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deur

Prof. dr. J. M. W. le Roux

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Die primêre doel by die studie van struktuur is om die kinderlike vrae te beantwoord: Waarvan is dit gemaak? Hoe is dit gemaak? Hoekom is dit so gemaak? As hierdie eenvoudige vrae in die biologie ingewikkelde antwoorde oplewer, is die rede daarvoor te vinde in die ingewikkeldheid van die biologiese struktuur. By die studie van struktuur is daar 'n sin van finaliteit. Die voorwerp moet blootgelê, beskryf en geïllustreer word. Die tegnieke wat aangewend word moet nougeset en krities wees, maar moet die ondersoeker in staat stel om op die ou end die vorm van die voorwerp te bepaal en sy moontlike funksie te vertolk. Daar is dus 'n finaliteit en eenvoud omtrent hierdie soort werk wat dit van ander dissiplines onderskei. Daar is waarskynlik geen ander wetenskaplike vakrigting waarin oorspronklike tekste wat 400 jaar oud is vandag nog gebruik kan word nie. Hierdie volledigheid van die eerste sorgvuldige studie beteken dat dit selde loon om dieselfde voorwerp weer met dieselfde metodes te bestudeer — foute in tegniek en interpretasie is vanselfsprekend uitsonderings. Die verhaal van die studie van struktuur getuig dus van afhanklikheid van nuwe tegnieke en metodes en 'n volgehoue poging om die bou van organismes steeds noukeuriger te bepaal.

'n Reeks aggregate en chemiese verbindings volg mekaar op vanaf die vlak van die atoom tot by groepe individue in die gemeenskap. Ons kan enigiets kies om hierdie opvolging te illustreer: 'n koolstofatoom, glukose, 'n glikogeenmolekuul, glikogeenkorreltjies in 'n lewersel, epiteelweefsel, lewer, spysverteringstelsel, soogdier, kudde. Dit is almal dele van 'n ongebroke reeks wat slegs vir beskrywing gegradeer is. In die reeks tree 'n aantal verskille na vore. Eerstens: belangstelling in die struktuur van onderdele kwyn namate ons na die groter eenhede toe beweeg. Alle wetenskaplikes ontmoet by die atoom; die kernfisikus wyk af as ons na die molekuul toe beweeg; ná die selorgaantjies verloor die plantkundige gemeenskaplike terrein met die dierkundige, en so bly steeds minder mense geïnteresseerd namate ons voortgaan tot by die hele liggaam. Hier vind ons belangstelling gewoonlik net by 'n nouer, professionele of toegepaste skool. Tweedens: in dié reeks word die suiwerheid en voorspelbaarheid van atome en klein molekule vervang deur onreëlmatigheid en onvoorspelbaarheid. Dit beteken dat die meer komplekse aggregate net aangetoon kan word deur direkte waarneming. Atoom- en molekulêre struktuur kan op grond van massagedrag en kristallyne suiwerheid en simmetrie vertolk word, maar die bloedvatpatroon in 'n orgaan of die rangskikking van die inwendige membrane in die sitoplasma moet gesien word voordat dit beskryf kan word. In biologiese sisteme vind hierdie verlies van reëlmatigheid reeds vroeg in die sfeer van makromolekule plaas. Enige groter vorms van geometriese gelykvormigheid is seldsaam en die res van ons genoemde reeks moet gevisualiseer word. Die groottes van hierdie strukture kom rofweg ooreen met die meter-, millimeter-, μ- en mμ-skale. Vooruitgang hang dan af van die beskikbaarheid van 'n werktuig om die struktuur op te los, en vordering was spasmodies as gevolg van die opeenvolgende ontwikkeling van die werktuie. Daar is drie duidelike stadia: die blote oog wat met mm-eenhede werk, die ligmikroskoop met μ en die elektronmikroskoop met mμ. Om gemeenplase, veralgemening en oordrywing te vermy, het ek as voorbeeld van die verband wat daar tussen makroskopiese, ligmikroskopiese en molekulêre anatomie bestaan, 'n orgaan gekies wat teenswoordig in ons volkshuishouding 'n lewensbelangrike rol speel, naamlik die herkouermaag. Ek sal kortliks probeer aantoon hoe waarneming van strukture op hierdie vlakke van organisasie onvermydelik moet lei tot 'n skatting van hulle funksie.

