

SOME QUANTITATIVE DATA ON THE ROLE OF THE RUMINANT PROVENTRICULI IN THE DIGESTION AND ABSORPTION OF NITROGEN-FREE ORGANIC MATTER

L. PALOHEIMO, A. MÄKELÄ and M.-L. SALO

Department of Animal Husbandry, University of Helsinki

Received April 25, 1955.

A critical review of earlier investigations

The earliest ideas regarding absorption from the ruminant stomach were based on anatomical findings. The enormous extension of the mucous membrane of the proventriculi led investigators to the view that absorption of digested food must occur in these compartments of the digestive apparatus (7, p. 66; 10, p. 145; 14, p. 189). KÜHN (l.c.), referring to the rich network of blood capillaries in the laminae of the omasum, ascribes to this stomach a special absorptive capacity. On the other hand, COLIN in 1873 (ref. 8, p. 187) on anatomical grounds denies any absorptive power to the proventriculi. He refers to the cutaneous and stratified character of the epithelia concerned and does not admit for them any greater absorptive capacity than for the epidermis of the skin. ELLENBERGER (1, p. 863) also denies that the proventriculi have any noteworthy absorptive capacity. The reason alleged by him is rather curious: »Wenn daselbst lebhaftere Aufsaugung stattfände, dann würde wegen Eintrocknung des Inhaltes das Wiederkauen unmöglich werden.» As for the omasum, ELLENBERGER refers to his own experiments, which had given negative results. According to MANGOLD (8, l.c.) these experiments were made *in vitro* with fragments of mucous membrane. Adopting Colin's and Ellenberger's line of reasoning, MANGOLD emphasizes the absence of absorptive power in the mucous membrane of the proventriculi. He postulates that the water-soluble substances formed in the proventriculi are absorbed by the portal blood only on reaching the small intestine.

TRAUTMAN (15, p. 178), re-examining the histology of the mucous membrane of the proventriculi, admits the possibility of a remarkable absorptive capacity. In his experiments a rapid absorption of some alkaloids was established. PHILIPSON and MCANALLY (12, p. 199) were the first to give evidence of the absorption

of volatile fatty acids from the proventriculi. In their experiments sheep with both rumen and abomasal fistulae were used. In the abomasum the concentration of volatile fatty acids was found to be insignificant and did not increase significantly after feeding, while in the rumen the concentration was considerable. It was concluded that at least the bulk of the acids were absorbed from the proventriculi. Later the same authors (ref. 13, p. 17) showed »that blood draining the rumen, reticulum, omasum, and caecum carried a higher concentration of volatile acids than peripheral blood.» Taking into consideration the volume of blood draining the rumen and reticulum, and the gross area of the surface of these compartments, BARCROFT, MCANALLY and PHILLIPSON (ref. 13, l.c.) established that in sheep from 1 to 5 g of volatile acids, expressed as acetic acid, were absorbed from the rumen and reticulum per hour.

Using the iron of the food as tracer and taking samples from the rumen contents of sheep at different intervals after feeding, RATHNOW (ref. 6, p. 255) found that in 3 hours 32 %, in 6 hours 48 %, and in 9 hours 59 % of the dry matter of hay was digested.

HALE, DUNCAN and HUFFMAN (3, p. 953) criticize the use of iron as tracer and are of the opinion that Rathnow's method is not reliable for determining rumen or total digestion coefficients. By a somewhat similar technic, but using lignin as tracer, these authors (ibid.) studied the digestion of alfalfa hay in the rumen of the cow. (Although the term »rumen» is used, rumen together with reticulum must be meant.) They used a cow with a rumen fistula, the rumen being evacuated before the first feeding with the hay to be examined. Then followed a preliminary feeding period of at least 12 days, and at the close of this period, 14 hours after a certain meal, the rumen contents were removed, weighed, sampled for chemical analysis, and replaced in the rumen. This procedure was repeated twice for each level of feeding (10, 20, or 30 lbs hay per day). Using the same hay, digestion trials for determining the coefficients of total digestion were performed with other cows. On the basis of the increase in the percentage of lignin, the »coefficients of rumen digestion» were calculated and compared with the »coefficients of total digestion». It is, however, apparent that these two groups of coefficients are incommensurable. The latter coefficients express the percentages of the different food constituents absorbed from the alimentary tract or disappeared in the form of CH_4 and CO_2 during passage. »The coefficients of rumen digestion», however, cannot reveal the amounts of food constituents absorbed from the rumen or disappeared from it in the form of gases. It is evident that the percentage of lignin in the rumen contents 14 hours after feeding is appreciably higher than in the food ingested, not only because a certain amount of food constituents have been absorbed from the rumen, but also because the products of digestion have been transferred from the rumen-reticulum to other compartments of the digestive tract. These transferred products of digestion may be included in the part of the food digested in the rumen, but this concept of digestion is not the same as in the usual digestion trials. It is evident, too, that the undigested particles transferred have not the same lignin content as the contents remaining in the rumen. On the contrary, it is probable that these

