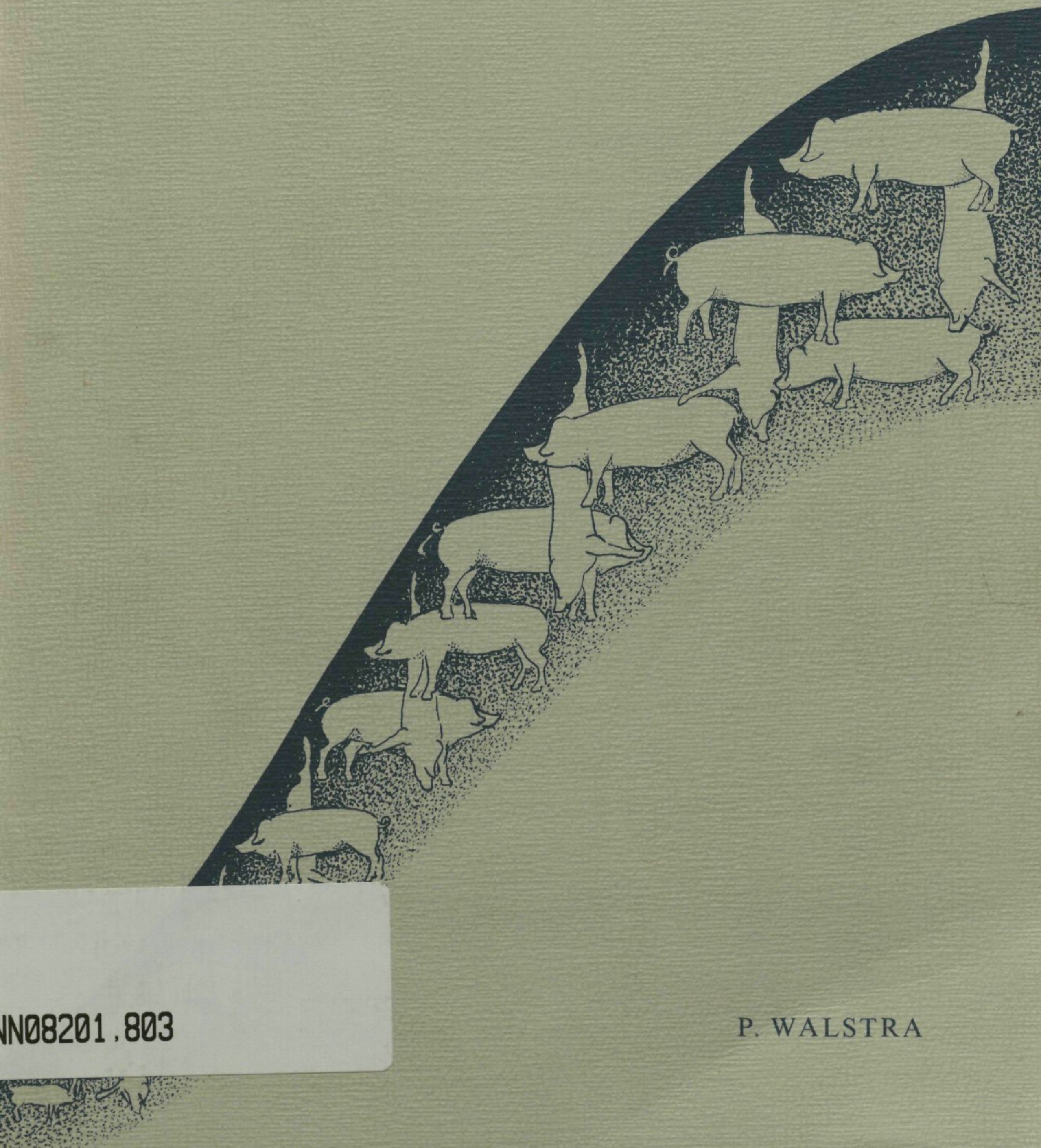
GROWTH AND CARCASS COMPOSITION FROM BIRTH TO MATURITY IN RELATION TO FEEDING LEVEL AND SEX IN DUTCH LANDRACE PIGS



P. WALSTRA

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GROWTH AND CARCASS COMPOSITION FROM BIRTH TO MATURITY IN RELATION TO FEEDING LEVEL AND SEX IN DUTCH LANDRACE PIGS

(with a summary in Dutch)

Proefschrift
ter verkrijging van de graad
van doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. H. C. van der Plas,
hoogleraar in de organische scheikunde,
in het openbaar te verdedigen
op vrijdag 2 mei 1980
des voormiddags te elf uur in de aula
van de Landbouwhogeschool te Wageningen

H. VEENMAN & ZONEN B.V. – WAGENINGEN – 1980

STELLINGEN

I

Voor het beschrijven van relatieve groei wordt te vanzelfsprekend gebruik gemaakt van de allometrische formule.

Dit proefschrift.

II

Bij het door velen ingenomen standpunt dat reeds in een jong stadium de uiteindelijke spiergewichtsverdeling bereikt wordt, is onvoldoende rekening gehouden met een op latere leeftijd optredend masculinisatieproces.

Dit proefschrift.

III

Sexeverschillen in spier- en vetgewichtsverdeling doen het geldelijke voordeel van een groter vleesaandeel bij het mesten van beren in plaats van borgen kleiner zijn dan veelal verondersteld wordt.

Dit proefschrift.

IV

De grotere mate van marmorering bij vlees van beren vergeleken met die van borgen gevonden in Amerikaanse proeven, is slechts ogenschijnlijk, tenzij gecorrigeerd wordt voor verschillen in algehele vetheid.

o.a. SIERS, D. G. J. Anim. Sci. **41** (1975) 522–526.
Dit proefschrift.

V

Het is twijfelachtig of de geconstateerde verbetering van de vleeskwaliteit van Deense selectiemesterijvarkens op basis van objectieve metingen vervat in een vleeskwaliteitsindex (KK-index), een gevolg is van directe selectie op dit kenmerk.

JENSEN, P. en E. ANDRESEN. Paper 30th Ann. Meeting E. A. A. P. Harrogate, juli 1979 en Livest. Prod. Sci. **7** (1980) (in druk).

VI

Het is gewenst om bij de indeling van vleeswaren in kwaliteitsklassen niet alleen te letten op de chemische samenstelling, maar ook op de bereiding volgens goed vakmanschap.

Kwaliteitsregelingen P.V.V.

VII

Bestrijding van mastitis via selectie op het voorkomen van lage celgetallen in melk is een riskante benadering.

VIII

De theorie van SELYE dat stressoren één algemeen aspecifiek reactiepatroon in mens en dier teweegbrengen is aanvechtbaar.

SELYE, H. The stress of life. McGraw-Hill, New York (1956).

IX

De bereidheid tot het nemen van wettelijke maatregelen ten aanzien van de wijze van houden van landbouwhuisdieren dient minder afhankelijk te worden gesteld van wetenschappelijk bepaalde, meetbare criteria voor het welzijn van dieren.

Nota Intensieve Veehouderij – Tweede Kamer, zitting 1974–1975, 13227, nrs. 1–2.

X

De algemeen gehuldigde opvatting dat de zgn. richels op visschubben des winters dichter bij elkaar worden afgezet dan gedurende een zomer is onjuist.

UTRECHT, W. L. VAN. Aquaculture 17 (1979) 159–174.

XI

Het is niet zonder risico's dat in brede kringen voetstoots wordt aangenomen dat op alternatieve wijze geproduceerd voedsel een betere kwaliteit heeft dan het op gangbare wijze voortgebrachte produkt.

XII

Het feit dat verondersteld werd dat de heilige Antonius de Kluizenaar, patroon van de varkens, niet alleen bescherming bood tegen het 'heilig' vuur bij varkens maar ook tegen dat bij de mens, berust waarschijnlijk op de symptomatische overeenkomst tussen respectievelijk vlekziekte en moederkorenvergiftiging.

P. WALSTRA
Wageningen, 2 mei 1980.

VOORWOORD

Een onderzoek als het beschrevene in deze dissertatie kan niet worden uitgevoerd zonder dat van velen hulp en steun wordt ondervonden. Iedereen die op enigerlei wijze heeft bijgedragen aan de totstandkoming van dit proefschrift wil ik gaarne daarvoor danken.

Het onderzoek werd uitgevoerd op het Instituut voor Veeteeltkundig Onderzoek 'Schoonoord' te Zeist. De directie van het instituut ben ik zeer erkentelijk voor de mij geboden mogelijkheden het geheel te kunnen doorvoeren en uit te werken.

Een woord van dank wil ik gaarne brengen aan de dierverzorgers op de 'Bantham', aan het personeel van de uitsnijruimte, aan degenen die de vele literatuuraanvragen hebben verwerkt en aan de dames die het typewerk verzorgden, waarvan met name mej. E. C. Kroeze en mevr. E. Barnard-de Vries het leeuwendeel voor hun rekening namen. De heer H. de Vries verrichtte het merendeel van het tekenwerk; voor de keurige verzorging daarvan wil ik hem hartelijk dankzeggen. De heren H. Schuitemaker en W. Buist van het Instituut T.N.O. voor Wiskunde, Informatieverwerking en Statistiek te Wageningen ben ik dank verschuldigd voor de computermatige verwerking van het materiaal. Mevr. M. H. de Stoppelaar-Rijsinge dank ik voor de accuratesse waarmee zij de Engelse tekst corrigeerde.

Dank ben ik tevens verschuldigd aan drs. P. L. Bergström en Dr. Ir. E. W. Brascamp (Instituut voor Veeteeltkundig Onderzoek 'Schoonoord' te Zeist), Ir. A. A. M. Jansen (Instituut T.N.O. voor Wiskunde, Informatieverwerking en Statistiek te Wageningen) en Ir. E. Kanis en ing. W. J. Koops (Vakgroep Veefokkerij, Landbouwhogeschool te Wageningen), niet alleen voor het kritisch doornemen van het manuscript of delen daarvan, maar ook voor hun waardevolle inbreng in de eropvolgende discussies.

Een woord van bijzondere dank geldt de heer G. Mateman. Van hem mocht ik veel technische assistentie ondervinden, zowel bij het voorbereiden van de figuren en van het materiaal voor de computermatige verwerking, alsmede voor het uitvoeren van vele berekeningen.

Zeer erkentelijk ben ik ook Ir. A. A. M. Jansen, die mij steeds tot steun is geweest bij de statistische verwerking. Zijn groeiende interesse voor het onderwerp en de veelal langdurige discussies heb ik zeer gewaardeerd.

Een speciaal woord van dank wil ik richten tot drs. P. L. Bergström. Met jou Peter had ik vele lange discussies. Ik mocht profiteren van jouw anatomische kennis, terwijl via jouw directe betrokkenheid bij het onderwerp mij inzicht werd gegeven in de interpretatie van de uitkomsten. Jij was steeds aanwezig wanneer moeilijkheden dreigden, ook op momenten die mogelijk wel eens ongelegen kwamen.

Mijn promotor, Prof. Dr. Ir. R. D. Politiek wil ik danken voor de suggesties bij de verwerking van het materiaal en de totstandkoming van het proefschrift. U hoorde mijn problemen aan en weerhield mij van het planten van nog meer bomen in dit reeds omvangrijke bos. Voor Uw belangstelling en voortdurend stimulerende invloed ben ik U zeer dankbaar.

Omslagontwerp Peter Bergström

CONTENTS

1. INTRODUCTION

In zootechnical studies the processes of growth usually have two main aspects. Firstly growth as such is considered to be the increase in body size (weight and length) per unit time. Differentiation, of which completion is achieved largely in the embryonic stage already, is included in the process. The second aspect is growth as a morphogenetic process: the increase of the different parts of the body or at least the changes in size and shape of the body components caused by different growth intensities of the various organs and tissues. This differential growth may be called development.

The developmental changes ultimately lead to a carcass of which its composition and the time over which it can be realized determine the ability for meat production in pigs. Environmental factors, of which climate and feeding level are the most important, interfere with the realization of the genetic potential.

Knowing the basic principles by which the changes in the body occur is of great value. Actual developmental changes, however, can only be accurately studied when anatomical dissections are carried out during growth. Such experiments in pigs were rather scarce in the literature at the start of the present study. These were the motives to set up an experiment with pigs in order to gain insight in the laws to which the processes of growth obey. Moreover, it would supplement similar work in cattle, which had already been started at the Institute by BERGSTRÖM.

The primary objective of the present study merely was the assessment and detailed description of the changes in body composition during growth. A second aim was to study whether and to what extent growth patterns would be influenced by sex as a genetic factor and by feeding level as an environmental factor.

Data on growth of the organism as a whole can be easily obtained, unlike data measuring the development of the body. The latter cannot be measured with sufficient accuracy unless dissections are carried out. Estimation of the body composition by any other method was not in the scope of this study. Other methods mostly measure composition indirectly, except chemical analysis. Chemical assessment, however, serves a somewhat distinct purpose, although it would give valuable supplementary information to complete the picture of the changes in a growing animal.

The dissection techniques used generally, are limited to the so-called standard methods, among which the Institute's (I.V.O.)-standard method (BERGSTRÖM and KROESKE, 1968). These methods are mainly based on commercial jointing. They are rather rough methods in which generally the tissue components bone, muscle and fat are separated incompletely. Moreover, such methods are different in the different countries and even within countries; therefore anatomical dissection has to be applied.

Because of the enormous amount of work and the fact that the value of the carcass is reduced, the examples of complete anatomical dissections in the literature are limited. HAMMOND initiated anatomical dissection work at Cambridge. The results of the Cambridge School became available in the period 1930–1955; they were published by HAMMOND (1932a) and PÁLSSON and VERGÉS (1952ab) for sheep, by MCMEEKAN (1940abc, 1941) and POMEROY (1941) for pigs and by WALLACE (1948abc) for lambs. This work was extended by WILSON (1952, 1954ab, 1958ab, 1960) who used the same type of experiment for poultry and for East-African dwarf goats.

After MCMEEKAN had finished his comprehensive studies, dissections in pigs at distinct stages were also published by others. In general, however, the dissections were incomplete, i.e. only the main tissues were dissected without proceeding to a within tissue basis, or only a few muscles were involved. In other cases only linear measurements were taken or the slaughterings took place only around the commercial slaughter weights. Dissections in pigs on a within tissue basis proceeding up to individual bones and muscle groups were carried out by RICHMOND and BERG (1971ab, 1972) and CARDEN and GOENAGA (1977).

Complete anatomical dissections up to individual muscles were only found by CUTHBERTSON and POMEROY (1962ab, 1964) and DAVIES (1974ab, 1975). Such dissections were carried out in sheep by LOHSE et al. (1971) and in cattle by BUTTERFIELD and BERG (1966ab), ROBELIN et al. (1974, 1977), BERGSTRÖM (1974b, 1978) and ANDERSEN (1975).

At the start of the present study (1969) in pigs only the work of MCMEEKAN (1940abc, 1941) and CUTHBERTSON and POMEROY (1962ab) had been published, while in addition ELSLEY et al. (1964) had re-analyzed MCMEEKAN's data and FOWLER (1965, 1968) had started investigations. Except by BERGSTRÖM and KROESKE (1969) no anatomical dissection work in pigs had been done in The Netherlands. Their examination was related to the normal slaughter weight and was designed to connect carcass composition with grading data of the carcass. So the knowledge with regard to changes during growth in pigs at that time was scarce. Moreover the whole range from birth to maturity had never been examined.

Therefore the present study was designed to try to assess the body composition as complete as possible proceeding to individual bones and muscles, and to the fat depots subcutaneous, intermuscular and flare fat. The dissection stages have covered the whole range from birth to maturity (except for subcutaneous fat and skin at birth).

The experiment was set up as a cross-sectional design with seven dissection stages to which later on the new-born stage was added. The pigs were slaughtered at 6 weeks intervals, except in the elder animals where longer intervals elapsed between the stages. Six treatment groups were formed comprising two feeding levels (*ad libitum vs* a restricted level) and the three 'sexes' (entire males, castrated males and females). The nutritional treatment was introduced at the first dissection stage when the animals were 10–12 weeks old. In principle eight animals per treatment group at each dissection stage were to be slaughtered resulting in a total of 328 planned animals.

The description of the growth of parts relative to given entities may be largely facilitated when the allometric equation is used. Preliminary calculations made clear that over longer trajectories high power terms needed to be added to the equation, which was used in its logarithmic form. Part to whole relationships were considered stepwise: – carcass related to live weight – main components related to carcass weight – and individual bones, muscles and fat depots related to the total respective tissue weights.