The ruminant stomach and the manner of its function are matters of great economic importance and of such direct interest to veterinarians that we are inclined to think of them as being unmatched in nature. But this is not so, and similar adaptations are to be found in other mammals. Although ruminants excel in this respect, all herbivores possess some ability to obtain nourishment from the digestion of fibrous plant material. This unpromising food consists largely of cellulose and other complex carbohydrates, which resist attack by the normal mammalian complement of digestive enzymes but may be broken down by micro-organisms within the alimentary canal. These micro-organisms may contribute to the nutrition of their hosts in two ways:

(a) They break down complex materials to simple products, which are directly absorbed, and

(b) in their growth and multiplication they build up a range of new materials, absent from the original diet, which may be digested lower in the digestive tract.

A suitable environment for the activities of these microbial symbionts may be provided either in the stomach or in the large intestine. The intestine has been favoured by most of the herbivorous species that we ordinarily encounter — the horse, the pig, the rabbit — and if we confine our attention to these familiar animals the ruminant stomach may well appear to be unique. However, no less striking adaptations of the stomach occur in many more exotic mammalian groups — among the whales and edentates, camels and marsupials, hippopotami and monkeys.

Certain features appear to be comon to all these species. The fermentation chambers correspond in origin to the fundic and adjacent parts of the simple stomach and are therefore entered directly from the esophagus. Their epithelial lining is either "esophageal" in character or, if it is glandular in whole or part, limited to the production of a mucous secretion. These chambers are divided from the lower parts of the organ by a region of constriction, which points to the existence of some mechanism for the regulation of the flow of ingesta, and they are succeeded by a compartment of smaller capacity provided with true "peptic" glands and connected through a pyloric passage with the intestine.

We know all too little about the comparative physiology of the multichambered stomach. From the resemblance to the situation in the ruminants it is reasonable to conjecture that there is this common pattern: the ingesta are stored as a sodden mass in the forechambers, where they undergo microbial fermentation. Microbial hydrolysis of the cellulose yields successively simpler products, the most important end products being volatile fatty acids which are absorbed through the stomach wall and carried, possibly after conversion, to the liver by the portal blood. It may be postulated that combustion of these volatile fatty acids provides a major part of the total energy requirements of all these so-called "polygastric" species.

The ruminants display some striking characteristics. They encompass features of stomach morphology, the processes that continue within the forechambers, the blood chemistry and, above all, the success with which they have adapted to an ecological niche by their ability not only to survive but also to thrive upon poor grazing.

The one certainty in the topographical anatomy of the abdomen is the inconsistency of size and form, and therefore of position and relationships, of the abdominal organs and especially the hollow viscera. This conception of an incessantly changing pattern, so very different from the impression obtained in the dissection room, is vital to our understanding of the physiology of these organs and is largely based upon results of radiological studies of normal living subjects. These alterations are made possible by the very restricted attachment of the rumen — by direct adhesion to the abdominal roof and indirectly by connections with the esophagus and omasum. These attachments, together with the great size and mass of the stomach, assure it a relatively constant general position but do not hamper the continuous and reciprocal contractions and relaxations of the different compartments whose outer surfaces, made smooth by the covering peritoneum and lubricated by the serous fluid, are able to slip freely over the lining of the abdominal wall and against neighbouring organs. The contractions of the rumen and reticulum necessarily lead to adjustments in the position of neighbouring organs, which in turn have further consequences throughout the abdomen. It is therefore absurd to speak of the position of these organs in precise terms. Dogmatic statements of form and position have no place in the description of the viscera — the average text stresses unduly the "standard" form assumed by these organs after death. Consideration of this mercurial behaviour makes it evident that additional adhesions resulting from surgery, trauma or infection must impair the normal working of the ruminoreticulum and are to be avoided whenever possible.

