Mo. Agr. Expt. Station, Research Bul. 7 (1913).

TABLE 82

Gross Efficiency of Swine as Converters

Data from Kansas Agricultural College

Lot	Experiment No.	Ration	Dry Matter Consumed Lbs.	Energy Consumed, Therms	Protein Stored, Lbs.	Fat Stored, Lbs.	Energy in Protein, Therms	Energy in Fat, Therms	Total Energy Stored	Percentage Gross Energy Stored
31	VI	Corn and ash	112.8	230.2	0.7	1.4	1.8	5.8	7.6	3.3
21	V	Corn alone	239.5	488.5	3.8	22.1	9.7	95.0	104.7	21.4
6	III	Corn alone	206.7	421.7	1.4	6.6	3.6	28.2	31.7	7.5
32	VI	Corn and ash-free blood protein	227.2	463.5	7.2	23.5	18.4	101.1	118.5	25.6
14	IV	Corn and ash	290.4	592.4	4.6	26.1	11.8	112.1	123.9	20.9
13	IV	Corn alone	383.5	792.2	4.9	38.9	12.5	167.4	179.9	22.7
2	II	Corn and ash	373.7	762.3	5.7	39.8	14.7	171.4	186.1	24.4
1	II	Corn alone	441.1	899.8	6.3	51.0	16.2	219.6	235.8	26.2
15	IV	Corn and protein-free skim milk	406.2	828.6	5.4	53.9	13.8	232.0	245.8	29.7
23	V	Corn and corn germ	424.1	865.2	13.4	50.5	34.4	217.3	251.7	29.9
34	VI	Corn, starch, casein, and ash	444.9	907.7	16.9	58.3	43.4	250.9	294.3	32.4
29	V	Corn and casein every 7th day	492.6	1,004.8	10.3	64.0	26.4	275.5	302.0	30.1
33	VI	Corn and ash-free blood protein, and ash	401.0	817.9	18.2	61.0	47.0	262.4	309.3	37.8
36	VI	Corn and casein 1 : 1½ and ash	492.1	1,003.9	21.5	77.4	55.3	332.9	388.2	38.7
35	VI	Corn and casein 1 : 3 and ash	533.4	1,088.2	22.9	78.8	59.0	339.2	398.2	36.6
17	IV	Corn and albumin	548.6	1,119.2	14.1	84.9	36.4	365.2	401.6	35.9
37	VI	Corn, casein reducing, and ash	516.9	1,054.6	21.5	83.1	55.2	357.6	412.8	39.1
22	V	Corn and casein	643.8	1,313.4	21.8	94.0	56.2	404.4	460.6	35.1
18	IV	Corn and milk protein every 7th day	618.4	1,261.6	15.7	102.4	40.4	440.6	481.0	38.1
26	V	Corn and albumin	746.0	1,520.8	24.3	110.2	62.6	474.2	536.8	35.3
16	IV	Corn and casein	846.8	1,727.5	20.2	126.6	51.9	544.9	596.9	34.6
9	III	Corn and milk protein	931.8	1,900.9	27.3	153.3	70.4	659.8	730.2	38.4
	III-V	Corn and protein-free skim milk	2,055.9	4,194.0	29.8	189.7	76.6	816.4	893.0	21.3
3	II	Corn and black-blood albumin	1,236.8	2,523.1	26.3	199.8	67.7	859.9	927.6	36.8
	III-V	Corn and synthetic ash	1,849.7	3,773.3	24.6	201.3	63.4	866.6	930.0	24.6
4	II	Corn, black-blood albumin, and ash	1,377.2	2,809.4	24.3	215.0	62.5	925.5	988.0	35.2

The data reported include feed and milk records for eight dairy cows for one year and two for about one third of a year. Four different breeds were represented in this lot of dairy cows. The animals were all mature and showed but slight changes in weight during the experiment. For the present purposes it is assumed that the slight changes in weight which were observed represented no significant change in protein or fat in the body of the animal. The rations consisted of alfalfa hay and silage and a grain mixture composed of corn meal, 4 parts, wheat bran, 2 parts, and linseed oil meal, 1 part. The feeds were fed as nearly as possible in the proportion of grain, 1 part, hay, 1 part, and silage, 4 parts. Some exceptions to this ration are given but are not considered to be of significance in this connection.

The data are given in Table 83. The therms consumed in the ration have been calculated for the present purposes by multiplying the total dry matter consumption by 2.04 therms per pound. This is derived from 4.5 therms per kilogram which is very close to the figure that would result if each individual feeding stuff were multiplied by its own factor for gross energy as determined by Armsby.[7] The results, while not strictly accurate, nevertheless serve our purpose as well as more accurate figures. The therms recovered in the milk are derived from the content of protein, fat, and sugar found by Eckles by the use of the factors: 5.65 for protein; 9.2 for fat; and 3.9 for lactose.