2. LITERATURE

2.1. GENERAL

Growth has many aspects. Not all aspects are fully elucidated, particularly the fundamental aspects of the mechanisms involved in regulating growth, how growth is initiated, and how it proceeds and then diminishes in early maturity. Since growth has so many aspects it is difficult to define, and it depends also on the purpose why, the professional area from which or the level at which growth is studied. Basic studies on growth, for example at cellular level, are not of direct interest for the pig breeder who shows his well-developed Pietrain boar at an exhibition.

According to BRODY (1945) growth is biologic synthesis, production of new biochemical units and thus the aspect of development concerned with increase in living substance or protoplasm, including the processes (a) cell multiplication, (b) cell enlargement, and (c) incorporation of material taken from the environment. Other terms used are (a) hyperplasia, (b) intussusception (NEEDHAM, 1964) and hypertrophy, and (c) accretionary growth, increase in non-cellular matter, respectively.

Where VON BERTALANFFY (1960) defines growth as 'the quantitative increase of a living system which results from the prevalence of anabolism of building materials over catabolism', growth is distinguished from differentiation. The latter being an increase in organisation and morphological heterogeneity within a living system. This distinction between the qualitative and quantitative aspect is elaborated by NEEDHAM (1964). Though in principle there is a considerable degree of independence in the course and control of growth and differentiation, a closer examination shows that there is no sharp borderline. NEEDHAM eventually states that both aspects are 'correlated directly rather than inversely, are complementary rather than reciprocal or even antagonistic'. VON BERTALANFFY (1960) arrived at a similar conclusion.

The morphogenetic processes work throughout the life of an animal, from the conception on to the adult state. The differentiation of organs and tissues mainly takes place in prenatal life. Also the relative increase in size is very rapid then. After birth growth and development of the animal is in cell enlargement and in different growth rates of the various body components, i.c. organs and tissues, relative to the body as a whole. Therefore shape of animals is continuously changing. An illustration is given in Fig. 2.1, derived from HAMMOND (1932b). At one week the pig is all head, neck and legs with a short shallow body as HAMMOND expressed it. During the growing period first length increases proportionally; then the body deepens and thickens so that ultimately the head, neck and legs become proportionally smaller. In this way an animal reaches its adult weight and form. Even when an animal has arrived at mature weight it still grows, i.e. a certain tissue grows at the expense of an other tissue.

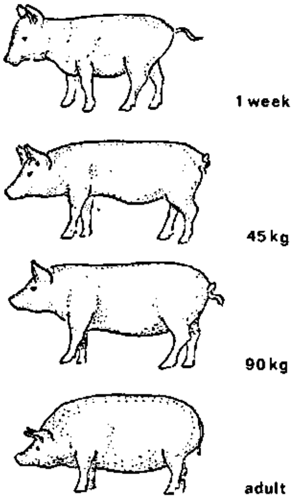

FIG. 2.1. The changes in proportions of the pig from birth to maturity. For comparison, the height at the shoulder is the same (from HAMMOND, 1932b).

Another definition of growth given by BRODY (1945) fits to these concepts, viz. that for purposes of quantitative analysis and under the condition of normal food supply, growth is defined as 'relatively irreversible time change in magnitude of the measured dimension or function'. As changes in proportions may have brought about evolutionary changes, they were also viewed in a more philosophical light (BERNARD, 1885; THOMPSON, 1917; HUXLEY, 1932; BRODY, 1945; VON BERTALANFFY, 1960; NEEDHAM, 1964).

A living organism is in continuous exchange of material with its environment. Interactions between the individual and its environment have also been discussed by the just mentioned authors. In ontogeny the external factors can influence form, size and body composition to a great extent. Climate, particularly temperature, and food supply are important factors. They also played a role in phylogenetic changes. Higher animals have to maintain a constant internal environment: 'la fixité du milieu intérieur est la condition de la vie libre, indépendante', first more extensively stressed by BERNARD (1885). This principle to maintain a steady state later on was named homeostasis by CANNON (1929).

Self-inhibition of growth in early maturity has been comprehensively discussed by NEEDHAM (1964). He reviewed the mechanisms of control of growth at different levels (cellular, tissue and organ, and at the level of the animal as an entity) in relation to various external factors, to hormones and to genetic control. According to him it seems that a particular hormonal ratio must be closely bound to a particular body size so that growth can be halted at any stage, and yet resume quite normally and go on to produce an invariable final size. Also VON BERTALANFFY (1960) concludes that in many physiological activities absolute size is the predominant factor governing the rate of processes.

The literature reviewed here will deal with the results obtained in pigs in the first place. Because the concept of differential growth seems to fit so well to all kinds of animals, much may be learned from work done in other species and therefore this will be cited as well.

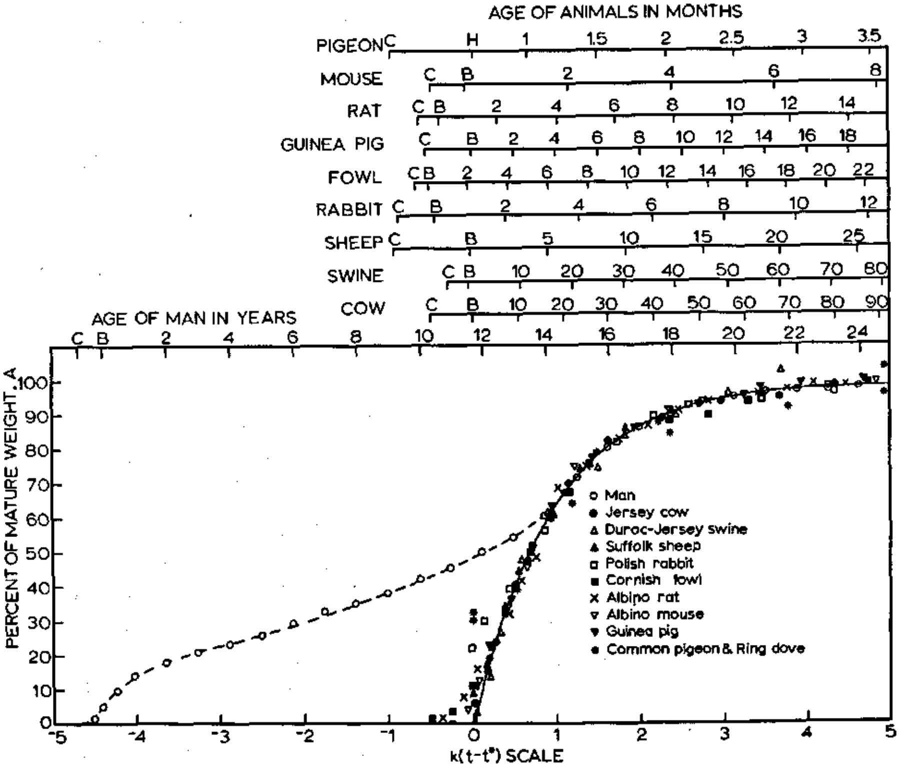

FIG. 2.2. Equivalence of weight growth curves in different species (from BRODY, 1945).

2.2. LIVE WEIGHT GROWTH

2.2.1. *General*

The literature concerning live weight growth will only be described briefly, since the primary objective was to describe relative growth. It was not within the scope of this study either to search for an equation that would fit best the live weight growth data measured.

The well-known weight-age growth curve is sigmoid from birth on in many animals. There is a close similarity between the curves of different species, if the scales for weight and age are appropriately chosen, which is shown in Fig. 2.2. The point of inflexion, which also indicates the age at puberty, is generally reached at about 30% of mature weight in higher animals. Only the human growth curve is unique with its long juvenile period and having the point of inflexion around 60% of mature weight (BRODY, 1945).

2.2.2. *Growth curves*

Absolute growth rate is the increase in size (weight, W, or length) per unit of time. For a very short interval this can be written as dW/dt, and is then called instantaneous growth rate (Brody, 1945). The specific growth rate is the increase in size per unit of time and per unit of size: $(dW/dt) \cdot {}^{1}/W$. It is proportional to the growth yet to be made in the self-accelerating phase as it was called by Brody (1945). Absolute growth is maximum in the point of inflexion. After that, in the self-inhibiting phase of growth, the specific growth rate is proportional to the growth already made.

Actual growth data may be fitted in different ways. Instead of using two different equations as developed by Brody (1945), an effort can be made to describe the whole trajectory by one equation. Many proposals are found in the literature. Two main groups of equations may be distinguished: empirical equations on the one hand and polynomials on the other. Their nature and when they may be used were discussed by Finney (1978), in particular in the case of polynomials.

The family of empirical equations, including the logistic and Gompertz equation, may be derived from a general form as was described by Richards (1959). Physiologists prefer such equations, because the parameters of the equations would have a biological interpretation. On the other hand polynomials may fit very well when the appropriate number of terms is chosen.

Except the equations that are related to the Richards function other empirical equations were developed as was discussed by Taylor (1978), e.g. those based on feed intake or intake of metabolizable energy. Beside the nutritional models, other quantitative models evolved, founded on physiological phenomena. The von Bertalanffy-model (1957, 1960) is based on the difference between the processes of building up and breaking down of material. Both anabolic and catabolic processes are expressed as a power function of weight. In this way they fit into the family of the Richards functions. One may also proceed from this basic idea and relate the other empirical equations to this as was summarized recently by Peil (1979).

The fitting of most of the empirical models generally raise some or other objection e.g. in that only a certain part of the whole trajectory is covered or in that the point of inflexion does not coincide. Except for polynomials it seems difficult to construct models that can be universally fitted to growth data of various species and various growth stages. Nutritional models are developed for a certain species in particular. A choice between empirical models is hampered by the fact that models have hardly been mutually compared (especially in the case of pigs) on actual growth data.

2.3. RELATIVE GROWTH

Organs and tissues, or parts of them, do not grow uniformly throughout their life span. They grow at different rates relative to each other and at different rates to the body as a whole. Moreover their maximum growth does not coincide, which leads to different growth curves. In all these cases this phenomenon will be considered here as relative growth. A definition of the actual concept of relative growth is given on p. 10 where allometry is defined. If required relative growth in the sense of the ratio of specific growth rates will be denominated growth ratio.

For physiological as well as mechanical reasons (BRODY, 1945; VON BERTALANFFY, 1960; NEEDHAM, 1964) the form of an animal necessarily changes in order to be able to function and to maintain homeostasis; organisms are physiologically similar rather than geometrically similar. Thus function is associated with form and structure. The changes in form can be understood because it is found that in various species surface area during growth increases proportionally with only a fractional power of the body weight, with about $W^{2/3}$ or slightly less as appearing empirically from work cited by BRODY (1945), VON BERTALANFFY (1960) and MCMAHON (1973) or theoretically with $W^{5/8}$ (MCMAHON, 1973). So larger animals have relatively smaller surfaces.

The proportionality of surface to $W^{5/8}$ was derived by MCMAHON (1973) starting from buckling and bending loads on trees and on branches of trees. He concluded that there are critical lengths to endure these forces and that length (l) then is proportional to the 2/3 power of diameter (d). This also holds for loads on animals standing and moving, which was mentioned by NEEDHAM (1964) as well. The weight of a limb is proportional to ld^2, also true for an animal as a whole, because as assumed proportions of limbs and trunk change with size in the same way. However, when l^3 is proportional to d^2, then l is proportional to $W^{1/4}$ and d is proportional to $W^{3/8}$. And since total surface is approximated by ld it is hence proportional to $W^{5/8}$. Since as appeared from work of others the inherent tensile strength of a contracting voluntary muscle fibre and the rate of shortening may be taken as constant, MCMAHON could conclude that then power output of a particular muscle is dependent only on the cross-sectional area. This area is proportional to d^2 and hence the maximal power output is proportional to $(W^{3/8})^2 = W^{0.75}$, with which the statement, especially proposed by KLEIBER (1961), that metabolic rates are proportional to the 3/4 power of body weight is theoretically supported.

The change in form also follows from the findings that the strength of the supporting structures (bones and muscles) increase with the cross-sectional area of these structures, i.e. with a fractional power lower than unity of body weight. Thus an animal should break down at a certain size; this point can be postponed by relatively larger increases of supporting tissues than of non-supporting visceral organs. Smaller animals, therefore, are more slender than larger animals.

People have long been fascinated by form. The differential patterns of growth, determined by functional requirements (NEEDHAM, 1964), are complex, and simple algebraic treatment was less feasible. To describe changes in proportions THOMPSON (1917) therefore used geometrical methods in transforming related forms by deformations of the coordinate system. Many examples are given, from the outer form of animals (mainly fishes), heads of man, the bony snouts of crocodiles and pelves and shoulder-girdles of prehistoric animals, to skulls of different animal species and man. The method was also used as appears from the enumeration to elucidate evolutionary changes.

2.3.1. *Growth of organs*

As metabolic processes are associated with surfaces smaller animals also have a higher metabolic rate. But the metabolic rate during growth also decreases since the ratio of visceral organ weight to body weight declines (BRODY, 1945; HOLLIDAY et al., 1967), and metabolic processes depend to a great extent on the metabolic activities of the principal internal organs. HOLLIDAY et al. (1967) found that the organ metabolic rate was about 80% from total basal metabolic rate, at least in humans and in the resting state. At low temperatures and under work stress the muscle tissue becomes relatively more important for heat production.

Interspecifically the internal organs are proportional to body weight with a fractional power: from 0.6 to 0.8 (BRODY, 1945), and as established on some laboratory animals and farm animals from 0.75 to 1.0 (HOLLIDAY et al., 1967). The latter also found that some of the highly active organs e.g. liver and kidneys had a lower organ metabolic rate with increasing size of the animal species. Within species, as measured also in liver and kidneys of rats, rabbits and humans there was a rather constancy in organ metabolic rate during growth.

Organs in general grow proportionally to body weight with a fractional power less than unity. Organs of the neuro-endocrine system, especially the brain including the pituitary, are in the middle of the range mentioned above. The weight of heart and blood are nearly directly proportional to body weight (BRODY, 1945; VON BERTALANFFY, 1960), but differences between and within species exist owing to the physical exertion.

On the log-log plot breaks in the slope are shown for liver, brain, lung and kidney growth relative to body weight growth in man, chicken and pigeon. Breaks also occurred in the growth of gonads; the slopes in their relative growth first rise slowly, then rapidly until the beginning of puberty. The adrenals follow the same course. BRODY (1945) also further showed that in dairy cattle the various organs grow with a power to body weight (360–725 kg) lower than hitherto mentioned, e.g. the value for heart is only 0.56. ROBELIN et al. (1974) as well in general found values varying between 0.55 and 0.90 for the organs of the thoracic and abdominal cavity in young bulls.

Relative growth of organs is determined genetically, but according to NEEDHAM (1964) there are also local controls acting between cells, tissues and organs. Within organs older parts should accelerate the growth of younger parts. The vascular system by means of vasodilatation and vasoconstriction not only regulates the supply of oxygen, but according to VON BERTALANFFY (1960) is also involved because of the competition of organs and tissues for material which also determines relative growth. Especially energy supply is important and competition exists between adjacent as well as between distant organs and tissues. Harmonious growth between parts, organs and tissues cannot only be controlled by local regulating systems; a completely efficient mechanism also needs more systemic control at the higher levels and according to NEEDHAM (1964) the endocrine system may have its own special modification of this mechanism.

Absolute growth, at the organ level fairly common by means of intussusception (NEEDHAM, 1964), is rather constant in most organs following S-shaped curves. The most deviating S-shaped curves as shown by VON BERTALANFFY (1960) from work of others on humans and rats are displayed by the reproductive organs and the thymus. The latter rapidly grows up to puberty and then shrinks. The former organs first lag behind with respect to other organs, but show a sharp rise preceding puberty. A quite different pattern is displayed by the brain which has an early rapid growth and a growth curve of the exponential decaying type.

Organs and body tissues have different growth rates and different metabolic rates, thus body composition affects the metabolic rate. The form of an animal then changes. It is noted that on the log-log plot breaks in the slopes appear in the case of growth of organs. A functional balance exists with respect to the ratio of the size of internal organs and the size of the body (VON BERTALANFFY, 1960). Because the stage of development at birth is different between species, this functional balance will be reached interspecifically only by different allometric growth intraspecifically. According to BRODY (1945) only animals which have evolved a form in harmony with physical or geometric laws on the one hand and physiological needs on the other hand have survived.

2.3.2. *Allometry*

A possibly oversimplifying, but none the less obviously useful relation in relative growth is the so-called allometric equation:

$$y = ax^b,$$

in which y mostly is the weight of a tissue or a part of a tissue or an organ related to x representing the weight of the whole or the weight of another sensible entity; a and b are constants. Allometry is sometimes called heterauxesis, but is then restricted to ontogenetic growth, being distinct from allomorphosis which is used in phylogenetic comparisons. This terminology has been proposed by HUXLEY et al. (1941). Allometry is accepted as the general covering term.