How can we reduce this multichambered stomach of apparent complexity to the more simple and understandable type we are acquainted with in animals like the dog or horse? The story of the development and maturation of the stomach must commence with its embryonic origin. At one time it was believed that the forechambers represented esophageal diverticula and that only the last compartment, the abomasum, developed from the gastric spindle that supplies the entire stomach of other species. This notion has long been disproved, and detailed embryological studies show that all four parts of the ruminant stomach are of gastric origin, an interpretation that is confirmed by the adult topography, the attachments of the omenta and the source and ramification of the gastric nerves and vessels. The embryological studies have demonstrated which parts of the spindle furnish origin to the different compartments. The rumen and reticulum enlarge from the fundic region facing the cardia, the omasum from the lesser curvature at a more distal level, and the abomasum from the terminal section, mainly from the aspect corresponding to the greater curvature of the simple stomach. The channel along which milk passes to the abomasum in the sucking calf thus follows the lesser curvature.

The arrangement of the smooth muscle bundles has been well described and it is established that the principal tracts can be homologised with the simpler pattern of the fibres of the simple-chambered organ. The three-layered arrangement of the fundus and body of the simple stomach is reflected in the muscular arrangement of the homologous ruminoreticulum. The third layer corresponding to the internal oblique fibres of the fundus and body of the simple stomach is present on the ruminoreticulum. The fibres radiate over the reticulum, surround in nearly circular fashion all parts of the rumen and continue into the pillars or inflexions of the walls; consideration of some of these tracts will show how the cranial pillar may be drawn dorsocaudally to shut off the atrium ruminis and how contraction of the fibres which invest the caudal blind sacs can lead to the obliteration of these diverticula.

The nerve supply to the ruminant stomach is distributed in essentially the same manner as in the simple stomach. The dorsal and ventral vagal trunks run along the lesser curvature; the dorsal trunk supplies the visceral surface and the ventral trunk supplies the parietal surface. Similarities are noted, both in the time of development and in the distribution of the gastric nerves, in man and ox. In both species, the vagal trunks reach the gastric primordium at approximately the same stage of gestation: at 7 mm or 31 days in man and at 11 mm or 30 days in the ox. By the 17 mm (37 days) stage in man and in the 14 mm (34 days) stage in the ox, both vagal trunks run along the lesser curvature of their respective primordia. The posterior vagal trunk in man supplies branches to the posterior surface of the stomach and gives branches which pass around the lesser curvature of the stomach to its anterior surface. The comparable dorsal vagal trunk in the ox innervates the dorsal surface of the ruminoreticular primordium and the developing omasum. The anterior vagal trunk in man supplies the anterior surface of the stomach and gives off a branch which passes to the liver and pylorus. The comparable ventral trunk in the ox supplies the ventral surface of the developing stomach and also gives off a branch to the liver and pylorus. Thus, between the 30th and 37th day of gestation the gastric nerves in man and ox parallel one another in development. The gastric primordia in both species also resemble one another at this period.

Of special interest for the orientation is the attachment of the mesenteria. During the course of ontogenesis the stomach primordium becomes subjected to considerable positional changes as a result of rotational incidents and differences in growth intensities. Both mesenteries, the dorsal and ventral mesogastrium, remain intact, with the stomach or mesenterial plane extending between their lines of attachment. This plane allows the distinction of left and right sides of the fully developed stomach, independent of changes in form and position. In the simple stomach the ventral mesogastrium regularly attaches to the lesser curvature and this criterion is also used to determine the lesser curvature of the ruminant stomach. The dorsal mesogastrium attaches regularly to the greater curvature only in the distal part of the stomach, while in the cardiac zone its line of attachment may deviate to a variable degree from the greater curvature. Its line of attachment on the simple stomach may appear rather complicated when it is projected on the ruminant stomach. Consideration of ontogenetic events, and by reconstruction according to methods of co-ordinates, this line can be reduced to the curvature seen in the simple stomach and stereometric principles thus translated into anatomical language.