TABLE 83

GROSS EFFICIENCY OF DAIRY COW AS A MILK PRODUCER

Animal		Days	Dry Subst. Consumed, Lbs.	Energy Consumed, Therms	Milk Yield, Lbs.	Energy in Milk, Therms	Percentage Recovery
Jersey	43	365	9,169.0	18,704.8	8,039.5	3,158.9	16.9
"	62	365	5,282.1	10,775.5	3,188.9	1,371.4	12.7
"	4	365	8,622.1	17,589.1	6,773.6	2,966.4	16.9
"	27	365	9,410.4	19,197.2	8,522.9	3,744.5	19.5
"	63	365	8,652.3	17,650.7	6,033.9	2,855.2	16.2
Holstein	206	365	10,783.9	21,999.2	11,986.9	3,715.3	16.9
Ayrshire	304	365	8,700.4	17,748.8	9,169.0	3,140.4	17.7
Shorthorn	400	365	7,372.9	15,040.7	5,573.0	1,972.7	13.1
Ayrshire	303	120	2,809.5	5,731.4	3,325.1	1,132.7	19.7
Holstein	211	110	3,420.9	6,978.6	4,393.4	1,339.6	19.2

The recovery of gross energy in the form of milk runs from 12.7 per cent to 19.7 per cent with an average of 16.9 per cent. This is a fairly uniform recovery and is fairly comparable to the gross efficiency of the young Missouri Group I cattle in producing body substance. The rations were both mixed rations and climatic and other local conditions were

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[7] *Jour. Agr. Research,* 3 (1915), 444.

alike. It should be borne in mind, however, that the figures for the dairy cow are for the product yielded after the animal had procured its growth while the values for the beef steer cover both the growth and the fattening periods.

The production of flesh by thin mature cattle would be more nearly comparable. Such data are furnished by two mature beef steers fattened at Missouri[8] on mixed rations. The efficiency of recovery of the metabolizable energy consumed above maintenance has been shown to be about 53 per cent for these two steers. Calculating the gross energy of the ration consumed by the use of the factor 2.04 therms per pound of dry matter consumed the gross energy consumption was as is shown in Table 84.

TABLE 84

Gross Efficiency of Mature Cattle

	Dry Matter Consumed, Lbs.	Gross Energy of Rations	Energy of Gains	Percentage Gross Recovery
Steer 121	3,531.45	7,144.15	1,067.61	14.9
Steer 48	12,292.05	25,075.78	2,558.10	10.2

Steer 48 was fattened to a greatly overdone condition. Gains were very slow during the latter part of the fattening period, and consequently the maintenance cost was relatively high. Steer 121 was slightly underdone and represented good feeding practice. The former shows a gross efficiency of 10.2 per cent and the latter 14.9 per cent. This figure for Steer 121 compares very favorably with 2 of the 10 figures for the dairy cow, and is not very greatly below the average for the ten dairy cows—16.9 per cent. The ration of the beef steer was rather richer in grain and therefore might have been expected to show a higher efficiency. On the whole these figures do not support the belief that the dairy cow is a more efficient transformer of energy than the beef steer. Since the beef steer had secured most of its growth at the time its feeding trial began a large part of the gains made were in edible flesh, fat, and organs. The calculation of true edible product would reduce the over-all efficiency of the mature beef steer somewhat. That is, however, another question and does not affect its efficiency as a converter of energy. It may be as much the fault of the consumer as of the beef animal that more of the product formed is not used as human food.

Factors Affecting the Gross Efficiency.

Character of Ration. The gross efficiency of the animal as a converter depends upon several factors. Table 85 gives a compilation of the

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[8] Missouri Agr. Expt. Station, Research Bulletin 30.

data given in detail in the preceding part of this chapter. For mixed rations the cattle give efficiencies running from 8.1 to 17.7 per cent. Typical figures for the mature animal are near 15 per cent for the beef steer and 17 per cent for the dairy cow.

For swine only concentrates have been used but here the effect of fat in the milk is distinctly shown. For skim milk the efficiency is 24.6 per cent, for milk with 2.5 per cent fat it is 32.2 per cent, while for milk with 5 per cent fat it is 39 per cent. Corn alone gives 20.2 per cent efficiency but corn supplemented with protein gives 35 per cent efficiency.

The richer, more concentrated, and more easily digested foods give greater efficiency.

TABLE 85

EFFECT OF CHARACTER OF RATION ON PERCENTAGE OF GROSS EFFICIENCY

Cattle		Swine	
Minnesota mixed ration	9.7 %	Skim milk	24.6%
Missouri mixed ration	8.1-17.7 %	Milk 2.5% fat	32.2%
Steer 121 mixed ration	14.9 %	Milk 5.0% fat	39.0%
Dairy cows mixed ration	16.9 %	Corn	20.2%
		Corn and protein supplement	35.0%

The Plane of Nutrition. That the plane of nutrition or the relative consumption of feed affects the gross efficiency is shown most strikingly by the Missouri data on cattle. The full fed Group I calves up to the age of one year showed 13.9 per cent average gross efficiency. For longer lengths of life the efficiency dropped and averaged 9.4 per cent. Table 86 shows the results. For the medium fed Group II cattle the figures are 9.5 and 5.0 per cent respectively and for the scant fed Group III cattle 6.5 and 3.9 per cent.