Allometry defines the specific growth rates of y and x whenever they stand in a constant ratio:

$$\left(\frac{dy}{dt}\cdot\frac{1}{y}\right) \Big/ \left(\frac{dx}{dt}\cdot\frac{1}{x}\right) = b$$

When this form is integrated then the logarithmic form of the allometric equation results:

$$ln\, y = ln\, a + b\, ln\, x$$

The constants a and b can be calculated by means of the least-squares method and have the normal meaning. So $ln\, a$ is the intercept and b is the slope of the regression line, but in this special case b is called the growth coefficient. The intercept has no particular biological meaning; it is the value of y when x equals unity. Positive allometry occurs if $b > 1$, y is then growing faster than x. Hence when the weight of x increases with $p\%$, the weight of y will increase with $bp\%$. In negative allometry ($b < 1$) the relative increase of y is smaller than that of x. If $b = 1$ the components y and x grow at the same rate, they grow isometrically.

The equation itself was already used before HUXLEY (1932) employed this form functional more systematically. HUXLEY also introduced the term growth gradient when different relative growth rates of parts of an organ or a limb exist. He found a growth gradient e.g. down the limb, meaning that the growth coefficients of the consecutive segments or parts of the limb were in an increasing order up to the distal end as found in insects and in the opposite order as found in sheep (analyzed from data of HAMMOND). According to HUXLEY (1932) a growth centre then should be located in the part with the highest growth coefficient.

The allometric equation has been widely used. Examples have already been given in the preceding sections in relating metabolic rates and weights of various organs to some power of body weight, and in fact both terms of the VON BERTALANFFY growth-model are allometric equations.

Several physiological characteristics as they were related to body weight and also the way they can be interrelated by means of the allometric equation were described by ADOLPH (1949). In a comprehensive review GOULD (1966) described the application of allometry in many different species throughout the animal kingdom. Not only the ontogenetic or growth allometry which we are most concerned with, but also the intra and interspecific allometry, and the evolutionary allometry were critically discussed, especially with regard to size.

The allometric relationship is strongly defended by VON BERTALANFFY (1960) who argues that because of the tremendous complexity of processes involved in growth, one would rather expect that parts grow in some irregular manner. Since the simple allometric relation does apply in many hundreds of cases from all animal classes, it is not trivial and it should be based upon general and fundamental principles. The allometric growth coefficient is given (1) a physiological interpretation and is called a distribution coefficient in that y is given the capacity to appropriate a certain share of the total increase (physiological competition) which is genetically governed, and (2) a functional interpretation in that the body has to function in such a way that homeostasis is maintained in spite of changes in size of the body (biological similarity).

In spite of the great extent to which use is made of and the wide applicability of the allometric equation objections against this formula exist from the mathematical and statistical as well as biological points of view. A first objection is that when the equation is applied to separate parts of e.g. organs and tissues or segments of limbs (thus leaving the relationship of the physiological phenomena with size intact) it cannot be applied to the sum of those parts, first expressed by HALDANE (HUXLEY, 1932), unless they have similar values for the exponent b. HUXLEY himself replies to this criticism (and it is also argued by LAIRD (1965)) that the dissimilarities in the b-values within certain entities will lead to a slight discrepancy only, because the specific growth rate at any age was found to be closely similar for nearly all parts of the body (LAIRD, 1965), and HUXLEY feels justified from the actual figures obtained. With regard to the organism as a whole the exponential values are much more diverse, but according to LAIRD (1965) such cases are in the distinct minority and then organs or parts with a relative small mass are involved.

As it is unlikely that the growth ratios from linear and gravimetric measurements will be constant throughout the body, they are not synchronous. It is also unlikely that the ratio for any pair of measurements is constant throughout life (PÁLSSON, 1955; NEEDHAM, 1964; LAIRD, 1965). Both statements were found to be true. And of course over defined periods and for certain parts or the whole a simple linear relation can be applied. BARTON and LAIRD (1969) showed that when exponential decay of growth ratios (i.e. multiplicative growth which was assumed by HUXLEY to obey to allometric growth) no longer dominates accretionary growth, as is the case from early maturity onwards, this linear growth becomes evident. The allometric equation therefore would not precisely describe the relation between y and x for the entire growth period and breaks or at least changes must often appear in the slope of the curve (BRODY, 1945; TAYLOR, 1978), so double logarithmic plotting in allometry does not automatically lead to a straight line.

According to VON BERTALANFFY (1960) the discontinuities usually are not accidental but connected with definable changes. Clear examples are changes as a consequence of moulting and of metamorphosis in the tadpole (GOULD, 1966); examples were also given in preceding sections. Since growth is a continuous process breaks (according to PÁLSSON, 1955) are a result of environmental changes. On the other hand the allometric equation should not be used in dividing a non-linear curve into a sequence of straight lines (GOULD, 1966). This is usually artificial because transformation of one of the variables may produce other apparently linear segments (TAYLOR, 1978), and because (according to LAIRD (1965)) there always is a smooth progression in the concerning relation, representation by two or more straight lines therefore is biologically meaningless. RICHARDS and KAVANAGH (1945) had also stated that in given cases a gradual change in slope may be a better characteristic than intersection of the curve into straight lines.

In cases where the decay of the specific growth rate of parts is not the same, a curved regression line will be found; the time scales of parts are different (LAIRD, 1965). When parts grow isometrically there is no displacement in time; in differential allometric growth there is a constant time interval between corresponding points on the shifted individual growth curves of parts passing these points at different times during growth as shown by LAIRD et al. (1968). BARTON and LAIRD (1969) elaborated this further in that they were able to estimate the displacement in relative units of time. It was then also stressed that erroneously curvilinearity particularly when present later in life may be unnoticed in the allometric log-log plot. This was emphasized by SHOLL (1954) and by TAYLOR (1978) as well, because the deviations of the straight line at later stages of growth are packed together and may obscure non-linearity, whereas in early stages there may be over-emphasis.

According to SHOLL (1954) the allometric equation is a too extensive generalization. He also stresses that this equation refers to sizes and it cannot be considered as a growth curve (also mentioned by JANSEN (1976) and TAYLOR (1978)) because absolute time is not included in the allometric equation. This is sometimes felt as a disadvantage (LAIRD, 1965). Since in allometry according to

ROSEN (1960), the growth of one part with regard to time is substituted by the growth of one part to another, a kind of 'physiological clock' is incorporated in the equation.

A last objection is that adequate statistical treatment in application of the allometric equation as a usual regression formula may give problems (SHOLL, 1954), because the components y and x can both be considered as independent variates subject to random variation (RICHARDS and KAVANAGH, 1945; GOULD, 1966; SEEBECK, 1968a; JANSEN, 1976). Therefore other approaches have also been chosen, such as e.g. allowance for error in x (HALDANE, 1950), but according to SEEBECK (1968a) based on results of REEVE (1950) too, there will be no alteration in the differences between groups as measured by the slopes if the difference in the variation about the regression lines between the groups is only small. Moreover slight differences in absolute values are of minor importance because calculating is done for comparative reasons. So a one-way analysis of covariance is also an appropriate procedure. BRODY (1945) reported that except for too short intervals of x in general the error in application of the least-squares method to the logarithms is insignificant.

Several other independent variates may be added to the allometric equation, e.g. a $(log\, x)^2$ term. This type was already used sometimes earlier (references cited by SEEBECK (1968a)) and very recently by MCFIE (1978) and ROBELIN et al. (1977) as well.

Furthermore, multivariate techniques are proposed or used by several authors. E.g. JOLICOEUR (1963) proposed the use of the first principal component of the covariance matrix of logarithms in testing whether proportions have been grown isometrically. According to MOSIMANN (1970) and shown by SEEBECK (1978) as well, this approach is too restricted. The former developed a more general concept which was further extended by SEEBECK (1978) because the concept too had its limitations, regarding the fact that (according to SEEBECK (1978)) it was particularly suited to size allometry rather than growth allometry (or at least to cross-sectional studies), and no single coefficient was summarizing the allometric relationships.

Factor analysis was advocated by GOULD (1966) and by HOPKINS (1966), but interpretational difficulties are still adherent to this method.

Given the limitations of the allometric equation – HUXLEY (1932) and REEVE and HUXLEY (1945) called it a first but useful approximation therefore – it nevertheless shows a wide use and applicability (many references were mentioned by HUXLEY (1932), VON BERTALANFFY (1960) and SEEBECK (1968a)). It is advocated, praised or defended by HUXLEY (1932), BRODY (1945), SHOLL (1954), VON BERTALANFFY (1960), ROSEN (1960), NEEDHAM (1964), LAIRD (1965), LAIRD et al. (1965), SEEBECK (1968a), ROUX (1976), SEEBECK (1978) and TAYLOR (1978) and each of them based this on one or more of the following merits of the allometric equation: usefulness in concisely describing observations very accurately in many cases, simplicity in calculation and interpretation and its independence of scale transformations.

The allometric equation may therefore be used although with caution, but still over rather extensive periods of growth. Even if growth would obey fixed rules, the allometric equation should not be glorified as an allometric law in nature, but it has to be seen as an empirical formula. As the equation has clearly proven its usefulness it should be considered as a tool to describe the results of multitudes of data from growth studies when complete anatomical dissections have been carried out, as will be shown in later sections.

2.4. GROWTH STUDIES WITH SPECIAL REFERENCE TO GROWTH IN PIGS

In a lot of growth studies in pigs hardly growth equations were used, neither for live weight growth nor for relative growth, especially in the latter type of studies. Particularly in older studies the growth of tissues and organs was compared by expressing their weights either as percentages of a certain entity or as relative percentages of a given reference weight, e.g. birth weight. Later on use was made of the allometric equation to compare carcass composition in growth rhythm experiments or to study relative growth within carcasses, within tissues and whether this could be influenced by genotype and environmental factors.

2.4.1. *Classic growth studies*

Except the exploratory work of HAMMOND the actual growth studies in pigs started with the comprehensive experiments carried out by MCMEEKAN (1940abc, 1941). The experiments were designed to study whether the constituent parts of the body are equally affected by external conditions or if these conditions, imposed during a particular period of growth, would result in differences in form and composition of the carcass.

For that purpose groups of uniform pigs belonging to an inbred strain of the Large White breed, were reared and fed on a high and low plane of nutrition from birth on up to 16 weeks of age. A number of the animals (12) were then killed and dissected. Of the remaining animals 10 continued on the high and low plane of nutrition, while the others (10 also) changed over to the other plane. All four resulting groups of pigs, viz. the high-high (HH), high-low (HL), low-high (LH) and low-low (LL) treatment groups, were killed at about 90 kg live weight. The HL and LH groups were fed in such a way, that they reached the same planned age at slaugher. The dissection not only included the different organs and main joints – head, neck, thorax, loin, pelvis, legs and shoulders – but also a further partition of the joints into the various tissues; and in addition the muscles of the leg were subdivided into the thigh muscles, the muscles round the tibia and those round the cannon, and individual bones were weighed.

The plane of nutrition had a marked differential effect on growth and development up to 16 weeks of age (MCMEEKAN, 1940b). The low-plane pigs were not miniatures of the high-plane ones and had not merely been growing slower. The low-plane animals more resembled the juvenile proportions, whereas the high-plane more approached those of the adult, because the regions of the body like head, limbs and neck were less affected than thorax and pelvis and these in turn less than the lumbar region. Moreover length measurements were less affected than depth or width measurements. The influence of the level of nutrition was highest on total fat, the influence on muscle was much less, but more than on the skeleton. The weight of the skeleton, however, was still more than doubled on the high-plane level as compared to the low plane. The effect upon the organs was in average slightly less than upon skeleton.

These differential effects are said to be closely related to the relative order of development of the parts. This order of development was established in an earlier preliminary experiment (McMEEKAN, 1940a) in which a number of boars and castrates, that were commercially fed, were killed at monthly intervals (except at 12 weeks of age) from birth on up to 28 weeks of age. The ranking of the anatomical units at 7 months of age from early to late developing was: head, fore limbs including the shoulders, hind limbs including the thighs, neck, pelvis, thorax and loin, and the ranking of the weights of the muscle tissue within these units was: head, cannon and arm region of the fore limb, cannon and leg region of the hind limb, neck, shoulder, thorax, thigh, pelvis and loin. It was shown that skeleton, muscle and fat develop differentially in that order. With respect to backfat it was noticed that the weight and the thickness of the inner layer increased more rapidly than those of the outer layer which was also reflected in the percentage of chemical fat at all ages. There is a rapid increase in fat deposition in the first 4 weeks of age after which a marked fall was shown. This rapid initial increase was ascribed to the need of temperature regulation after birth. The development of muscle tissue was clearly due to an increase of the fibre diameter; there might only be a slight increase in the number of muscle fibres. The relative development of parts and organs is given a functional basis. The well-developed parts at birth are stated essential to life processes and body functions. Those parts and organs that are more associated with growth and storage functions will therefore develop proportionally more in postnatal life.

Continuing the results referred to earlier, it appeared that a restricted supply of nutrients does inflict later developing parts more than earlier developing due to a superior competitive capacity of the latter parts (McMEEKAN, 1940b). As in the preceding paragraph, growth gradients were obtained extending from the extremities (head, limbs and tail) and terminating in the latest-developing part – the lumbar region –, and in addition an outward trend from skeleton to subcutaneous fat was shown. This order of increasing effect was found for the anatomical units as well as separately for the muscle and fatty tissue. The total weight of the bones of the fore limbs, however, just as the individual bones of both fore and hind limbs, were not affected consonant with the general picture. According to McMEEKAN (1940b) only at later stages of growth the upper limb bones will show marked differences. The late developing thickness growth of bones in comparison to the length growth, however, could already be noticed at this stage.

It was further found that the total subcutaneous fat was influenced to a greater extent than the total intermuscular fat which is reflected in the anatomical units, except in neck and thorax. This is not in agreement with the results of the age series, because there the intermuscular fat should be later developing as shown at 28 and at 16 weeks of age as well.

Neglecting some hesitation as to the limited number of animals, both sexes show the same order of development of the main tissues; muscle and bone tissue were affected most in gilts while fat was affected most in castrates by the higher level of nutrition.

After the change-over at 16 weeks of age and the ultimate slaughter at about 90 kg it still could be stated as a general result that the nutritional environment differentially affects the development of the animal body (McMEEKAN, 1940c). The HH and LH pigs were of rather similar type showing higher proportions of late-developing parts in comparison to the HL and LL groups which were also of rather similar type and having relatively higher proportions of the early-developing parts. Within these types the effects were exhibited to a greater extent by the groups which were already on the low plane of nutrition before the change-over.

The development of the main tissues was also differentially affected. In comparison to the LL group all three other groups had less bone and muscle, but more fat (again more subcutaneous than intermuscular fat); the greatest effect was demonstrated by the LH group and the smallest by the HL group. With regard to the organs corresponding results to those of the former period up to 16 weeks of age were obtained.

The view that earlier developing parts had a superior capacity to compete for nutrients under conditions of restricted food supply could now be extended. As was indicated (McMEEKAN, 1940c) the competitive capacity of the late-developing parts increased as growth proceeded, also under the continued low plane of nutrition, due to a relatively reduced growth intensity of the earlier developing parts. The ultimate effect thus is also determined by the period of life or stage of development over which the nutritional treatment is extended, not only observed under continuously restricted food supply, but also after recovery from undernutrition.

But for an occasional exception the same picture as between the main tissues could be observed as to the results within the anatomical units for each of these tissues with regard to the ranking of the treatment groups as well as the extent of the effect as related to the stage of development.

Again muscle weight increase was closely related to the muscle fibre diameter.

With regard to sex differences castrates were found to have more fat and less bone and muscle than gilts, the extent of the differences being also differentially influenced by the plane of nutrition.

If the weight of the muscle of e.g. the joints loin and legs is expressed as a percentage of total muscle weight then a percentage of about 35 results for each of the four treatment groups. McMEEKAN was not aware of this constancy. On the other hand he was convinced that the major modifications in form and anatomical composition did not occur as isolated effects but rather as orderly changes spread over correlated parts and originating in 'some deep-seated rhythm of growth', as stated in a more contemplative review at the conclusion of his study (McMEEKAN, 1941) and adopted from HAMMOND (1932a). He also stated that the mature size and form of the animal might be permanently affected by prolonged and severe undernutrition. In fact this was confirmed later on by LISTER and McCANCE (1967).