To complete the homologies between the simple and ruminant stomach, mention should be made of the arterial blood vessels which supply homologous sections of the intestinal tract in mammals. The celiac artery is the main source of supply and trifurcates into hepatic, splenic and left gastric arteries, the main branches of which run along both curvatures. The greater curvature is supplied by the gastroepiploic arteries, the lesser curvature by the gastric arteries. In the ruminant the mode of origin is distorted by the great development of the arteries of the rumen and reticulum, which correspond to branches of the splenic and left gastric arteries on the simple stomach.

We know that the ruminoreticulum is not merely a fermentation chamber but also an important absorptive organ, and it is necessary to consider the structure of the mucous membrane a little more carefully. In natural conditions newborn lambs and calves subsist upon their mothers' milk like the young of other species, and in their digestive physiology they resemble these more closely than they do adults of their own kind. This period does not last long — no one with experience of young ruminants can have failed to be impressed by the avidity with which they seek out and consume solid food when only a few days old — and an adult regimen can be established within a very short time because all parts of the stomach present a relatively advanced state of development at birth. The changes that occur during the transition from a milk diet to one of forage are mainly in the proportions of the several compartments and in the details of the mucosa; they constitute one of the most interesting aspects of the anatomy and physiology of these animals and are also of great economic importance as the efficiency and precocity with which adult feeding habits are acquired is of practical concern to the stockraiser.

The four chambers are established early in embryonic life, and while all continue to enlarge they do so at very unequal rates, first one having the advantage and then another. Birth finds the abomasum manifestly the largest compartment and it is of course only this part that has an immediate function to perform. Before we consider the proportions at different ages a reminder of the problems connected with the measurement of the hollow organs may be useful. There is no general agreement whether it is best for this purpose to use their masses, their potential capacities when artificially distended or the actual volume of their contents at a given time. Each of these parameters has certain advantages and disadvantages and each has its supporters. All must be used with discretion, for it is evident that some of the figures given in the literature are ridiculous — for example the statement that the volume of the rumen of a kid weighing five koligrams amounts to more than five litres. One is reminded that, while all science may be measurement, all measurement is not necessarily science. Probably the volume of the contents is the most useful and physiological measurement, and with appropriate reference substances and sampling techniques, it is adaptable to longitudinal studies in which the same animals are examined at successive stages of development.

In lambs the abomasum increases in mass fourfold during the first two months of life and at a more leisurely pace thereafter. It is doubtful whether mass is the most useful description of this organ, and if we consider the volume of its natural contents we find that this hardly changes during the first eight or nine weeks and then increases slowly but steadily until maturity. Thus, while the abomasum dominates abdominal topography at birth, extending from one flank to the other and from the diaphragm almost to the pelvic inlet, the picture is quite different only a few weeks later: at two months the topography is hardly to be distinguished from that seen in the adult. These anatomical changes are accompanied by alterations in the motor physiology. The neonatal abomasum is the seat of vigorous activity in which deep peristaltic waves course over the distal part of the organ to transform into antral systoles as they approach the pylorus; these movements are more sluggish after a bare month of postnatal life and continue to abate in vigour and intensity.

The growth of the rumen and reticulum follows a rather different pattern. These organs increase in mass by a factor of fifteen during the first two months and then grow more slowly until the adult mass is reached. They contain very little ingesta during the first two or three weeks but when the animal first evinces a serious interest in solid food, they gain in volume very quickly. In lambs of two weeks age the ruminoreticulum holds less than half the content of the abomasum: it contains an equal volume one week later and almost twenty times as much before two months have elapsed. The latter is approximately the adult ratio and the volume of the rumen now maintains a steady relationship with the abomasal volume and the live mass of the animal. Most of the increase in ruminal mass is accounted for by growth of the muscularis propria, but the more interesting changes occur in the mucosa. At birth the rumen is thickly carpeted with small, conical and incompletely separated papillae, and the epithelium, though not yet fully differentiated, posesses all the main features of its adult structure. By three weeks the papillae are individually distinct and are beginning to acquire their familiar tongue-like form, while the epithelium is thicker and the surface layers are more heavily keratinised than before. Shortly after this the basal layer begins to fold and forms the characteristic indentations that mark its junction with the underlying connective tissue.