particles have on the average a lower content of lignin because the more tender parts of the hay and easily suspended particles may be transferred sooner than the coarser fragments. Thus it is not surprising that in some cases in the experiments of Hale et al. the digestibility of protein in the rumen appears to be nearly 100 % (in one case 99.5 %) of the total digestibility of the protein. Errors of the same kind must also be included in the figures pertaining to other food constituents. Later the named authors (4, p. 733) have criticized their method described above, but they still maintain that »it is unlikely that any appreciable passage of plant particles not yet thoroughly subjected to the disintegrative action of the rumen would take place». This statement, however, can hardly be valid. In their following paper (5, p. 747) they describe investigations made with two rumen fistula cows. The method used was in principle the same as in the experiments related above. Samples were removed from one of the cows at 6 and 12 hours and from the other cow at 14 and 24 hours after feeding. A period of from 1 to 2 weeks was allowed between the removals of rumen contents to ensure complete resumption of the normal function of the rumen. Alfalfa hay was used also in these experiments. In the interpretation of their findings the authors are this time more cautious than in their previous paper. But much of the criticism directed above at the earlier experiments of Hale et al. must also be applied to their later investigation and especially to the interpretation of its results. Moreover, the terms used are highly misleading: they still speak of »rumen digestion coefficients» and of disintegration of alfalfa hay in the rumen. Both expressions are alike misleading. However, because the inaccuracy of the method used tends to give, in our opinion, too high »rumen digestion coefficients», the figures relating to the disappearance of cellulose from the rumen in all probability have the right tendency. They give the impression that during the first 6 hours after feeding the disintegration of cellulose is rather slight. During the following 6 hours it is most intensive and from the 12th to the 24th hour almost negligible. To the question of the absorption of the products of digestion from the rumen the investigations of Hale et al. do not give any answer.

GRAY (2, p. 15) has also used the lignin ratio method in investigating the extension of the digestion of cellulose in the rumen of sheep. The number of experimental animals was four. Gray determined not only the digestibility in the rumen but also the total digestibility and the digestibility in the omasum, abomasum, small intestine, caecum, and colon. The technic used by him differed in principle from that of Hale et al. The sheep were fed for some weeks on a constant ration composed of wheat straw and alfalfa hay. Then the animals were slaughtered, samples of ingesta taken from different compartments of the digestive tract, and cellulose and lignin determined from the samples. The principle in determining the digestibility in different compartments was the same as is generally used in determination of total digestibility. For instance, in determining the digestibility in the rumen-reticulum, Gray compared the cellulose-lignin ratio of the food with the corresponding figures of the ingesta in the omasum. However, as a considerable absorption of volatile fatty acids probably occurs in the omasum and as the omasum functions as a filter press, the figures proposed by Gray as rumen digestion coefficients must

be somewhat too high if these coefficients are to be understood in the same way as the usual coefficients for total digestion. As the absorption from the abomasum is minimal and as the separation of solid and fluid fractions of the ingesta brought about by the omasum is reversed in considerable degree in the abomasum, it is possible, using the figures presented by Gray, to compute the digestion coefficients for the proventriculi as a whole. Thus it appears that there disappeared in the proventriculi 40—45 % of the cellulose of the food eaten, which makes 67—75 % of the total digestibility of this component. But there is still one obscure point in Gray's experiments. It is evident that the results obtained are in some degree influenced by the time elapsing between the last feeding and the slaughtering of the animal. In our opinion slaughtering should take place in the middle of the period between two feeding times. On this point Gray gives no information, but one must suppose that he has arranged his experiments in the said way.

MARSHALL (9, p. 1) has used Gray's technic in investigating the digestion of the pentosans in hay by two sheep. The digestion in the proventriculi was about 30 %, which makes about 67 % of the total digestion of pentosans. As the author mentions that the rumen contained much recently ingested material, one may conclude that the slaughtering did not take place in the middle of the period between two feeding times.