Results similar in almost all aspects to those described by McMEEKAN (1940abc) were reported by PÁLSSON and VERGÉS (1952ab) who carried out an experiment on sheep with about the similar experimental design. The only substantial difference was that bone weight was lowest in the LL group while this was highest in this group in McMEEKAN's experiment. Furthermore the percept of growth gradients was refined somewhat more.

Parts of these basic ideas from the work of McMEEKAN and PÁLSSON and VERGÉS were already formulated by HAMMOND (1932ab), extensively worked out in sheep but less in pigs. Differential growth was said to be influenced by age, breed, sex and state of fatness.

Breed and sex differences were also recorded by SCHMIDT et al. (1933) in tabulating the body composition of pigs at 30, 100 and 150 kg live weight in four different German breeds. The various joints, however, are hardly comparable (also because in most cases fat was left on them) with those of the previous work reported. Growth of belly plus shoulder, backfat layer, hind leg, back, head and flare fat increased in that order, nevertheless in reasonable accordance with the previous results in the age series. On the basis of empty body weight there was a pronounced decrease of the percentage of total organs, and also a decrease in bone and skin percentages. On the basis of carcass weight the percentages of flare fat and backfat layer largely increased, belly plus shoulder slightly increased, whereas hind leg and back decreased, and the percentage of head first decreased and then stabilized.

Dissection of individual muscles of the hind limb from sheep (HAMMOND, 1932a) showed differences in development of the individual muscles. In addition to the percept of the growth gradients it was stated that the largest muscles have the greatest post-natal development due to their function; and furthermore that long muscles ultimately tend to increase more than short muscles. HAMMOND also demonstrated that the evolution from the primitive breed to the improved breed had resulted in development of later developing parts.

The reverse of the processes described in the preceding paragraphs is evoked when animals starve or are kept under sub-maintenance levels of feeding as shown by POMEROY (1941) who started an experiment with pigs that had already been grown up to about 150 kg live weight. The tissues and the organs, as well as the different joints and of each tissue within these joints, are affected then in the reverse order of their development. E.g. bone even at first still grows before it slowly loses weight. Before that there is already a rapid loss of fat, and also although more slowly of muscle. The organs lose weight in a varying degree according to their necessity for life functions. Early maturing organs like the brain, however, continued to grow during the experimental period.

WALLACE (1948abc) studied the influence of nutritional level on the development of the pregnant ewe, and as a consequence on the growth and development of the lambs at given intervals before and after birth. The type of experimental design and the method of dissection again were about similar as used by the other representatives of the Cambridge School. WALLACE, however, was the only one of this School who doubted the view that the variations in the nutritional environment affected parts of the body differently. With regard to the presentation of the results WALLACE applied double logarithmic plots and therefore was able to compare directly the ratio in the specific growth rates of parts in successive intervals or that of parts in the same period.

Especially in the foetus differentiation and development first followed the anterior to posterior direction as described above, but changes in the order occurred as growth proceeded, particularly true in postnatal intervals for development of the organs. As long as the various joints in the age series were concerned similar results as the above mentioned were reached. WALLACE (1948c), however, found that the pattern of development within the tissues was the same – the proportion of each part to the whole depended upon the total weight increase of the corresponding tissue – for slowly and rapidly grown foetuses and therefore disagreed with the previous results. He also re-examined the data given by MCMEEKAN and postulated that the development of those tissues within the joints would not have been differentially affected if the weights of the parts had been compared to equal total tissue weight instead of to equal body weight.

A similar type of experimental design as described earlier was also used by WILSON (1954a). He showed that the results on the growth and development in chickens also were partly in agreement with those referred to earlier. Treatment effect on bone and muscle was significant at the same age, but not at the same body weight. Because of the variability of weight of fat between individuals WILSON (1954a) proposed to conduct comparisons on a fat-free carcass basis. He demonstrated that the treatment differences on percentage bone weight in MCMEEKAN's experiment were no longer present when bone weight was expressed on a fat-free carcass basis. WILSON argued that though zoologically fat is regarded as a tissue, fat deposition is not of the nature of growth of organs and other tissues. POMEROY (1955), however, sustained that fatty tissue is not merely a storage depot, but that at least part of the subcutaneous fat has an insulating function, while according to HAMMOND (1932a) part of the intermuscular fat acts as a pad between the muscles in protecting nerves and blood vessels. Later on FOWLER (1976) suggested that the fatty tissue would be built up of variable fat and target fat. The latter is laid down associated with the normal increase of lean tissue. It also would include part of the subcutaneous fat having an insulative function and it will only be changed on very low levels of feeding.

WILSON (1958ab, 1960) continued the series of the same kind of experiments on East African dwarf goats. Contrary to the earlier mentioned experiments, however, animals were slaughtered at, as closely as possible, estimated equal fatless empty body weights. The results were calculated both on a fat-free carcass and a carcass-plus-fat basis. With regard to age changes in growth of organs and tissues the results concerning the extent and order of development in most respects were in accordance with those of the other farm animals hitherto discussed. However, the results calculated on a fat-free weight basis showed only slight treatment differences. So hardly any influence of the level of nutrition on body composition was found following this procedure and thus the results were dissimilar to the earlier work reported.

Growth as described in this section is the development of the animal's body to different shapes affected by the plane of nutrition. According to the Cambridge School of workers the differential effect results in a given order of development of regions and tissues; growth gradients migrate over the body in anterior to posterior direction and in centripetal direction. In spite of the sometimes limited number of animals and the unequal distribution of the sexes, the results between different farm animals agreed reasonably well. One of the reasons of these similar results is already implied in the use of the same dissection technique. A dissection technique in itself, however, when only based on joints, may give misleading interpretations. Muscles of low and high commercial value may appear in the same joint, and late developing abdominal muscles, like in the present technique, together with the lumbar muscles led to the conclusion that the latter were also late developing (POMEROY, 1978).

The order of development remains as long as age series are involved, but studying compositional changes demands calculation of the data on a within tissue basis as proposed by WALLACE (1948c) who first doubted the differential effects of the level of nutrition on body composition. Dissection into anatomical units, or better regional units, thus should be followed by further dissection or replaced by complete anatomical dissection into the different tissues and individual muscles and bones.

2.4.2. *Results of some other growth studies*

2.4.2.1. Comparison of body composition at different live weights

In comparing breeds of pigs for efficiency of growth and gross body composition HOFMANN and RITTER (1958) and HOFMANN and BARFUSS (1962) tabulated the results from 50 to 210 kg live weight and from 20 to 200 kg respectively. The dressing percentage clearly increased as body weight increased; the increase was highest in the fattier type of breeds. The meat to fat ratio first rapidly decreased, but after about 150 kg only slightly. The same pattern was found for the percentage of bone. The percentages of ham, back and shoulder slightly decreased, whereas the percentages of backfat and flare fat gradually increased more during growth. The weights of the joints mentioned were expressed as percentages of carcass weight. According to HOFMANN and RITTER (1958) the accretion of flare fat relative to backfat became higher with increasing body weight. The increase in carcass length and backfat thickness was highest in the first part of the period at issue. Breed differences were demonstrated for all characteristics mentioned.

About similar results were attained by WENIGER et al. (1967) who studied gross body composition from 20 to 140 kg live weight. The decrease in the percentage of the various meaty joints, however, seemed to halt between 120 and 140 kg, and consequently so did the increase of backfat and flare fat. Most of the characteristics mentioned above were also studied by LOHSE et al. (1969) at 20 kg intervals from 90 to 150 kg. In addition they reported a similar pattern within the joints for the percentages of increase in fat and of decrease in muscle and bone, while the percentage of skin decreased as well. The absolute increase in weight of muscle during the period examined was relatively slightly less in the ham as compared to the other joints.

Pigs of 68, 91 and 118 kg live weight were compared by BUCK (1963). With increasing weight the dressing percentage increased (with a total of 5%), the percentages of muscle and bone decreased, and the percentage of fat plus skin increased. The weights of the tissues are expressed as percentages of carcass weight. There were only little changes in the percentages of the cuts; ham and shoulder slightly decreased, whereas back increased. Within the cuts the absolute gain in weight of muscle and fat was about equal in shoulder and ham, but in back and belly the gain of fat was higher than that of lean meat. The percentage of gain in muscle in the first interval was somewhat higher than in the second one, and conversely the gain in fat was higher in the latter interval. The favourable carcass composition of the sows over the castrates was more pronounced in the second interval and was demonstrated especially in the back.

SIDOR (1969) published results on changes of body composition of pigs slaughtered at 20, 50, 90 and 120 kg live weight. The percentage muscle on the basis of carcass weight was highest at 50 kg; however, it was not uniform in the various joints during the growth process. The proportion of fat augmented with body weight, especially at the later stages of growth. The gain of fat also varied in the various parts; it was highest in the flank from 20 to 50 kg, in the back from 50 to 90 kg and in the shoulder from 90 to 120 kg. A rapid decrease up to 50 kg was found for the percentage of bone. The percentage of skin followed a similar pattern.

A much more comprehensive study was carried out by PEDERSEN (1973). About 900 pigs were slaughtered at live weights from 80 to 150 kg, most of them in the weight range of 80 to 120 kg. Various nutritional treatments were applied: (I) normally increasing levels of energy and protein throughout the period examined, (II) as I but only up to 80 kg, after which energy and protein levels were held constant, (III) as I but only up to 80 kg, after which energy levels were held constant, (IV) as II, but with the threshold at 70 kg and (V) as III, but with the threshold at 70 kg. During the period from 80 to 120 kg the dressing percentage rose from 69.5 to 74.5. With regard to the joints it appeared that loin and belly increased most with increasing weight, whereas shoulder and ham did so the least. So those parts with the lowest meat content gained most in weight. In addition the amount of fat rose the most in these parts. Since fat increased more than muscle during the growth period at issue, the meat to fat ratio became continuously more unfavourable. The decrease in daily energy intake supplemented with higher protein intake counteracted these effects. The sexes, however, reacted differentially in this respect. In sows a steady rise in the gain of muscle in the carcass along the treatments I to V was shown, but in castrates no substantial increase after treatment III was seen any more. The meat to bone ratio became more favourable with increasing weight. The ratio in sows was about 0.2 higher than in castrates. The nutritional treatment hardly affected it, so the proportions remained constant in the fat-free carcass.

Piglets slaughtered from birth on at monthly intervals up to 3 months of age already exposed changes in body composition (OTTO et al., 1961). A marked decrease in the percentage of bone, owing to a considerable decrease in the percentage of head, was found between birth and 4 weeks of age. The percentage of muscle first increased, but between 8 and 12 weeks it already started to decrease along with the increase in fat, the percentage of which was still low (about 7%). The percentage of skin did not change much. The weight of the organs (as a percentage of live weight) decreased, whereas that of the alimentary tract increased up to 2 months of age, then decreased, except for the stomach which showed a continuous increase.

From these studies it may be concluded that with increasing weight there is an increase in dressing percentage and in the percentage of fat, and there is a decrease in the percentages of muscle, bone and skin. As a consequence the muscle to fat ratio is getting worse continuously. The muscle to bone ratio, however, increases during growth. Within the various joints (expressed as percentages of carcass weight) the same pattern is found, although e.g. the decrease in muscle is not uniform in the various joints and the increase in fat in the various joints is highest at different intervals.

The formation of fat is more pronounced in the later stages of growth. Most studies, however, did not include live weights beyond 150 kg. HOFMANN and BARFUSS (1962) noticed that after 150 kg the meat to fat ratio still diminished, but to a smaller extent than in earlier stages. An indication of this feature can also be found in the work of WENIGER et al. (1967) who found that the decrease in meaty joints seemed to be less in the interval from 120 to 140 kg than in earlier intervals.

The joints containing the lowest percentage of muscle (back and belly) increased most, contrary to shoulder and ham which increased the least. Within the joints fat increased most in back and belly. The finding of HOFMANN and RITTER (1958) that the ratio of flare fat to backfat increases is in accordance with the finding of McMEEKAN (1940a).

The unfavourable changes in gross body composition during growth can be counteracted by nutritional treatment, the more so as energy intake is restricted, supplemented with higher intake of protein (PEDERSEN, 1973). From such treatments sows benefit more than castrates. These nutritional treatments, however, hardly influence the muscle to bone ratio.

Breed and sex differences do occur with respect to the compositional changes of the body during growth. The more unfavourable carcass composition of castrates over sows is more pronounced at later stages of growth and particularly in the fattiest parts.

The changes in body composition already start in early postnatal life. Since fat formation is still low, a dramatic decrease in bone percentage causes an increase in muscle percentage in the first weeks after birth.

2.4.2.2. The influence of feeding level in early postnatal life on subsequent performance

Groups of piglets grew along different curves until they weighed about 23 kg in an experiment carried out by LUCAS et al. (1959). After that weight all pigs up to slaughter at about 93 kg live weight were kept on the same high plane of feeding. Three groups consisted of early-weaned (at 10 days of age) piglets; piglets in one of these groups were fed *ad libitum*, as were those of a fourth group that were weaned at an age of 8 weeks. The subsequent growth rate was lowest in the group with the early-weaned pigs fed *ad libitum*, after the animals had changed to the same level of feeding. The carcasses of the pigs at 93 kg from this group also contained the highest amount of fat. The pigs from the other three groups were slightly fatter when they had reached weaning weight earlier. Thus this result is not in line with the one reported by MCMEEKAN (1940c), for in his experiment the LH group showed the fattest carcasses. The pigs in MCMEEKAN'S experiment, however, were more severely restricted than those in that of LUCAS et al. (1959).

In a similar type of experiment (ELSLEY, 1963a) pigs of the same age were slaughtered at weaning (8 weeks), but of different predetermined live weights, viz. about 14, 18 and 23 kg. The sow-reared piglets and the early-weaned piglets on the highest feeding level (both groups were also of the same live weight) did not differ in body proportion as was indicated by the joints (the same joints as in MCMEEKAN'S experiments) expressed as a percentage of carcass weight. Both groups, however, differed significantly in composition in that the sow-reared piglets contained more bone, more muscle and less fat, but the muscle to bone ratio was equal. With respect to the three early-weaned groups it appeared that with increasing carcass weight the proportion of head, shoulder and ham joints decreased, whereas thorax, loin and pelvis increased. The percentages of bone and muscle decreased and the percentage of fat (subcutaneous fat more than intermuscular) rose with increasing carcass weight. The muscle to bone ratio slightly increased. All these results were in general agreement with those of MCMEEKAN (1940b), and likewise that no differential growth of parts of the skeleton could be clearly demonstrated. And besides it was noticed that the treatment differences in the tissues within the later-maturing joints were larger than in the earlier-maturing ones.

Pigs with the same history up to weaning at 8 weeks, as described in the preceding paragraph, were given equal amounts of feed up to slaughter at about 90 kg live weight (BOAZ and ELSLEY, 1962; ELSLEY, 1963b). The subsequent growth rate and the carcass quality of the sow-reared and the early-weaned pigs of 23 kg at 8 weeks were very similar, in contrast to the findings of LUCAS et al. (1959). The amount of subcutaneous fat at 90 kg went up significantly with increasing weight at 8 weeks, again in contrast to the results of MCMEEKAN (1940c).

Three experiments of the same nature were carried out by NIELSEN (1973). Somewhat contradictory results were found. Growth seemed to slow down somewhat from 20 to 90 kg when the pigs had reached a weight of 20 kg at a younger age. Both very high and very low energy rations, fed in the period from 6 to 20 kg, negatively influenced meat formation during the fattening period up to 90 kg. Instead of increasing energy levels increasing protein levels in the same type of experiments were also studied by NIELSEN (1973). As to subsequent growth and meat formation during the fattening period up to 90 kg the four experiments gave contradictory results. Up to 20 kg there was a clear positive effect of the higher protein levels on growth and on percentage meat of the carcass.

Severe undernutrition in early postnatal life was examined by DICKERSON and MCCANCE (1964) in that pigs and cockerels were undernourished from about two weeks of age for one year and 6 months respectively. Assessment of the body composition of pigs after the one year of undernourishment – when they still had a body weight of about 5 kg – revealed that hardly any fat was present (0.2%), as compared to 12.6% in normally fed piglets with the same fat-free body weight and of 3 to 5 weeks of age. The undernourished pigs further contained less muscle, but more bone and skin than the normal ones. Partial rehabilitation (assessed after 14 days of rehabilitation and at the time the animals had almost doubled their body weight) of pigs resulted in proportions of fat, muscle, bone and skin moving towards those of normal animals of about the same weight, but they did not yet reach the normal values. In cockerels the rehabilitation until doubling of body weight practically led to restoration of the body composition.