The continuation of these processes completes the transformation within two months of birth. The maturation of the reticular lining runs parallel. The appearance of the structures depends to some extent upon the usage they receive: in animals fed on contaminated forage or harsh material containing abrasive phytoliths they are worn and ragged. The characteristic pattern of ruminoreticular activity is not developed at birth. Relatively little study has been given to these movements in the youngest animals but as they have an influence on abdominal topography we cannot neglect them entirely. Activity, irregular and uncoordinated, is exhibited by animals only a few days old, and by three weeks there are reticular contractions which, however, are not associated with contraction of the atrial compartment of the rumen. The interplay at first involves the ventral sac of the rumen and the reticulum, and it may be noted that the gross development of the atrium ruminis is also retarded. The mature, more regular pattern of behaviour appears to be established at some stage in the second month, considerable individual variation being displayed. A brief mention of the digestive processes within the rumen may be allowed to round off these few remarks. In grazing lambs the concentration of volatile fatty acids within the ruminal contents is at first very low and remains so for two weeks: from this age there is a very rapid increase, and two months old lambs on pasture differ little from their dams in this respect. It is interesting to note that the behavioral, anatomical, mechanical and chemical aspects of ruminoreticular development follow the same time-table, a schedule that is also observed by the parotid gland, whose secretion provides the meduim in which microbial digestion takes place. Taken in conjunction, these various factors enable us to recognise three distinct phases in the development of the ruminant. There is first a neonatal phase, which in the lamb lasts until three weeks, and this is followed by a transitional period, which extends from the third to the eighth week, when the definitive ruminant state is attained.

There have been many experiments designed to isolate the factors that stimulate the postnatal development of the forechambers. It seems that the changes that occur in the first three weeks are little affected by the nature of the diet, although they will be slowed if the rations are grossly inadequate in amount. Further increase in the size of the ruminoreticulum and in the thickness of its wall depends on the inclusion of some form of roughage — even if only inert material — in the food, and if this is deficient growth is slow and does not proceed beyond the stage reached by normally reared animals after four or five weeks. The omasum is particularly dependent upon this mechanical stimulation and if not exercised advances little beyond its neonatal dimensions. The time at which chemical and physical influences are effective does not appear to be narrowly defined, for animals maintained on artificial diets quickly acquire a normal gastric structure and confirmation when transferred to normal rations.

The mucosal linings of the rumen and reticulum are made rough and irregular, each in its own fashion, by the projection into the interior of numerous papillae. The primary function of these projections is to increase the mucosal surface area — a conclusion based on the demonstration that the development of the papillae is dependent upon the chemical nature of the diet and not upon its physical properties. Reaching this degree of development is stimulated by the presence of a sufficient quantity of butyric acid in the rumen contents. Butyric acid is taken up and utilized by the epithelial cells. Beta-hydroxybutyric acid is released into the blood as a residue. The stimulating effect of this butyric acid metabolism in the epithelial cells will also enhance the permeability to other fatty acids, although these do not appear to interfere actively in tissue metabolism. Passing reference must be made to the very rich network of capillaries that is to be found within the papillae, both within the central core and also in the connective tissue extensions that project into the thickness of the epithelium, much like the papillary bodies of the skin. The plexus lies immediately below the deepest stratum of the epithelium, only 50μ from the cavity, and is obviously well placed to carry away absorbed products. Less is known of the lymphatics of the rumen papillae but these also appear to be generously developed and it has been suggested that their arrangement resembles that of the lacteals of the intestinal villi. The destination of the blood that is carried from the rumen into the portal vein is of great interest. It is well known that there is a streamlining of the portal flow in some animals and that the blood conveyed from various parts of the gastro-intestinal tract is differentially distributed in the liver. It would be interesting to have convincing evidence of the occurrence of this phenomenon in ruminant species, for it has a potential importance to workers in many fields of ruminant biology. The omasum is a less obviously active organ than the preceding chambers. The omasal lumen is subdivided into a series of recesses by the projection of many plates of different length, except along the lesser curvature, where the omasal sulcus provides an open passage. These laminae increase the mucosal area and also impede the passage of the larger fragments of ingesta. Contractions of the omasal canal and body are attended with a drop in pressure and cause a suction effect which facilitates the passage of ingesta. The motility of the laminae are independent — contractions start at the free border and proceed to the base in a caudal direction. Recent observations on omasal motility contradict the popular view that solid feed particles only pass in between the laminae while the fluid part flows freely through the omasal canal from the reticulum to the abomasum. It is now well established that not only water but also electrolytes and volatile fatty acids are absorbed here. The epithelial and vascular arrangements of the mucosa are basically similar to corresponding features of ruminal structure. Of particular interest is the demonstration of valves in the veins and the existence of arteriovenous anastomoses, two haemodynamic mechanisms of value for the reflux of blood in this vascular area. Subepithelial capillaries are replaced by venules in certain areas which have particular significance as "exchange partners" for the transport of products through the mucosa. The endothelium of these vessels possesses ponicytosis vesicles and pores — structures currently considered as possible transport routes for the exchange of substances through the vessel wall.