TABLE 86

EFFECT OF PLANE OF NUTRITION AND RAPIDITY OF GAIN ON GROSS EFFICIENCY OF CATTLE

	Full Fed	Medium Fed	Scant Fed
Young	13.9%	9.5%	6.5%
Over 1 year	9.4%	5.0%	3.9%

It would appear then that the plane of nutrition and rate of gain affect the economy of the gain. This is, of course, a trite observation and is confirmed by the experience of all practical feeders. However, it may not be out of place of discuss this question further. The gross efficiency does not seem to vary as the daily gain in live or empty weight or as the daily recovery of energy in the gains. It is, then, more than a question of daily gain. The last column of Table 79 gives the percentage of metabolizable energy consumed above the maintenance requirements to the gross energy consumption. In a fairly uniform manner these figures follow the gross efficiency. In other words gross efficiency is a question of the relative food consumption above the maintenance cost. The greater the proportion of the total feed not needed for maintenance the greater will be the efficiency of the conversion. This is a prime factor in the efficiency of the pure-bred beef animal compared to the scrub as has been shown by Armsby and Fries.[9]

Kind of Animal. There are no data that bear conclusively on the relative ability of different kinds of animals to convert energy. The data presented for the hog show the highest efficiency but these are for concentrated, easily digested foods. If one animal can be fed on concentrated rations while another must be given considerable roughage the former animal might well receive the credit for the resulting economy. On the other hand the animal that consumes much roughage and the offals from grain is utilizing material that would otherwise be lost as human food and is consequently of the highest economic value.

The Efficiency of the Animal Compared with the Steam Engine. It is of interest in studying the efficiency of the animal as a converter of energy in work and food production to compare it with a mechanical energy converter such as the steam engine. We have recently been confronted with the phenomenon of the burning of corn for fuel in place of the usual use as a food for animals or man. The economy of this substitute conversion might help solve the question of the ethics of such a substitution. Van de Velde[10] has presented some figures to show that not more than 13 per cent of the chemical energy of the fuel can be transformed by the steam engine into work while in the muscular work done by man the output of the chemical energy of the food is 25 per cent. These figures are valid only while both machines are in use. While at rest the steam engine uses no energy and suffers little deterioration. Man, on the other hand, always needs some food to make up for metabolism.

Armsby[11] has presented similar figures for our domestic animals and shows that the efficiency of the animal as a converter of potential energy into mechanical work is about one third compared to 15 per cent for the steam engine. In ordinary practice one half of this efficiency for the steam engine is considered a good result. He further points out, however, that when gross in place of net energy is used, when the constant use of energy by the animal whether work is done or not is considered, and when

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[9] United States Dept. of Agr., Bur. of Animal Industry, Bul. 128 (1911), 15.
[10] *Natuurwetenschapp. Tijdschr.*, 4 (1922), 25 and 49.
[11] "Principles of Animal Nutrition," New York, 1910, 511.

the expenditure of energy in locomotion is taken into account but little remains of the apparent superiority of the animal as a prime motor. Of course, the greater cost of the fuel (food) for the animal is still another question.

In a later publication Armsby[12] calculates the overall efficiency of a work animal to be in one case 5.1 per cent. This efficiency will increase with the intensity of the work and decrease with the number of hours the animal is idle per day. In other words, it will vary as the ratio of useful work to maintenance requirement varies.

Given the machine and the fully grown food-producing animal, the relative economy of the conversion of energy during the period of its useful production can well be answered by the figures presented under milk production above. The dairy cow can convert 17 per cent of the gross energy in the form of milk and the beef steer can convert 15 per cent of the gross energy of the ration fed during five months into energy in the form of body substance.

The young animal is an economical converter of energy as shown by the young full fed Missouri cattle. They showed an average recovery in body substance of 14 per cent of the gross energy of the ration fed. This represents the economy of production of the machine itself to some extent as well as the economy of flesh production.

Over shorter periods of time and with concentrated foods the hog shows much greater efficiency.

Under other systems of feeding, *e.g.*, mixed rations in limited amounts or full rations after early growth, the efficiency of cattle drops to 9.5 per cent. Still less efficient feeding, where less liberal rations are consumed so that the maintenance cost amounts to larger and larger proportions of the ration consumed, reduces the gross efficiency to 3.9 per cent.

It would appear then, that the animal under favorable conditions is more efficient than the steam engine and under medium conditions fully as efficient as the steam engine in ordinary practice.

[12] "The Nutrition of Farm Animals," New York, 1917, 567.

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