In the experiment of LISTER and MCCANCE (1967) similarly undernourished pigs were rehabilitated until growth stopped (at about two years of age). After rehabilitation the weights of the organs per unit fat-free body weight in general did not differ much from those of normally grown pigs. Since growth of the rehabilitated pigs stopped at the same chronological age as that of the normal ones, the skeleton remained smaller and thus the length measurements of the individual bones as well. In general the sows showed a better recovery than the boars or the castrates. The rehabilitated pigs (possibly except for the boars) appeared to be relatively fatter, but still were less muscular and had lighter bones than the normal controls. These results were thus in agreement with the view on the order of development (MCMEEKAN, 1940c), but when the results were expressed as percentages of fat-free carcass weight the body composition was said to be appropriate for its size.

As stated at the end of the preceding section body composition already changes in early postnatal life, sometimes even dramatically. In this section it is shown that these changes may be influenced by nutritional treatment. As weaning weight at 8 weeks increased the percentages of the joints with the higher percentage of bone or muscle (head, shoulder, ham) decreased accordingly and those with the higher percentage of fat (thorax, loin, pelvis) increased. Besides, the largest differences were found in these later-maturing joints.

The results as to subsequent growth rate after piglets had been grown along different curves up to weaning in general show, although in some cases contradictory results were found, that pigs seem to have a somewhat higher growth rate when they had reached weaning at an older age or at a lower weight. The carcasses of the pigs at 90 kg were fatter as the animals were younger or were heavier at weaning. In contrast McMEEKAN (1940c) found the fattest carcasses in the restrictedly fed group early in life. The experiments, however, are not strictly comparable, because in McMEEKAN's experiment the change-over of the diets took place at an age of 16 weeks and before that age the animals were more severely restricted in their feed intake than in the experiments mentioned above. More extreme conditions like severe undernutrition may lead indeed to alteration of proportions, even of muscle and bone on a fat-free basis. But as is also shown proportions will be largely restored after rehabilitation.

2.4.3. *Newer concepts of growth*

2.4.3.1. Re-analysis of the work of the Cambridge School and choice of the independent variate

The first reservations with respect to the interpretation of the results of the Cambridge School of workers came from WALLACE (1948c) and WILSON (1954a) as described in section 2.4.1. They already noticed that many of the nutritional treatment effects would not be present when the calculations had been carried out on a within-tissue basis or on a fat-free carcass basis respectively. In his experiment with East African dwarf goats WILSON (1960) showed that the nutritional treatments hardly had any differential effects on the muscle components.

TULLOH (1963) also re-examined the work of the Cambridge School on sheep using the allometric equation as regression equation to estimate body composition from empty live weight. The growth coefficients showed that with increasing empty live weight the percentage of fat increased, the percentage of muscle almost remained constant, whereas that of bone decreased. The deviations, however, from the regression lines were rather large, presumably due to the inclusion of the variable fatty tissue. Nevertheless TULLOH (1963) concluded that the various planes of nutrition only had small effects on carcass composition.

ELSLEY et al. (1964) re-analyzed the results of McMEEKAN (1940c) and those of PÁLSSON and VERGÉS (1952b). They standardized the data using muscle plus bone weight as the independent variate. Using the allometric equation in their regression analyses ELSLEY et al. (1964) noticed that the regressions fitted the data very well. The growth coefficients indicated that the order of development found for the tissues as well as for the joints were in agreement with those described by the workers of the Cambridge School – so when fat is excluded as well. The growth coefficients in sheep had a greater spread than in pigs, particularly for the fat components. However, from the adjusted means based on the fat-free carcass ELSLEY et al. (1964), in contrast to the results obtained by the original authors, had to conclude that the plane of nutrition did not differentially influence the tissues muscle and bone in pigs and sheep. The treatment differences for the fat components, however, were highly significant (at least in pigs), so that they could state that fat deposition is not closely related to the growth of fat-free body mass. With regard to the various joints it was demonstrated that treatment differences generally disappeared after adjustment, at least in pigs. ELSLEY et al. (1964) did not find clear evidence that after restricted feeding a relationship between relative retardation of development of the joints and their order of development existed.

FOWLER (1968) pointed at discrepancies in this respect. For example expressing bone weight as a percentage of muscle weight (using data from MCMEEKAN (1940c) and PÁLSSON and VERGÉS (1952b)) he showed that restricted feeding tended to increase the proportion of muscle relative to bone, which conflicts with the theories of the Cambridge School. He further concluded from the results of the re-analysis by ELSLEY et al. (1964) that the functionally important relationships between tissues and parts is maintained by adjusting the variable amount of fat when e.g. energy intake would be reduced. Using again data from PÁLSSON and VERGÉS (1952b), FOWLER (1968), however, also demonstrated that after adjustment based on total bone weight the nutritional treatment still affected significantly the relationship between the skeletal parts. Restricted feeding had by far the largest effect on the bones of the head. (This is another example of the discrepancy referred to earlier, because the head is adopted as an early maturing part of the body.) The head continued its growth. According to FOWLER (1968), however, this relative change might have caused the significant results in other bones, being merely a mirrored effect.

In experiments of his own FOWLER (1965, 1968) further elucidated the choice of the independent variate. Piglets of 56, 70 and 91 days of age which had been grown along three different growth curves up to 23 kg live weight were then placed on a high or low plane of feeding up to slaughter at 70 kg live weight, thus giving 6 nutritional treatment groups. From 48 kg of live weight onwards pigs were also slaughtered at 5 equal weight intervals. Total carcass weight, weight of muscle in the ham and weight of femur plus tibia-fibula were taken as independent variates in adjusting weight of components. The treatments significantly affected the muscle to fat ratio in the ham joint consistent for each of the three independent variates. If, however, a component of the fat-free carcass (i.c. the femur) was taken as the dependent variate, only a significant result was found (the fatter pigs had smaller femurs) for the independent variate total carcass weight, hence solely for the independent variate that included fat.

Like FOWLER (1968) also SEEBECK (1968a) discussed the choice of the independent variate. The latter stated that empty body weight should be the independent variate if the major components of the body are to be studied. In examining the major parts of the carcass or the distribution of parts of the musculature, carcass weight and total muscle weight should be used as the independent variates respectively.

SEEBECK (1968b) himself used multivariate analysis in testing distribution of muscle, bone, subcutaneous and intermuscular fat by measuring these tissues in each of five joints. For that purpose rams, whethers and ewes of two breeds were slaughtered from 13.5 kg live weight onwards at 4 intervals of equal weight up to 35.5 kg. Between sexes practically no significant differences were found in distribution in any of the tissues mentioned. Except for bone highly significant differences in distribution between breeds were shown. The shoulder and leg joint seemed rather constant in this respect. During growth of these lambs changes in the distribution of all tissues occurred as measured by the growth coefficients. Increase in total weight of any of the tissues was followed best by their respective tissue weight in the shoulder, particularly true for muscle weight. With respect to muscle weight distribution it appeared that with increasing total muscle weight the weight of muscle in the leg and thorax decreased, whereas it increased in neck and loin plus flank. But for one exception the same pattern was found for the other tissues.

WILSON (1968a) did not find that distribution of muscle and fat among shoulder, middle and ham joints, adjusted for weight of muscle and fat respectively, significantly differed between treatments. Here distribution was not, however, studied during growth but only at the end of the experiment. The treatments being that pigs were grown along three different curves by means of high-low (HL), medium-medium (MM) and low-high (LH) feeding patterns from about 20 to about 73 kg live weight. Muscle weight between the LH- and HL-treatment did not differ but the LH-pigs contained significantly more fat which was also reflected in various fat depth measurements being thus in agreement with the results of MCMEEKAN (1940c). After adjustment for weight of muscle plus bone it appeared that treatment effects neither on weights of muscle and fat nor on the distribution of muscle plus bone among the three joints were found. This is thus in agreement with the conclusions formulated by ELSLEY et al. (1964), except that also fat was unaffected by the nutrional treatment.

In the same experiment 6 individual muscles from the proximal pelvic limb were dissected (WILSON, 1968b). The various means were all adjusted for total muscle weight. Like total weight of muscles in the ham, the weight of the six muscles as a group was not influenced by nutritional treatment or sex. Three out of the six individual muscles, however, showed a significant nutritional treatment effect and one of them a sex effect as well. The nutritional effect could not be explained in view of an order of development, because in another experiment (WILSON, 1968b) the weights of these muscles were not affected by increasing weight at slaughter. This other experiment comprised two nutritional treatments and four slaughter weights from 32 to 73 kg live weight. With increasing slaughter weight only the percentage of *m. semimembranosus* significantly decreased, while the six muscles as a group kept pace with the total muscle weight. The nutritional treatment significantly affected the weight of the *m. biceps femoris* having a higher percentage of total muscle weight on the higher feeding level. Both muscles mentioned and the group of six as a whole showed sex effects, the castrates having the higher percentages. Thus the results of both experiments just described with respect to sex differences are contradictory. In addition it was found by WILSON (1966) that the weights of *m. biceps femoris*, *m. adductor* and that of the group of six were higher in females than in castrates. Furhter composition of the diet significantly influenced the weights of the six muscles as a group.

COLE et al. (1976) using the allometric equation regressed weights of the various tissues on total side weight as well as on muscle plus bone weight in the live weight range of pigs from 25 to 65 kg. They found, like many others, that bone was earlier maturing than muscle, and muscle earlier than fat irrespective of the independent variate chosen. The *b*-values found were in the range as calculated in pigs by others (ELSLEY et al., 1964; RICHMOND and BERG, 1971a; DAVIES, 1974a). They also concluded that *b*-values for the tissues mentioned did not differ much between cattle, sheep and pigs. The growth of the leg joint did not significantly differ from the growth of the whole carcass side. Fat, muscle and bone in the leg regressed on the corresponding tissues in the side showed *b*-values also near to unity, just like the *b*-value for the femur related to bone in the side. Only in the case of bone the *b*-value was significantly lower than unity.

2.4.3.2. Functional aspects and the choice of the independent variate

As described in the first paragraph of section 2.3. changes in form are not achieved only for mechanical reasons; physiological and functional aspects are involved as well. Looking for independent variates and in view of the results described in the preceding section FOWLER (1968) chose functional entities as base-lines, so meaning that changes in form are related to functional priorities. He exemplified this (again by using data from PÁLSSON and VERGÉS (1952b)) by taking total weight of the limb bones, and the weight of ribs plus sternum expressed as a percentage of total weight of the organs of the thorax plus anterior alimentary tract as base-lines. In the former case treatment effects for the individual limb bones disappeared in contrast with the result mentioned earlier. In the latter case the treatment effect on the weight of ribs plus sternum was also eliminated, whereas the original result was that the weight of the ribs of the LH-group related to total skeleton weight was higher than that of the other groups. Since the weights of the organs mentioned were heavier in the LH-group there was a functional need for heavier ribs.

The functional aspect was further extended by FOWLER and LIVINGSTONE (1972). They introduced a successive relationship-testing, meaning that they eliminated successively from the analysis those body components which were most sensitive to nutritional or environmental changes, thus ending up with a difficult modifiable 'hard core of interrelationships'. This was exemplified with data of an experiment in which boars, castrates and sows from 20 kg onwards, had been allocated to three nutritional treatments: high energy, high protein (H,HP), high energy, low protein (H, LP) and low energy, high protein (L,HP). Pigs were slaughtered from birth to 120 kg or to 140 kg in the case of the H,LP-group. The logarithmic form of the allometric equation was used to calculate regressions.

As a first step FOWLER and LIVINGSTONE (1972) showed that characteristics representing fatness were significantly affected by the nutritional treatments, animals on the H,LP-treatment being the fattest. In a further step in addition to subcutaneous fat (+ skin) and flare fat all other superficial soft tissues from head, trunk and limbs (including metatarsals and metacarpals) were removed, and what was left was called the basic animal. It consisted of six functional units: head, ribs plus intercostal tissue, fore limbs, hind limbs, abdominal wall and *m. longissimus dorsi*. In this order they were classified from early to late maturing according to the overall growth coefficients: about 0.70 for the head and about 1.20 for the *m. longissimus dorsi*, while all others were intermediate from 0.90 to 1.10. Of these six units only hind limb and ribs plus intercostal tissue were not influenced by the nutritional treatments when regressed on basic animal. Functional adaptation was apparent in the case of a heavier head and a lighter abdominal wall on the L,HP-treatment. The treatment effect on the other two units could only be explained in that the basic animal still contained relatively a considerable amount of inter and intramuscular fat. These sorts of fat, however, seemed to be metabolic active as tested by regression of active organs (liver, lungs plus trachea and heart) on the basic animal as well as on the fat-free basic animal. In the latter case significant treatment effects were found for each of the three organs, but they disappeared when related to the basic animal. Thus the basic animal could be accepted as a metabolic active mass. A further step was to study relationships on a within-tissue basis or even on a within selected group of muscles or bones. Examples show that treatment effects are significant when a particular muscle or bone does not belong to a functional group which is chosen as the independent variate, e.g. when the longissimus dorsi muscle is regressed on a selected group of muscles, and when bones of the head and pelvis are regressed on total limb bones.

FOWLER and LIVINGSTONE (1972) finally postulated that at each stage of life, animals have specific growth targets that must be largely fulfilled before moving on to the next stage. Birth, weaning and puberty are clear growth targets by which functional needs determine the form of the body. At maturity the close relationship between form and function diminishes. BERG and BUTTERFIELD (1976c) stated that in the early post-natal phase functional demands are the major factor in relative growth of muscles. According to FOWLER (1968) form is most critical somewhere between puberty and early maturity. The stress of reproduction – competition for the right to reproduce – is then superimposed on the animal's already existing functional demands.

According to LOHSE et al. (1971) the concept of functional units may be applicable to some anatomical regions including to their bones, but in regions with more complex functions functional grouping of muscles will be distinct from anatomical grouping. This is because the growth impetuses (for the explanation of the term see p. 32) of the individual muscles within some groups differ markedly from each other and/or from the group as a whole. Examples elucidated these statements. The groups of muscles of the proximal and distal thoracic limb and those of the distal pelvic limb all have an average-low or low growth impetus and could be considered as the unit of locomotion. The proximal muscles of the pelvic limb, however, which have a high impetus do not fit in, and this group was given the function of providing driving power added to the locomotion unit. This power should largely proceed from the larger and superficial muscles with the high-average impetuses, and the deeper situated muscles with a low or low-average impetus might form part of the locomotion unit. Although the muscles of the abdominal wall can be regarded as a functional unit, the muscles of the shoulder girdle could not. The trunk is mainly supported by the large muscles *m. serratus ventralis* and *m. pectoralis profundus* having a high impetus in the growth phase after birth. Other muscles in this anatomical region with a less clear bearing function, however, start with a lower impetus postnatally.

BERG and BUTTERFIELD (1975, 1976abc) again raised the concept of functional demand in explaining the large differences in muscle distribution found between species and demonstrated this on dissection data of the various muscle groups of cattle, pigs, sheep, horse, water buffalo, banteng, moose, deer, bison and the data of BRYDEN (1969) on elephant seals. Factors as weight of the body to be borne, mobility, agility and aggressiveness are important in determining muscle weight distribution. It was concluded that the possibilities to change the muscle distribution within a species seem to be not very promising, for the functional relationships have to be changed.

JOHNSON (1974) also tried to give a functional basis to the results reached in calves. In his study the prenatal stage from 150 days of gestation with its relatively constant maternal environment was involved. Considerable changes already occurred between two prenatal phases in growth impetuses of the various tissues. Bone and connective tissue had a high growth impetus from 150 to 210 days of gestation needed for a supportive role in this stage of development. But at birth the growth impetus is already average or low as is normally seen postnatally. The growth pattern of muscle at birth also has already its postnatal impetus, but is enhanced in the perinatal period. Differential growth between the standard muscle groups was mainly noticed in the prenatal periods. There was a greater (preparatory) development of the muscles of both fore and hind limb relative to total muscle. The muscles of the abdominal wall had a low impetus prenatally, but they change to a higher impetus after birth when a supportive role is required for the increased contents of the abdominal cavity.

A supportive function for increased contents of the abdominal cavity could also explain the findings of HEAP and LODGE (1967). During a 110 day period, pregnant and non-pregnant sows were given the same amount of feed. In addition to the higher weights of the contents of the reproductive organs pregnant sows also had a higher carcass weight, mainly accounted for by higher weights of fat, muscle and mammary gland. Of the four joints the shoulder remained practically unchanged. The increased amount of the fat was found in all three other joints. The higher muscle weight in the pregnant sows was mainly due to a higher muscle weight in the belly joint, indicating the supportive function.