An explanation of the relative infrequency with which the abomasal contents reflux through the wide omaso-abomasal opening may be found in the development of the abomasal plicae, which rise abruptly around the margin of the opening and, acting like a ball valve, close the orifice when the pressure within the abomasum rises.

Aangesien ons belangstelling oorwegend op die funksie gerig is, moet die ultrastruktuur nog ten slotte kortliks genoem word. Sentraal daarby staan die uitgangspunt dat die verhoornde meerlaagepiteel nie slegs as 'n skans funksioneer nie, maar dat dit 'n selektiewe deurlaatbaarheid vertoon en selfs tot aktiewe transport in staat is. Die ultrastruktuur moet geprojekteer word teen die agtergrond van die volgende vrae: Kan uit die ultrastrukturele beeld die transepiteliale transportweg afgelei word? Gee hierdie beeld insig in regulasie- en omsettingsmoontlikhede? Hoe is die skans gekombineer met die transportvermoë? Gee die ultrastruktuur opheldering oor die moontlike optrede van bepaalde patologiese reaksiepatrone?

Die stratum basale bestaan uit een laag silindriese epiteelselle. Die selkern lê weggedring van die apikale helfte; sentrobasaal word baie mitochondria en groepe ribosome aangetref. Endoplasmatiese reticulum en golgisisteem is redelik goed ontwikkel en 'n duidelike basaalmembraan begrens dié sellaag teen die kapillêrryke bindweefsel daaronder. Die membraan lê nie in 'n plat vlak nie en toon lokale diep instulpings wat deur sitoplasmatiese uitlopers van die basaalselle gevul word. Die teenwoordigheid van nie-epiteliale selle bewys dat die basaalmembraan hulle deurgang nie verhinder nie. Die basaalselle is d.m.v. halfdesmosome aan die basaalmembraan geheg. Soms rus 'n gedeelte van die selmembraan op die basaalmembraan. Dit is egter hoofsaaklik vertakkende sitoplasmatiese uitlopers wat basaalwaarts uitstulp en met voetjies op die basaalmembraan eindig. Dit val ook op dat enkele uitlopers vanaf die stratum spinosum die basaalmembraan bereik. Die lateroapikale oppervlak van die basaalselle gee eweneens talryke uitlopers af. Laasgenoemde eindig d.m.v. demosome op soortgelyke uitlopers van naburige selle (basaalselle of spinosumselle) of eweneens via desmosome direk up 'n buursel. Somige uitlopers eindig vry. Die baie wye intersellulêre ruimte en die opvallende oppervlaktevergroting, asook die rykdom aan mitochondria, dui stellig op 'n aktiewe transportfunksie. Belangrik is ook dat in die stratum basale sowel as in die stratum spinosum 'n hoë B-hidroksiebottersuurdehidrogenase-aktiwiteit teenwoordig is.