Own experiments

In their investigation on the rate of passage of food in the digestive tract of cattle, PALOHEIMO and MÄKELÄ (11, p. 165) have determined the percentage of lignin, N-free organic matter, and N-free non-lignin organic matter in hay and in the corresponding ingesta of the abomasum. The animals, 14 cows and 5 young bulls of about 7 months old, were fed with hay (mainly timothy) thrice daily during a period of 10 days. The individual animals received the same amount of hay at every feeding time (three times daily) and the feeding intervals were uniform. After 10 days the animals were slaughtered 4 hours after the last feeding and the contents of the different parts of the alimentary tract were measured and examined. The experiments were spread over a longish period and for this reason the quality of the hay was not quite the same for the different animals. The method of lignin determination used by us gives, when applied to hay, lignin which is indigestible in ruminants.

As one may see, the results of our experiments make it possible to calculate the digestibility of N-free organic matter and N-free non-lignin organic matter in the proventriculi according to the principle used by Gray. In table 1 the results for individual animals are shown. One sees that, although the hay eaten by individual animals was not of exactly the same quality, the results are fairly uniform. As the amount of ingesta in the abomasum is always relatively small, it is presumable that the sample taken from this compartment cannot always be representative of the material transferred from the proventriculi. This inaccuracy, however, seems not to have had any greater detrimental effect on the results of the experiments.

Table 1. Digestibility of N-free organic matter and of N-free non-lignin organic matter in the proventriculi and in the whole digestive tract of cows and young bulls.

Animal	Hay dry-matter daily kg	Digestibility of N-free organic matter		Digestibility of N-free non-lignin organic matter		Ratio a:b
		a) in the proventri- culi %	b) in the whole digestive tract %	a) in the proventri- culi %	b) in the whole digestive tract %	
Cow 1	10.67	52.23	60.52	57.47	66.60	0.86
» 2	4.14	56.26	62.94	61.89	69.31	0.89
» 3	2.48	57.74	63.29	63.59	69.61	0.91
» 4	2.48	52.87	67.93	58.18	74.72	0.78
» 5	6.30	56.46	64.81	62.61	71.93	0.87
» 6	6.76	50.55	57.47	56.67	64.44	0.88
» 7	3.38	53.70	61.37	60.19	68.81	0.87
» 8	3.38	49.37	56.96	55.34	63.83	0.87
» 9	6.00	56.43	63.23	62.37	69.87	0.89
» 10	6.00	57.13	64.64	63.21	71.46	0.88
» 11	4.08	53.39	62.14	59.14	88.86	0.86
» 12	4.08	57.61	66.03	63.64	73.04	0.87
» 13	2.40	48.31	63.53	53.51	70.38	0.76
» 14	2.40	53.01	62.65	58.81	69.41	0.85
Young bull 1	3.49	55.37	60.68	58.91	65.15	0.90
» 2	4.12	59.57	60.22	63.80	64.59	0.99
» 3	3.53	54.74	63.11	58.12	67.99	0.86
» 4	3.77	57.99	61.40	61.98	65.95	0.94
» 5	4.26	55.92	60.52	59.48	64.93	0.92

As the lignin is considered to be indigestible, it follows on arithmetical grounds that the ratio between the digestibility in the proventriculi and the total digestibility must be the same independently if the calculation is made on the basis of N-free organic matter or on the basis of N-free non-lignin organic matter. The table shows that of the total amount of N-free non-lignin organic matter digested in the whole digestive tract, 76—99 % is digested in the proventriculi. If the cows Nos. 4 and 13 are left out, the limits in the cows are 85 and 91 %. The average for the cows is 86 % and for the heifers 92 %. The ratio in question seems to be independent of the amount of hay eaten.

The amount of dry matter in the ingesta of the abomasum was determined in the ordinary way, without taking into consideration the volatile fatty acids. As the amount of these substances in the ingesta of the abomasum is very small, the inaccuracy caused by this omission must be negligible. According to some later studies by one of us (Mäkelä) the total of volatile fatty acids, both free and bound, calculated as acetic acid, in the contents of the abomasum varied in 5 cows and 2 calves from 0.17—0.98 % of the dry matter.

As hay contains only a small amount of lipids in proportion to carbohydrates, the fraction »N-free non-lignin matter» amounts to almost the same as carbohydrates. Thus the figures pertaining to the first-named fraction must be nearly the same as those pertaining to the carbohydrates.

The terms »digested» and »digestibility» are used in this investigation in the same sense as in the usual digestion trials. Hence the percentage of N-free non-lignin organic matter digested in the proventriculi means the relative amount of the fraction in question which disappears from the alimentary tract during the sojourn in the proventriculi. As the main part of what disappears is absorbed in the blood vessels and a smaller part is removed as gases, the results of our investigation strongly support the view that in cattle the carbohydrates are digested mainly in the proventriculi and their degradation products are absorbed principally from these stomachs.