The concept of functional demands leading to changes in body composition is strongly supported by dissections of elephant seals from birth to maturity as reported by BRYDEN (1969). These animals, indeed, have a growth pattern which markedly differs from terrestrial mammals. Elephant seals grow rapidly in early postnatal life with deposition of fat relatively exceeding that of the other tissues which is the reversed order of development. In a fasting period after weaning, tissues lose weight, except blood volume that relatively increases which is associated with adaptation to diving. A third period is characterized by the changeover from the terrestrial habitat to a mainly aquatic life. Dramatic changes are then found in the allometric relationships of blood, muscle and skeleton; the muscles surrounding the spinal cord become more important in swimming, so the functional demand results in a higher growth coefficient. According to BRYDEN (1969) the development of fat must be under genetic control since in terrestrial (domesticated) mammals there is no direct relationship with a functional demand and in the elephant seal it already developed in anticipation of its subsequent insulating role. Therefore domestication and selective breeding will influence the form of the body mainly by changing the distribution of fat. However, the allometric relationships of tissues will be hardly changeable by selective breeding when they are dependent on functional demands.

2.4.3.3. The first complete anatomical dissection in pigs

CUTHBERTSON and POMEROY (1962ab, 1964) carried through an almost complete anatomical dissection of the carcass into the individual bones and muscles and the major fatty parts (CUTHBERTSON and POMEROY, 1962a). This method may be used as a means to yield additional insight in distribution of the components of the different tissues during the growth process.

Ten castrated pigs were dissected at each of the live weight stages 68, 91 and 118 kg resulting in carcass weights of 50, 68 and 92 kg respectively. The percentages of bone and muscle decreased from stage to stage (with a slight increase in muscle to bone ratio) and the percentage of fat increased (CUTHBERTSON and POMEROY, 1962b). The gain of muscle and bone was more pronounced in the first period, contrary to that of fat which was higher in the second period.

The weights of the major regions of the skeleton as well as those of the individual bones were expressed as percentages of total bone weight (CUTHBERTSON and POMEROY, 1962b). Likewise groups of muscles and individual muscles were related to total muscle weight, and the fatty parts to total fat weight (CUTHBERTSON and POMEROY, 1964). The changes from stage to stage were only small and in general often statistically insignificant. Within the major groups of the skeleton and within those of total muscles the individual bones or muscles followed the general trend of their group or subgroup. There were only a few exceptions. Of the 5 major anatomical regions of the skeleton the fore and hind limb decreased from stage to stage, whereas those of thorax plus loin, sacrum and cervical vertebrae increased. Correspondingly the muscles of the thoracic and pelvic limb slightly decreased, whereas those of abdomen, thorax, back plus loin and neck and the cutaneous muscles slightly increased.

The growth of the various groups, that of the individual bones and muscles, and that of the fatty parts was calculated as the percentage increase from 50 to 68 kg and from 68 to 92 kg carcass weight. Of the anatomical regions of the skeleton the thorax and loin had a faster growth than both limb regions. The fastest growth in the second period was produced by the cervical vertebrae which had been growing intermediately in the first period. Consonant with these findings the growth of muscle groups of the limbs was slower than those of the axial skeleton. These findings in general are in reasonable agreement with those of McMEEKAN (1940a). The group of muscles of the neck, however, was the slowest growing group in McMEEKAN's experiment. The comparison with the results found by McMEEKAN bears some difficulties. Although the ages are about comparable, the weights in the present experiment, however, go beyond those in McMEEKAN's experiment. The groups of muscles in particular are less comparable, because of the commercial cuts made by McMEEKAN.

Within both limbs, apart from some exceptions, the proximal muscles and bones tended to grow faster than the more distal ones, especially in the first period. In the second period, however, the differences were smaller and in some cases the pattern reversed; particularly with respect to the hind limb bones, but also the metatarsal and metacarpal muscles were the fastest growing muscles now. It further appeared that mainly in the first period growth in length of bones predominated over growth in thickness, which was more pronounced in the fore than in the hind limb. In the second period a relatively more thickening (and ossification) process had taken place. The results in this paragraph in general are also in agreement with those of McMEEKAN (1940a).

Within the thorax and loin group of bones the ribs were growing slowest at least in the first period, while the thoracic vertebrae grew faster than the lumbar vertebrae particularly in the second period. The muscles of back and loin grew fastest in this region, while the abdominal group grew slower than the thoracic group. Such results may be calculated from the data of McMEEKAN (1940a) as well.

Within the muscles of the neck the ventral and lateral ones grew at about the same rate in the first period, but in the second period the lateral group grew faster, about as fast as the muscles of back and loin. This might not have been expected in the view of McMEEKAN's work, but on the other hand it corresponds to the faster growth of the cervical vertebrae in this period.

With respect to the individual muscles it appeared that some muscles grew faster than the muscles of the group to which they belonged. In many cases this could be explained in that errors in splitting the carcass might have influenced their weight or only small muscles were involved. Both categories therefore showed higher standard errors. To the deviating growth rate of other muscles some meaning could be given. The faster growth of the metatarsal and metacarpal muscles, and that of the lateral muscles of the neck (especially the *mm. intertransversarii*) are directly connected to faster growing parts of the skeleton. CUTHBERTSON and POMEROY (1962b, 1964) suggested that in these regions a second phase of active growth had taken place. Within the medial hip and thigh group of muscles those firmly attached to the pelvis and femur (*m. obturator* *internus, m. pectineus, m. adductor*) also grew faster than other muscles of this subgroup. The scapula was fast growing, but also the *m. subscapularis*. Slower growing muscles like *m. scalenus dorsalis* and the diaphragm are connected with the ribs. The thoracic part of the *m. longissimus dorsi* had a faster growth than the lumbar part especially in the second period. On the other hand less consonant examples may be found also, e.g. the fast growing *mm. intercostales*.

Based on the results described, CUTHBERTSON and POMEROY (1964) found some evidence of differential growth within the muscular tissue. Apart from the muscles round the cannons and lower regions, some muscles clearly exemplified a faster growth in the second period than in the first period. The main finding, however, was that the increase of most muscles in the second period was in general considerably less than in the first period. The authors therefore concluded that the differential growth as described by MCMEEKAN (1940a) in pigs and also by PÁLSSON and VERGÉS (1952a) in sheep must have taken place before the periods covered by their experiment.

With respect to the fatty parts it appeared that the percentages of subcutaneous and intermuscular fat did not change much from stage to stage. Flare fat grew fastest in accordance with MCMEEKAN's (1940a) data. The increase of subcutaneous and intermuscular fat is higher in the second period than in the first. The latter fat depot grows slowest which is in agreement with the data of PÁLSSON and VERGÉS (1952a) for sheep but not with the results found by McMEEKAN (1940a). Considering, however, the data of MCMEEKAN (1940b) the same trend may be found. Most of the subcutaneous fat was found in the middle region; the increase in this region in both periods was also higher than in the ham and shoulder region. The intermuscular fat also had the highest proportion in the middle region.

2.4.3.4. Classification of muscles and growth patterns in farm animals other than pigs

BUTTERFIELD and BERG (1966a) started to classify the growth of individual muscles relative to total muscle weight using the allometric equation. Thirty calves and 62 steers were dissected spread over the whole age range from birth to maturity and were divided into 5 age phases. When no significant differences among the phases could be found muscles had a monophasic growth pattern. In that case it was tested whether the overall growth coefficient was significantly greater than 1.0, not significantly different from 1.0 or significantly less than 1.0, resulting in muscles with what was called a high, average or low growth impetus respectively. Of the 95 muscles dissected more than 60% were ascribed a monophasic pattern.

A second category of muscles was formed by those showing a diphasic pattern. The changes in growth impetus between phases mainly occurred in the first phases. This finding is also reported by BERGSTRÖM (1978). Within the diphasic pattern muscles were classified as having a low-average, average-high and high-average growth impetus. A third category comprised muscles which were problematical to classify because of a higher variability due to their small size, to difficulties in separation at dissection or to damage at slaughter. The authors further stated that a number of muscles could be easily defined, but that others due to their higher standard error were tentatively classified. They also suggested that determination based on total muscle weight rather than on age might have been more justified. In addition the steers were rather heterogeneous with regard to genetic background and nutritional history. Although the standard error is sometimes rather high, particularly in the last phase of growth (which is also found by BERGSTRÖM (1978)), it seems that upon further consideration a number of muscles could have been grouped into other impetus classes or even that another than a mono or diphasic pattern could have been established. In fact BERGSTRÖM (1978) found that for a relatively large number of muscles the classification was different from that of BUTTERFIELD and BERG (1966a). The results with regard to the distribution of individual muscles from the work of BERGSTRÖM (1978) were similar to those from the experiments on bulls carried out by ANDERSEN (1975) when corresponding trajectories are compared. BERGSTRÖM (1978) also found less evidence for a diphasic growth pattern and stated that the growth coefficients rather tended to change continuously. The animals, however, in his experiment differed from those of BUTTERFIELD and BERG (1966a) according to e.g. sex. BRÄNNÄNG (1971) and BERGSTRÖM (1978) showed some differences in muscle distribution between bulls and steers. BUTTERFIELD and BERG (1966a) also noticed that unpublished results of BUTTERFIELD had given the impression that in bulls, particularly in the later phases of growth because of the onset of sexual maturity, the growth patterns might differ from those of steers. This was confirmed later on (BERG and MUKHOTY, 1970).

The individual muscles were brought together in standard muscle groups (BUTTERFIELD and BERG, 1966b), primarily based on anatomical regions, but were also given a more or less commercial basis. Analogous to what is described for the individual muscles the groups were classified accordingly. In Table 2.1 the various groups are listed together with their classification into growth impetus groups and the overall growth coefficient. Besides they are compared with the IVO-method of anatomical dissection as measured on results derived from BERGSTRÖM (1978). The IVO-method was developed by BERGSTRÖM. He modified the classification originally worked out by WALKER (1961). This modified method has also been applied to the pigs in the present study. A more detailed comparison of the method of BUTTERFIELD and BERG (1966ab) and the IVO-method was described by BERGSTRÖM (1974a) including all individual muscles. From Table 2.1 it can be seen that the growth coefficients for the various groups between the methods are very similar, although the groups are not quite comparable. The proximal and distal muscle groups both of fore and hind limb coincide with each other. Furthermore, according to BERGSTRÖM (1974a), about similar groups may be made when the IVO-groups F + G, I and E + H + J are compared with the 3, 7 + 8 and 4 + 9 of those of BUTTERFIELD and BERG (1966b) respectively.

The growth impetus of the various groups is the result of the growth impetuses of the constituent muscles. This, however, also means that a muscle group can

TABLE 2.1. Classification of the standard muscle groups with their growth impetus; comparison of the growth coefficients (measured as overall-coefficient *b*) of two methods of anatomical dissection in cattle (from BERGSTRÖM, 1978).

BUTTERFIELD and BERG (1966b)			BERGSTRÖM (1978)		
Standard muscle group	Growth impetus	*b* steers	Standard muscle group	*b* males	*b* females
1. Proximal pelvic limb	High-average or low	0.99	A. Proximal pelvic limb	0.98	0.99
2. Distal pelvic limb	Low	0.86	B. Distal pelvic limb	0.83	0.82
3. Surrounding spinal column	Average	1.01	F. Back and loin	1.03	1.05
			G. Sublumbar muscles	1.01	1.03
4. Abdominal wall	High-average or high	1.10	H. Thorax and abdomen	1.11	
5. Proximal thoracic limb	Low-average	0.99	C. Proximal thoracic limb	0.97	0.95
6. Distal thoracic limb	Low-average or low	0.84	D. Distal thoracic limb	0.82	0.82
7. Thorax to thoracic limb	High	1.03	I. Shoulder girdle	1.04	1.04
8. Neck to thoracic limb	Average-high	1.07			
9. Neck to thorax	Low-average	1.01	E. Neck	1.03	0.98
			J. Skin muscles	1.21	1.34

have an average growth impetus while parts of it may have a low and parts a high impetus. In fact such a group was found, viz. the group of muscles surrounding the spinal column. The proximal muscles of the pelvic limb were also difficult to classify, witness the fact that they were described as having a high-average or low growth impetus. With some exceptions there was less variability within the other groups. The distal muscles of both the fore and hind limb gave the least variability.

From the growth impetus given it further appeared that in many cases the larger and superficial muscles had a higher impetus, whereas the smaller and deeper situated ones in addition to the muscles of the distal limb showed a lower impetus. These results look like those of HAMMOND (1932a) when he stated (see also p. 17) that longer muscles tend to increase more than short ones and that the largest muscles have the greatest post-natal development. Likewise the low growth impetus of the distal muscles of the limb is in agreement with the conclusions of the Cambridge School in that these parts are early developing. As a general conclusion BERG and BUTTERFIELD (1976c) formulated that the muscles with a low or low-average impetus are mostly closely related to the skeleton and would have a vital survival function. The more superficial muscles on the other hand have only a minimal contact with the skeleton. These fastest growing muscles which have a high, high-average or average-high growth pattern are involved in productive work rather than in survival of the animal.

Groups of calves were imposed to a low-high or a high-high plane of nutrition up to 22 weeks of age (BUTTERFIELD and BERG, 1966c) to study the relative growth of muscles having a high-average growth impetus. Before the total muscle weight of the calves was doubled the change-over from high to average impetus was completed. The completion was postponed by restricted nutrition. The treatment affected the muscles differentially when they were related to age. Such results in fact then confirm the statements of the workers of the Cambridge School. However, when related to total muscle weight restricted nutrition uniformly retarded the growth of these muscles. From data of the same animals it was further shown (BUTTERFIELD and JOHNSON, 1968) that muscles which have a low growth impetus were also differentially affected in early post-natal life, at least on an age basis, in that these muscles were less retarded by restricted nutrition. But again these muscles are uniformly retarded when considered on the basis of total muscle weight. The relative growth rate of muscles having an average growth impetus was not influenced by restricted nutrition neither on an age nor on a weight basis. Even when larger differences in growth rates of groups of calves were introduced and all muscles of the carcass (brought together in the six impetus groups) were included (BUTTERFIELD and JOHNSON, 1971) the conclusions remained unchanged. Solely the low-average impetus group had a significantly lower b-value on the high plane of feeding, but this group only comprises about 9% of total muscle weight and contains muscles from different regions of the body. BERGSTRÖM (1978), however, demonstrated that retardation in the young stage influenced the muscle distribution also on the basis of total muscle weight. He worked with identical twin pairs in comparing extreme restriction (maintenance level) with well-fed animals. The high plane animals showed a higher proportion of the expensive muscles, especially those of the proximal pelvic limb. After rehabilitation the animals hardly differed any more in muscle weight distribution.

BUTTERFIELD and BERG (1966c) also noticed after re-analysis of data of other work of the former, that in adult cattle the percentage of total muscle weight particularly of muscles which have a relatively high growth impetus in early life, was lower after severe restriction (which resulted in loss of body weight) than after normal feeding. This was elucidated by BERG and BUTTERFIELD (1976c). They concluded that after severe restriction, particularly when weight loss is involved, the muscles are differentially affected in such a way that muscle groups having a low impetus are most protected from weight loss and those with a high impetus the least. This was explained as the need for the animal to protect those which are most vital for survival; thus the animal tends to return to its new-born muscle weight distribution. So the distal muscles of the limbs, well-developed at birth, will relatively gain in importance, and for example the abdominal muscles will relatively decrease, as will those of the proximal pelvic limb, also found by BERGSTRÖM (1978) in the identical twins. The normal proportions will be restored after rehabilitation.

Analogous to BUTTERFIELD and BERG (1966ab) 96 muscles from sheep carcasses were dissected and classified similarly (LOHSE et al., 1971). Ewes, whethers and rams were slaughtered from birth on at various intervals up to one year, and only whethers up to 517 days of age. The test for a mono or diphasic pattern was carried out at two points, viz. when the minimum value recorded for total muscle weight was doubled or quadrupled. Nearly 60% of the muscles dissected had a monophasic pattern. It could be stated that there was a general agreement with the results obtained in cattle. Some distinct differences, however, were also shown. The group of proximal muscles of the pelvic limb and the one surrounding the spinal column grew relatively slower in cattle, while the muscles of both neck and thorax to thoracic limb were found to be relatively slower growing in sheep. Not only the growth impetus but also the growth pattern in all four groups just mentioned differed from that in cattle. The proximal muscles of the pelvic limb had a monophasic pattern with a high growth impetus. During growth this group thus continuously increases relative to total muscle which is not in agreement with the results of others.