Die statum spinosum word verdeel in 'n dieper laag parabasaalselle en 'n oppervlakkige laag intermediêre selle. Die polihedriese spinosumselle is opvallend ryk aan mitochondria en ribosome. Golgisisteem en endoplasmatiese reticulum is ontwikkel. Radiaal en onder die seloppervlak word heelwat tonofribrille aangetref. Die spinosumselle se oppervlak vertoon ook talryke uitlopers waarvan die meeste d.m.v. desmosome verbind is met die uitlopers van naburige selle. Sommige strek tot op die basaalmembraan en sommige eindig vry. Die wye intersellulêre ruimte van die meergelaagde stratum spinosum sluit aan by dié van die stratum basale. Tesame vorm hulle 'n egte labirint wat op talryke plekke deurkruis word deur vry eindigende sitoplasmatiese uitlopers. Sommige van die uitlopers toon vesikulasie, wat dui op 'n sekresie na die intersellulêre ruimte toe. Daar is egter ook morfologiese aanduidings van so 'n proses in omgekeerde rigting. Hoog in die stratum spinosum begin die selle afplat.

In die stratum intermedium (granulosum plus lucidum) begin keratinisasie plaasvind: direk onder die apikale selmembraan word 'n korrelrige materiaal aangetref wat ongetwyfeld keratohialien is. Voorts wys hierdie laag 'n geprogrammeerde degenerasie van die selorgaantjies, veral van die mitochondria. In die stratum intermeduim word lisosome aangetref — selorgaantjies ryk aan hidrolase, veral suurfosfatase. Dieper in hierdie laag is daar ook 'n positiwiteit m.b.t. alkaliese fosfatase. Die intersellulêre ruimte is vernou m.b.t. die labirint daaronder; hierdie tendens word verstrek in die stratum corneum. Origens is die intermediumselle kragtig d.m.v. desmosome aan mekaar sowel as aan selle van die aangrensende lae gekoppel.

In die stratum corneum kan drie seltipes onderskei word. Die selkontoere is nouliks sigbaar en selorgaantjies is slegs as skimme waarneembaar. Die struktuurbeeld laat geen ruimte vir die veronderstelling van vitale prosesse nie. Die diepste laag bestaan uit plat selle, die middelste laag uit skyfvormige selle en die oppervlaklaag uit ballonvormige selle. Die morfologiese substraat van die skans wat in die stratum corneum gevorm word, moet gesoek word in die plat selle. Die selmateriaal bestaan uit 'n digte osmiofiele keratien wat waarskynlik as gevolg van lisosomale ensieme uit die sitoplasma van die intermediumselle onstaan. Die selle is stewig aan mekaar geanker en d.m.v. intakte desmosome aan selle daarbo en daaronder verbind. 'n Lipiedagtige stof wat deur die intermediumselle in die intersellulêre ruimtes afgeskei word, bedek die selle. Aan hierdie materiaal word 'n weerstand teen keratolitiese invloede toegeskryf. Die skyfvormige selle word nie deur die lipiedagtige stof bedek nie en kan in bepaalde omstandighede opswel en uit verband los raak. Bakterieë is ook nog nie dieper as die skyfvormige selle gevind nie. As geheel vorm die plat selle dus 'n ondeurdringbare skans.

'n Vergelyking van die morfologiese beeld van die epiteelskans in die grootpens met dié van die epidermis in die vel (teen hitte, koue, water, chemikalieë, meganiese en elektriese besering en deels teen ultravioletbestraling) toon ooreenkomste en verskille. Die ooreenkoms lê daarin dat die diepere horingselle uit digte keratien bestaan en dat hulle stewig aan mekaar geanker is. Die verskille lê eerstens by die desmosome wat in die pensepiteel intak bly, in die epidermis by die verhoorningsproses betrek word; tweedens, die lipiedagtige stof in die interdesmosomale ruimtes van die pensepiteel dien as 'n beskermende mantellaag, in die epidermis dien dit blykbaar bloot as vulmateriaal; in die derde plek bly die boonste verhoornde selle van die pensepiteel swelbaar, terwyl hulle by die epidermis verdroog.