S u m m a r y

Fourteen cows and five young bulls were fed with hay uniformly during 10 days. After slaughtering, the ingesta of the abomasum were removed and sampled. From the hay, from the contents of the abomasum, and from the feces lignin, N-free organic matter, and N-free non-lignin organic matter were determined. Using the lignin ratio principle, the digestibility of the two N-free fractions was calculated both for the proventriculi and for the whole digestive tract. It appeared that of the total amount of the N-free non-lignin organic matter digested in the whole digestive tract, 76—99 % was digested in the proventriculi. If the results for two of the cows are discarded, the limits in the cows are 85 and 91 %. On the basis of this investigation it can be concluded that in cattle carbohydrates are digested mainly in the proventriculi and their degradation products are absorbed principally from these stomachs.

REFERENCES

- (1) ELLENBERGER, W. 1890. Vergleichende Physiologie der Haussäugethiere I. Berlin.
- (2) GRAY, F. V. 1947. The digestion of cellulose by sheep. The extent of cellulose digestion at successive levels of the alimentary tract. *J. Exp. Biol.* 24.
- (3) HALE, E. B. & DUNCAN, C. W. & HUFFMAN, C. F. 1940. Rumen digestion in the bovine with some observations on the digestibility of alfalfa hay. *J. Dairy Sci.* 23.
- (4) HALE, E. B. & DUNCAN, C. W. & HUFFMAN, C. F. 1947 a. Rumen digestion studies I. *J. Nutrition* 34.
- (5) HALE, E. B. & DUNCAN, C. W. & HUFFMAN, C. F. 1947 b. Rumen digestion studies II. *Ibid.*
- (6) JARRIGE, R. 1953. L'utilisation des glucides alimentaires par les ruminants. *Ann. de la nutrition et de l'alimentation* 7.
- (7) KÜHN, JULIUS. 1873. Die zweckmässigste Ernährung des Rindviehes. Dresden.
- (8) MANGOLD, E. 1929. Handbuch der Ernährung und des Stoffwechsels der landwirtschaftlichen Nutztiere II. Berlin.

- (9) MARSHALL, R. A. 1949. The digestion of pentosans in hay by sheep. *Brit. J. Nutrition* 3.
- (10) MÜLLER, C. F. 1876. *Die Rindviehzucht*. Berlin.
- (11) PALOHEIMO, L. & MÄKELÄ, A. 1952. The rate of passage of food in the digestive tract of ruminants. *Maataloustiet. aikak. (J. Scient. Agr. Soc. Finland)* 24.
- (12) PHILLIPSON, A. T. 1947. Fermentation in the alimentary tract and the metabolism of the derived fatty acids. *Nutrition Abstr. Rev.* 17.
- (13) PHILLIPSON, A. T. & McANALLY, R. A. 1942. Studies on the fate of carbohydrates in the rumen of the sheep. *J. Exp. Biol.* 19.
- (14) SCHMIDT-MÜLHEIM, ADOLF 1879. *Grundriss der speciellen Physiologie der Haussäugetiere*. Leipzig.
- (15) TRAUTMAN, A. 1933. Beiträge zur Physiologie des Wiederkauermagens VI. *Arch. für Tierernährung und Tierzucht* 9.

SELOSTUS:

ERÄITÄ KVANTITATIIVISIA TIETOJA MÄREHTIJÖIDEN ESIMAHOJEN OSUUDESTA
TYPETTÖMÄN ORGAANISEN AINEEN SULATUKSESSA JA IMEYTYMISESSÄ

L. PALOHEIMO, A. MÄKELÄ ja M.-L. SALO

Kotieläintieteellinen laitos, Helsingin Yliopisto

Neljätoista lehmää ja viisi nuorta sonnimullia ruokittiin 10 päivän aikana määräsuuruksilla heinäannoksilla. Teurastuksen jälkeen juoksutusmahan sisältö punnittiin ja siitä otettiin näyte. Heinästä, juoksutusmahan sisällöstä ja sonnasta määritettiin ligniini, typetön orgaaninen aine sekä typetön ligniinivapaa orgaaninen aine. Ligniiniä johtoaineena pitäen laskettiin mainittujen typettömien fraktioiden sulavuus sekä pötsissä että koko ruoansulatuskanavassa. Tutkimuksessa kävi ilmi, että koko ruoansulatuskanavassa sulaneesta typettömästä ligniinivapaasta orgaanisesta aineesta oli esimahoissa sulanut 76—99 %. Jos kaksi lehmistä jätetään laskuista pois, saadaan lehmille raja-arvot 85 ja 91 %. Tämän tutkimuksen perusteella voidaan päätellä, että naudalla hiilihydraattien sulatus ja hajoamistulosten imeytyminen tapahtuvat pääasiassa esimahoissa.