LOHSE et al. (1971) also found that some muscles and one muscle group had a triphasic pattern and they stated therefore that multiphasic patterns may be needed as well to describe growth when the growth phases cover the whole of life.

2.4.3.5. Factors influencing muscle, bone and fat weight distribution in farm animals other than pigs

Within species the muscle weight distribution seems to be only influenced by the stage of development which may be sex-linked. The influence of breed and the rate of growth appeared to be remarkably small, taking into account comparisons at similar stages of development and at similar total muscle weight respectively (BERG and BUTTERFIELD, 1975, 1976ac). These authors also discussed the factors influencing the growth patterns of the tissues. This pattern is weight dependent, while age is only of minor importance. Breed differences exist with respect to the pattern of growth (earliness of fattening and ultimate proportions) and deposition of fat. The growth of muscle relative to bone is under genetic influence as well. Sex also influences the pattern of growth of fat, but at given muscle plus bone weights the ratio between growth of muscle and bone does not differ. Nutrition plays an important role on carcass composition. Especially the level of energy intake may markedly influence the fat growth in that the surplus of digestible energy over the requirements for maintenance and growth of muscle and bone is deposited as fat. BERG and BUTTERFIELD (1975) stated that with increasing pressure by a higher energy intake during fattening the depots with more resistance (intra-muscular areas) will also increase deposition of fat. FOWLER and ROSS (1974) comparing extreme feeding levels in pigs, also found that intramuscular fat was the most stable fat depot.

BERGSTRÖM (1974b, 1978) worked with entire male and female cattle of the Dutch Friesian breed which were slaughtered from one week of age with intervals up to 500 and 390 kg respectively. The studies also comprised Dutch Red and White and crossings with Charolais and Limousin. Gross carcass composition, particularly fat deposition is clearly influenced by sex. Only small differences between sexes were noticed for muscle and bone distribution when compared on the basis of total muscle or bone weight respectively. Some specific sex differences, however, occurred with regard to the muscle groups of the neck and shoulder girdle region being heavier in bulls. The muscles of the proximal pelvic limb were heavier in cows, at least in earlier stages. In the latest stages of growth also the muscles of the thorax and abdominal wall were heavier in cows. When compared on the basis of the same physiological age the differences between the sexes were more pronounced.

BERGSTRÖM (1974b) further found that the muscle to bone ratio appeared to be a function of weight rather than of age, and the distribution of fat was found to be a function of total fatness which is also the conclusion of BERG and BUTTERFIELD (1976c).

Bringing together their results obtained in the course of years BERG and BUTTERFIELD, 1976c) and their co-workers in some cases changed the growth impetuses originally given to the various muscle groups (cf. Table 2.1 on p. 34), especially because they also included bulls and heifers in the comparisons. The major changes being that the low-average impetus for the muscle group neck to thorax was only valid for steers and heifers, but bulls end up with a high impetus; and the group of muscles surrounding the spinal column changed into a high-average impetus. Of the original high-average or high impetus for the abdominal muscles high-average is now reserved for bulls and steers and high for heifers. Furthermore, the proximal and distal muscles of the hind limb were modified into high-low and low-average respectively.

BERGSTRÖM (1978) stated that differences in muscle weight distribution, if present, are hardly of commercial importance. He also indicated that the growth pattern of muscles in entire males and females was more similar than that between bulls and steers. With increasing total muscle weight the weight of the groups of muscles from the neck region, shoulder girdle region, and thorax and abdomen increased, whereas those from the pelvic limb decreased. Steers, however, may react differently. BERG and BUTTERFIELD (1976c), however, supposed a greater similarity between steers and heifers. BERGSTRÖM (1978) further noticed that, although based on limited information, the degree of fatness would not influence muscle distribution to a great extent either. Apart from factors which may have an influence on muscle weight distribution BERGSTRÖM (1978) stressed that an individual variation was always found. Clear evidence was illustrated by the identical twin pairs in that the between-pair variation in muscle weight distribution was much larger than the within-pair variation.

After 1970 many studies in cattle on anatomical dissections and relative growth have been published, particularly in the last few years. Since in many of these studies the main results are in general agreement with the results in cattle hitherto described, they will not be referred to in much detail.

Deviations from the pattern, however, may occur when e.g. certain parts of growth trajectories have been studied. Thus ROBELIN et al. (1974, 1977) and ROBELIN and GEAY (1976), considering relative growth of young bulls from 8 to 19 months of age, found growth coefficients for muscle groups that differed from those given in Table 2.1 (p. 34). Not only differences in constant terms, but also a reverse pattern was found in some cases. Since the earlier periods have been excluded, the neck and pectoral region is clearly more pronounced and the weight of the hind limb muscles has relatively decreased. ROBELIN et al. (1977) claim breed differences in muscle weight distribution when Limousin is compared to the more dairy breeds; the former having heavier muscles in the loin and hind limb region. The same was shown by KEMPSTER et al. (1976b) in that out of 17 breed-types only the more extreme ones exibited a difference. BERG et al. (1978b) comparing young bulls from eight sire breeds as well found significant differences in the distribution of muscle over the various joints at the same total muscle weight. Again the largest difference was revealed in the most extreme sire breeds in this experiment, Hereford and Chianina. The growth pattern over the (limited) range of the experiment as expressed by the growth coefficients was similar among breeds of sire. Growth gradients ran in centripetal direction over the limbs and on the trunk in dorsoventral direction, but also in posterior-anterior direction (most pronounced dorsally), explained as the growth impetus shifting to the fore quarter especially in bulls as referred to earlier (BERG and BUTTERFIELD, 1976c; BERGSTRÖM, 1978). TRUSCOTT et al. (1976) also found significant differences in 4 out of the 9 standard muscle groups, resulting in a higher proportion of expensive muscle groups in Friesian as compared to Angus steers in the range of ca. 350 to 520 kg live weight. Another example of a deviating muscle distribution is found in double muscled animals (ANSAY, 1976).

In addition to the influence of feeding level studied by BUTTERFIELD and BERG (1966c) and BUTTERFIELD and JOHNSON (1968, 1971), as described on p. 35, only ANDERSEN (1975) examined this aspect. He carried out an experiment that comprised bulls from 180 to 540 kg live weight fattened on four feeding levels. In contrast to the former workers, however, ANDERSEN (1975) did find that feeding level differentially influenced muscle weight distribution. Some muscles from the shoulder, thorax and abdominal wall and also the *m. longissimus dorsi* showed a higher proportion at the *ad libitum* feeding level, whereas some muscles from the neck had a higher percentage of total muscle weight at a restricted level (70% of *ad libitum*). Although the differences were significant, they were all small and remained within 1% of total muscle weight.

With respect to bone weight distribution in cattle, breed may influence it (TRUSCOTT et al., 1976; KEMPSTER et al., 1977; BERG et al., 1978d and JONES et al., 1978). According to JONES et al. (1978) sex also influenced the bone weight distribution. The small but significant differences between the breed-types were considered as commercially unimportant. The differences were attributed to differences in stage of maturity. According to KEMPSTER et al. (1977) the tibia-fibula and the radius-ulna grew significantly slower, whereas the lumbar vertebrae grew significantly faster than total bone weight. The other bones could not be compared very well, because joints had been dissected. This was also the case in the experiment of BERG et al. (1978d), but they nevertheless indicated growth gradients for the bones in the various joints running centripetally from the limbs and in the posterior-anterior direction with the highest *b*-value in the lumbar region. The growth pattern did not differ among the breeds of sire. JONES et al. (1978) found *b*-values significantly lower than unity for all limb bones and for the cervical vertebrae. The ribs, scapula and pelvis + sacral vertebrae grew faster than total bone, while the thoracic and lumbar vertebrae and sternum did not differ from total bone growth. With some exceptions (e.g. atlas and femur) anterior-posterior and centripetal growth gradients were found as well. There was no influence of either breed-type or sex on the growth pattern.

Various breeds of a weight range from 4 to 650 kg empty body weight were involved in an experiment carried out by ROBELIN (1978). The prenatal pattern of growth, was mostly the inverse of that after birth. ROBELIN (1978) did attach economical importance to the breed differences in bone weight distribution.

BERG et al. (1978d) tried to associate the growth coefficients of bone and muscle in the same joints. However, they had to conclude that, except for the limb joints, rather dissimilar patterns of growth of the tissues occurred. This is in contrast to the examples (with anatomical dissections) in pigs given by CUTHBERTSON and POMEROY (1964).

The partition of fat between fat depots changed during growth (JOHNSON et al., 1972). With increasing carcass weight intermuscular and subcutaneous fat increased relative to total fat, whereas intramuscular, kidney and channel fat decreased. It was further found (JOHNSON et al., 1973) that intramuscular fat content differed between the individual muscles and the standard muscle groups. It was highest in the muscles of neck and thorax, and in those of the abdominal wall. The distal muscle groups of both fore and hind limb contained the lowest amount. With increasing total dissectable fat, however, the distribution of intramuscular fat between the different muscle groups was not affected (except for both distal limb groups, but they together only contain about 4% of total intramuscular fat). The muscle weight distribution between the various muscle groups did not change when instead of total dissected muscle weight as the independent variate the intramuscular fat was subtracted from it.

The distribution of fat between the various depots was found to be influenced by breed (CHARLES and JOHNSON, 1976). Differences in weight of both intermuscular and subcutaneous fat in each of the joints tested, adjusted to equal total weight of these depots respectively, were significantly different between breedtypes (KEMPSTER et al., 1976a), but the differences were thought to be relatively unimportant. The latter further found a growth gradient for subcutaneous fat running from the proximal limb anteriorly along the dorsal joints. BERG et al. (1978c) in their experiment also found minor, but significant differences between breeds of sire in distribution of fat over the various joints. These differences, however, could be related to the maturity type of the sire breed groups. They further noticed similar growth coefficients among the breeds of sire. Growth gradients were indicated centripetally on the limbs, and further increasing from the neck to loin and rib area with the highest b-value in the flank, in contrast to the results found by KEMPSTER et al. (1976a). Friesian and Angus steers (TRUSCOTT et al., 1976) did not show differences in fat distribution between intermuscular and subcutaneous fat. If, however, kidney and channel fat were included breed did influence the fat distribution. Some sex differences in fat distribution were shown by BERG and BUTTERFIELD (1976c).

In sheep the distribution of muscle weight as influenced by nutritional treatment was examined by MURRAY and SLEZACEK (1975). Three groups of crossbred wethers were fed up to 40 kg live weight along three different growth curves. One group was fed *ad libitum* and another was kept on a low scale. A third group was fed *ad libitum* up to 25 kg and then held at maintenance level during 50 days, after which the *ad libitum* level was restored. The group of muscles of the proximal pelvic limb and that of muscles connecting the thorax to the thoracic limb grew fastest on the low level treatment. Further significant differences were found in proportions of the group of distal muscles of the thoracic limb and that of the intrinsic muscles of neck and thorax, being greater on the low treatment than on the *ad libitum* treatment. The latter group of muscles was also higher in the rehabilitated animals than in those fed *ad libitum*. The effects were attributed to a greater skeletal size in the older animals. Finally the group of abdominal muscles had a higher proportion in the *ad libitum* fed animals and in the rehabilitated animals, explained as a result of a supposed higher content of intramuscular fat in these muscles under these treatments.

The pattern of bone growth in sheep (PRUD'HON et al., 1978) rendered about the same picture as in cattle. A sex difference for the b-value of atlas, axis and skull was found. Since these bones had a high value in the males accompanied with a high value for the remainder of the cervical vertebrae it disturbed the anterior-posterior growth gradient in the males. Clear centripetal gradients were noticed in the limb bones in various breed or breed crosses. There was, however, a genotypic influence in that the development of the hindlimb bones relative to the forelimb bones was earlier in Berruchon du Cher, but in Merinos d'Arles there was no difference in development. This was said to coincide with the muscular development in these regions in comparing both breeds.

Changes in growth patterns were also obtained in rabbits by a French group of workers. The growth gradients found, as expressed by the growth coefficients of the various muscle groups (VEZINHET et al., 1972), were similar to those already described. There were only small differences between the sexes. The growth gradients were particularly consistent in the skeleton (DULOR et al., 1976), where in addition a gradient was found from the carpus and tarsus directed to the digits, which was also described by PÁLSSON and VERGÉS 1952a). With respect to the individual muscles (CANTIER et al., 1974) no clear gradient pattern could be found, which was in agreement with the results obtained in the large farm animals. The growth pattern of some of the individual muscles and bones was described by a straight line throughout the period at issue (a monophasic pattern); other muscles and bones grew along a diphasic pattern, while also the growth of some was better described by a curvilinear pattern.

Curvilinear patterns were also noticed by TRUSCOTT et al. (1976) and by ROBELIN et al. (1974, 1977). The former workers did not use the allometric equation in this respect; the latter, however, added a quadratic term to the allometric formula and explicitly tested for a linear or curvilinear pattern. With respect to the possible ways of describing growth patterns of tissues some information can be drawn from a study by BERG et al. (1978a) intended to compare growth patterns of young bulls from various sire breeds. They stated that use of the allometric equation (in its logarithmic form) was superior to the normal linear regression in describing the relationship between the weights of the tissues and the carcass weight or live weight.

2.4.3.6. Complete anatomical dissection and growth patterns in pigs

Like in cattle (BUTTERFIELD and BERG, 1966ab) and in sheep (LOHSE et al., 1971) complete anatomical dissections were also carried out in pigs and reported by CUTHBERTSON and POMEROY (1962ab, 1964) and by DAVIES (1974ab, 1975).

In the work of DAVIES two extreme breeds were involved, viz. Pietrain and Large White. From each breed 18 females were slaughtered equally distributed over the live weights 2, 4, 8, 16, 32 and 64 kg. The allometric equation was used to describe the relative growth of the various tissues and their parts. With respect to gross carcass composition (DAVIES, 1974a) the familiar pattern was found in that fat and muscle grew faster and bone slower than the carcass. In the case of fat in Large White, however, this was not significantly so. The carcass itself grew at a similar rate as empty body weight. The growth coefficients of the tissues were significantly different from each other, except the difference found between muscle and fat in the Large White. Breed differences were only significant for the growth of bone, being faster in Large White.

At the same empty body weight the weight of muscle and the muscle to bone ratio were higher in Pietrain than in Large White. When regressed on total muscle plus bone weight the difference in muscle weight between the breeds disappeared, even when data of the Large Whites from McMEEKAN's experiments (1940bc) was included in the calculations. Bone weight, however, was significantly different between Pietrain and the modern Large White. Comparing the extremities of the trajectory the muscle to bone ratio significantly increased with increasing muscle plus bone weight. At both ends the Large White groups did not significantly differ from each other, but Pietrain showed a higher muscle to bone ratio than these groups. DAVIES (1974a) also demonstrated that the muscle to bone ratio was rather similar when species were confronted at comparable stages of development. He concluded that genotype influences the proportion of muscle and bone, not only between species but also within species. The difference found between Pietrain and Large White was attributed to Pietrain being more mature at the same empty body weight.

A number of 62 individual muscles were grouped into 10 major muscle groups (DAVIES, 1974b). Since the grouping of the muscles was based on the articulations over which they act, differences with the classification of BUTTERFIELD and BERG (1966b) occur. An important difference is that the *m. iliopsoas* is regarded as a muscle of the hip and not as one of the back or sublumbar region.

The growth coefficients found were highest for the muscles of the lumbar, abdominal and femoral region. Somewhat lower values were calculated for the muscles of the distal hind limb, the pectoral, brachial and neck region, while the muscles from the head and distal fore limb had the lowest values. In this material clear growth gradients were established proceeding from anterior to posterior and from distal to proximal direction, and this was more pronounced in the Pietrain. Significant breed differences were only found for 11 muscles, among which the *m. iliopsoas* which has a higher growth impetus in Pietrain. Of the groups of muscles, the femoral muscles and the total *m. longissimus* (thoracic and lumbar part) had significantly higher growth coefficients in Pietrain, whereas those of the brachial region, i.e. the proximal muscles, were significantly higher in Large White.

The breed differences of the muscle groups were also given as their ratio. At birth the ratio for all 10 major groups was significantly in favour of Pietrain, but the higher total muscle weight of Pietrain could not be attributed to relatively high weights of muscles in particular regions. At 60 kg empty body weight, however, the higher total muscle weight in Pietrain appeared not to be the result of a higher overall muscle weight, but had to be ascribed to the heavier high growth impetus muscles.

COLE et al. (1976) only dissected six individual muscles, all of them from the hind limb. Comparing the growth coefficients found (as related to total muscle weight) with those reported by BUTTERFIELD and BERG (1966a), LOHSE et al. (1971) and DAVIES (1974b) a reasonable agreement appeared to exist. Only the low impetus given to the *m. adductor* seemed to be not in accordance with the other data, but also the average impetus of the *m. semimembranosus* tended to be somewhat low compared to the pig data of DAVIES (1974b).