Met die selektiewe deurlatendheid van die pensepiteel as sentrale probleem, vestig ons die aandag op die intersellulêre ruimte wat, soos 'n omgekeerde tregter wyd uitloop na die basaalmembraan toe, stellig geleentheid bied tot passiewe diffusie. Die swelbare elemente van die stratum corneum speel die rol van 'n deurlatende bakteriese filter. Die belang van die filter word duidelik wanneer die bakteriële komplikasies van ruminitis ter sprake kom. Die epiteelselle ondergaan hidropiese degenerasie, veral in die dieper lae. Skeurtjies ontstaan en die selle vloei saam tot blasies, wat vergroot en uitbrei tot in die oppervlaklae, waar die epiteel loslaat. Tegelykertyd vind 'n infiltrasie van neutrofiele plaas en die skans tussen kapillêre en pensholte bestaan nog net uit klein blasies. Op dié oomblik is daar 'n invasie van bakterieë. Die gevolg is vorming van swere, selfs perforasie en uiteindelik lewerabsesse. En waar juis by ruminitis die epiteel ten gronde gaan, ontstaan die vermoede dat die lisosomale hidrolases van die stratum intermedium hierby moontlik 'n hoofrol speel.

Wat die epiteel onder die stratum corneum betref, word die moontlikheid gestel van 'n gedeeltelik (passiewe) translabirintêre en 'n gedeeltelik (aktiewe) transellulêre transport. En hierby kan mens dan veronderstel dat die basaal- en spinosumselle wat so besonder ryk aan mitochondria is bepaalde molekules uit die intersellulêre labirint opneem om hulle, omgesit al dan nie, elders weer aan die labirint af te gee. So 'n meganisme sou sekerlik moontlikhede tot regulering van die transport kan bied. Transport via die transsellulêre roete veronderstel deurlatendheid van die sellulêre kontakpunte, nl. die desmosome, wat dan 'n ander funksie as 'n blote meganiese funksie aanneem. Daar is reeds sterk vermoedens dat dit wel die geval is.

Ek het hier en daar melding gemaak van histochemiese aspekte. Dit is 'n vakgebied wat ontstaan het a.g.v. die tegniese vordering op die gebied van die histologie en fisiologiese chemie, waardeur lokalisering van die chemiese stowwe in bepaalde dele van weefsels en selle vasgestel kan word en waarvan weer verklarings vir die bou en funksie afgelei kan word. Verdere verfynings het ons gebring tot die gebied van die ultrahistochemie. Van enige verdere bespreking in hierdie verband, soos van toepassing op die herkouermaag, wil ek voorlopig afsien.

En so word die vergelykende anatomie, die ontwikkelingsgeskiedenis, die makroskopiese en ligmikroskopiese anatomie, elektronmikroskopie en histochemie bygehaal om die vrae wat inleidend gestel is, te beantwoord, naamlik: hoe lyk dit, en wat doen dit?

Dit gaan dus hier oor vorm en funksie. Vorm op sigself is net belangrik omdat dit 'n weerspieëling is van die inwendige aktiwiteite van die lewende organisme. Die funksie dien as vormbepalende prikkel, as leitmotiv om selelemente en selle vanaf die molekulêre vlak in funksionele en morfologiese verband te rangskik, hulle te kristalliseer tot die vorm waarin ons die struktuur of orgaan uiteindelik met die blote oog waarneem. Met ander woorde: vorm is gekristalliseerde funksie!

Mnr. die Rektor, laat my toe om hierdie voordrag op te dra aan H.P.A. de Boom, wat sy natuurlike aanvoeling en diepe insig in die veeartsenykundige anatomie ingrypend, ten goede en blywend gestempel het op die onderrig in: Vorm is gekristalliseerde funksie.

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