A study of DUMONT et al. (1973) concerns the composition of the leg at the live weights 80, 100, 120 and 140 kg of Large White boars. The percentage of muscle remained constant up to 120 kg, but thereafter it decreased, whereas the percentage of fat continuously increased. The percentages of bone and skin decreased from 80 to 100 kg, but remained fairly constant thereafter. Most individual muscles as percentages of the total muscle weight of the leg revealed only very slight changes. A few tended to increase, like the *m. semitendinosus* and the *m. semimembranosus*, whereas the *m. vastus lateralis* and the distal muscles tended to decrease. This seems to be in agreement with the growth coefficients given by DAVIES (1974b).

The growth gradients found by DAVIES (1974b) were more pronounced than those reported by BUTTERFIELD and BERG (1966b) in cattle and by LOHSE et al. (1971) in sheep. In addition only a monophasic pattern was found, but this may be due to the limited range studied. It was concluded that the changes in muscle weight distribution of these pigs might be solely dependent on the functional demands when the body increased in size, i.e. the preferential development of the high impetus muscles are located in such a way that they meet best the propulsive effort in the growing animal. Besides a clear breed influence on muscle weight distribution was stressed. The more pronounced gradient of muscle growth in Pietrain compared to Large White was said to be sufficient in effectuating the greater muscle development in Pietrain.

The same animals were used to study the changes in bone distribution (DAVIES, 1975). Growth coefficients for individual bones or groups of bones did not differ between the breeds. Like in muscles an increasing anterior to posterior and distoproximal growth gradient was found in the bones as well, with the exception of the humerus and radius-ulna having a reversed order in the Large White, but this difference was not significant. At birth only the weight of the carpus plus metacarpus was significantly heavier in Large White, but at 60 kg empty body weight the weights of all bones were. No topographical pattern could be discovered. This means, given the preferential development of the high impetus muscles in the Pietrain (DAVIES, 1974b) that the difference between Pietrain and Large White in the ratio of muscle to bone was greatest at 60 kg in the femoral region. This was also found by DUMONT et al. (1969). The ratio of the weight of the brachial muscles to that of the humerus was also significantly different in favour of the Pietrain.

RICHMOND and BERG (1971abc, 1972) studied the growth of the various tissues and their distributions as influenced by live weight, breed, sex and ration. Up to 109 castrates and gilts of different Yorkshire-crosses, fed a high or low energy diet, were slaughtered at 23, 68, 91 and 114 kg live weight.

Gross carcass composition (RICHMOND and BERG, 1971a) at the different weights showed the well-known pattern of slow bone growth and faster growth of muscle. After 91 kg the fat tissue started to grow faster than muscle. The dressing percentage increased with increasing weight at slaughter. Breed of sire, sex and ration did not significantly influence the percentage of bone or the muscle to bone ratio. The proportion of bone, muscle and fat was not significantly affected by breed, but breed did influence the growth of the different tissues when expressed as growth per day of age. Sex and ration had a significant influence on the proportions of muscle and fat in the carcass. The carcasses from gilts or pigs, which were fed the lower energy ration contained more muscle and less fat, and had the same composition at 114 kg live weight as the carcasses from castrates or pigs fed the higher energy ration at 91 kg. Genotype-environment interactions were found to exist.

With respect to muscle weight distribution (RICHMOND and BERG, 1971b) there appeared to be slight changes between 23 and 68 kg live weight, but percentages of muscle groups (according to BUTTERFIELD'S classification) relative to total muscle weight did not change significantly thereafter, except that the percentage of the muscles from neck plus thorax was higher at 91 kg live weight. In this study as well as in the following ones of this series the 23 kg-group was excluded from statistical evaluation. Breed of sire only significantly influenced the group of muscles surrounding the spinal column in that Duroc × Yorkshire pigs had a higher percentage of this group than purebred Yorkshire. Sex did influence more muscle groups. Castrates not only had a higher percentage of the group just mentioned, but the whole of the expensive groups of muscles (a combination of the muscles of the proximal and distal pelvic limb and those surrounding the spinal column) was higher in castrates. The relatively less important group of muscles of the distal thoracic limb revealed a higher percentage in gilts. The group of muscles of the distal pelvic limb was the only group of muscles influenced by ration, being higher at the higher energy level, which is in general agreement with the calculations made by ELSLEY et al. (1964). In one of the groups significant interactions were found.

The distribution of the muscle groups was tested separately at the stage of 23 kg live weight. It then appeared that the percentage of muscles surrounding the spinal column and that of the proximal pelvic limb muscles was higher for gilts, whereas that of the muscles of neck and thorax was higher in castrates. Besides at 23 kg the percentage of muscles from the expensive groups was significantly in favour of the gilts. It was stated that already at 23 kg gilts had almost reached the proportions found at later stages, where castrates were still less mature. In general the muscle differentiation was completed at the stage of 23 kg live weight.

The results were compared with those of the age series of MCMEEKAN (1940a) and were found to be in accord with them. In view of this and also when comparing the results with those of cattle, it was concluded that diphasic growth patterns in pigs may be less pronounced than in cattle. Since muscle weight distribution was hardly influenced by sex and breed groups, selection in pigs would be only successful with regard to gross carcass composition and should not be directed towards muscle distribution.

The very small breed differences found by RICHMOND and BERG (1971b) were in contrast to the results as assessed by DAVIES (1974b), but the latter compared the more extreme breeds Pietrain and Large White. Five subjects of each of these breeds were also compared by DUMONT et al. (1969), at one stage of development, however, viz. at a half-carcass weight of 35 kg. The higher total percentage of muscle in Pietrain was not evenly distributed. The percentage of muscles grouped as neck, shoulder and fore limb was higher in Large White, while the percentage of muscles grouped as lumbar and hind limb was higher in Pietrain. So these results are in perfect agreement with those of Davies (1974b). The main individual muscles followed this pattern, but the breed difference in other individual muscles may be less bound to topographical regions.

Bone growth and distribution was also studied by RICHMOND and BERG (1972). The length and circumference of the scapula and the long bones increased significantly from stage to stage, except for the circumference of the femur. The increase relatively slowed down after 91 kg live weight, except for the humerus. Bone circumference increased more than bone length only between 23 and 68 kg live weight. Thereafter the ratio between length and circumference remained rather constant. So the thickening relative to lengthening occurred much earlier than reported by MCMEEKAN (1940a) and CUTHBERTSON and POMEROY (1962b). But for a single exception no breed influence was indicated for the lengths and circumferences measured. The length of the scapula was effected by sex and feeding level; it was shorter in the fattier pigs. Sex also influenced the length of femur and tibia, these bones being shorter in castrates.

All individual bones were expressed as a percentage of total bone weight (RICHMOND and BERG, 1972). Most of the bones followed the decreasing trend of total bone during growth, the bones of the hind limb and the humerus significantly so. Some increased (lumbar vertebrae) or tended to increase, like the cervical vertebrae and the ribs. An anterior to posterior growth pattern could be observed. The cervical vertebrae, however, did not fit in, but that was also true in the results of CUTHBERTSON and POMEROY (1962b). The faster growth of thoracic vertebrae relative to lumbar vertebrae in the period from 68 to 92 kg as indicated by the last-named workers was not confirmed in this study. The distoproximal pattern, if present, was very weak and was thus in general agreement with the results of CUTHBERTSON and POMEROY (1962b), but not with those of DAVIES (1975) and MCMEEKAN (1940a).

The weak differential effect of feeding level as indicated by MCMEEKAN (1940b), more pronounced in heavier animals (MCMEEKAN, 1940c) could not be confirmed. But for an occasional exception this is because feeding level (and sex and breed as well) did not significantly influence the bone distribution. The rather great extend of invariability of bone tissue was stressed. It was further stated that the differentiation in bone distribution was essentially complete at or before 23 kg live weight which corresponded to the findings for muscle distribution (RICHMOND and BERG, 1971b).

The invariability of bones is supported by work of WENHAM et al. (1973). They measured growth in length (diaphyseal length) and width of bones performed by means of radiographic techniques on 34 Large White crossbred pigs slaughtered from birth to 120 kg live weight. In addition 83 foetuses of different ages were also radiographed. The Gompertz equation was applied in order to be able to calculate the age at which length and width reached a certain proportion of the asymptotic measure. Of the bones measured the ulna attained 1/3 of the postnatal asymptotic length first, and at 3/4 the ulna again was one of the first. However, the ulna and scapula were by far the last bones in reaching 3/4 of the asymptotic width. This particular example of the ulna exhibits the early length growth and the later thickening of the bone, in accordance with the view of the workers of the Cambridge School. Most other bones, however, did not show this pattern. Rather the reverse was found, thus being more in agreement with the results of RICHMOND and BERG (1972), just like the weak order of development which could be elicited from the figures given. WENHAM et al. (1973) had to conclude that length and breadth of bones changed in a regular and orderly manner with the age of the pig. They further suggested a steady and persistent growth for the skull, rather than the misleading description early maturing. Like the ulna the skull indeed stood out at 1/3 of the post-natal asymptote, indicating the early maturing nature of the head, but of all bones studied the skull was the latest bone reaching 3/4 of the asymptotic length. From the radiographic pictures further estimates were made of the age of appearance of the various ossification centres. It was thus possible to state that, when compared with other large farm animals, the skeleton of the pig is relatively immature at birth.

With respect to fat distribution RICHMOND and BERG (1971c) featured that the percentage subcutaneous fat significantly increased between 91 and 114 kg live weight with a corresponding decrease of intermuscular fat. However, the increase in subcutaneous fat was highest from 23 to 68 kg. In this period intermuscular and body cavity fat decreased. The percentage of body cavity fat significantly increased between 68 and 91 kg. These findings seem to be in agreement with the results of DUMONT et al. (1973) who showed a slight increase in the percentage of subcutaneous fat between 80 and 100 kg and a corresponding decrease in intermuscular fat. Thereafter up to 140 kg the percentages remained rather constant. Breed of sire and sex did not influence the partition between the fat depots during the growth period studied (RICHMOND and BERG, 1971c). The higher energy level, however, resulted in a higher percentage of intermuscular fat during growth, but the decrease in subcutaneous fat was not significant. There was a significant ration by live weight interaction for both fat depots.

Within the different fat depots the changes were studied in the fore and hind quarters. For the main depots changes were noticed most between 23 and 68 kg in that more subcutaneous fat was deposited in the hind quarter and less in the fore quarter, likewise for intermuscular fat. No further significant changes occurred with increasing weight. Breed of sire, sex nor ration significantly influenced the partition of subcutaneous fat between fore and hind quarter. But they did with respect to intermuscular fat in that the fatter carcasses (belonging to the Duroc × Yorkshire cross, castrates and pigs on the high energy level) had a higher proportion of intermuscular fat in the hind quarter. Interactions were demonstrated as well.

DAVIES and PRYOR (1977) studied the distribution of fat in 15 castrated crossbred pigs slaughtered over a range from 8 to 62 kg live weight. The growth of subcutaneous, intermuscular and intramuscular fat appeared to be similar relative to total fat. The cavity fat, which is of minor importance, only significantly differed from intramuscular fat. These findings, however, are not in agreement with those of McMEEKAN (1940ab) and RICHMOND and BERG (1971c) and not with those of JOHNSON et al. (1972) in cattle either. About 70 individual muscles were also dissected. Although the growth coefficients of several groups showed growth gradients in general agreement as described by DAVIES (1974b), they were less discrete. The pattern of differences between the groups did not change when calculated on a non-fat dry matter basis. This means that intramuscular fat and water content of the muscles do not disturb the relationships, in accordance with the results of JOHNSON et al. (1973) in cattle. Furthermore, the intramuscular fat within a muscle group grew faster than the group as a whole, except for the neck, cutaneous and abdominal muscle group. The same, though less pronounced, was found for the weight of non-fat dry matter within the muscle groups. Since (but for a single exception) the *b*-values did not differ significantly between the muscle groups, a clear topographical pattern in this respect was not apparent. When the growth of intramuscular fat within a muscle group was related to total intramuscular fat growth gradients were found similar to those of muscles, i.e. increasing from neck to longissimus and from distal to proximal direction in the limbs. When related to total fat these gradients almost disappeared.

The percentage of intramuscular fat between the individual muscles showed a large variability, also noticed by JOHNSON et al. (1973) in cattle. The percentage non-fat dry matter varied very little between muscles. The highest fat content was assessed in the muscles of the fore quarter, in the cutaneous muscles and in the superficial muscles that are not clearly overlaid by a fascia.

FOWLER and ROSS (1974) attempted to influence the changes in the various fat depots by means of composition and level of intake of the diet. From about 80 kg live weight onwards groups of pigs were given a very low protein (4%) diet but with amply sufficient intake, or a submaintenance diet but rich in protein (29%). After 4 weeks the amounts of subcutaneous, perinephric and mesenteric fat were about doubled in the pigs fed the energy-rich diet as compared to a control group. After 8 weeks there was about a three-fold increase. Inter- and intramuscular fat only slightly increased. On the other hand the amounts of fat in all depots (per kg fat-free body weight) had not changed in the underfed pigs in the first 4 weeks. But slimming for 8 weeks resulted in mobilization of fat from the subcutaneous and perinephric fat, whereas the inter and intramuscular depots still seemed to be rather stable. Hence the various depots were differentially affected. The high protein diet, however, could not prevent that the fat-free body weight decreased after the first 4 weeks and to a lesser extent also in the second 4 week period. Also based on these results FOWLER (1976) supposed that a part of the fat-free body was relatively labile (called the variable lean tissue) and could easily be converted under conditions of sub-maintenance diets in contrast to the essential lean tissue.

The effect of nutrition on distribution of the various tissues was also studied by CARDEN and GOENAGA (1977). From 30 kg onwards each of a group of 12 castrates was restrictedly fed according to live weight and given one of four nutritional treatments, being diets with high energy-high protein (HEHP), high energy-low protein (HELP), low energy-high protein (LEHP) or low energy-low protein (LELP) levels. Animals were slaughtered evenly spread over the live weight range of 60 to 110 kg. In the regression analysis the linear regression was applied because in the weight range studied, the allometric equation did not result in smaller variation around the fitted lines.

Gross carcass composition was clearly influenced by the nutritional treatments. The high energy diets produced fatter animals (HEHP more pronounced than HELP) and the animals on a low energy level thus had more muscle and bone and less fat (LEHP more pronounced than LELP). The growth rate of fat, muscle or bone relative to carcass weight did not significantly differ between the high energy diets or between the low energy diets.

After dissection of the individual muscles 8 groups were made. The groups up to and including group 6 were practically the same as dealt with by BUTTERFIELD and BERG (1966b) (cf. Table 2.1 on p. 34) and by LOHSE et al. (1971). Group 7, however, comprised the muscles connecting the fore limb to the thorax and therefore coincided with the IVO-group of muscles of the shoulder girdle region. Group 8 was a combination of remaining muscles and contained the intrinsic muscles of the neck and thorax and those connecting the fore limb to the neck.

Like in other work the major effects of nutrition were found in the ratio between fat and fat-free carcass tissue. But in this study also differential effects were established for distribution within the tissues. The distal group of muscles of the hind limb on the LEHP treatment grew faster relative to total muscle than on the other treatments, likewise those of the fore limb on the HEHP and LEHP grew faster than on the low protein treatments. Significant differences were also found in the adjusted means for the muscles of the abdominal wall, those of the proximal muscles of the hind limb, those of the muscles connecting the fore limb to the thorax and for the total of expensive muscles (group $1+3+5$). The finding of a lighter proportion of the muscles of the abdominal wall on the low energy treatments, also found by FOWLER and LIVINGSTONE (1972), was ascribed to lower contents of the abdominal cavity. The authors tried to find out whether a mirrorred effect had influenced the other groups, by excluding the muscles of the abdominal wall from total muscle weight. The nutritional effect on the proximal muscles of the hind limb then disappeared, but the effect on the others (slope of groups 2 and 6, and adjusted means of group 7) remained. Thus these findings are not in agreement with those of RICHMOND and BERG (1971b) and only for some characteristics consistent with those of FOWLER and LIVINGSTONE (1972). Restriction of energy resulted in a higher proportion of expensive muscles, which was not found earlier, though MURRAY and SLEZACEK (1975) reported a higher b-value for the group of muscles of the proximal pelvic limb. The greatest difference amounted to 1.8% of total muscle weight and was said to be probably of little commercial importance.

With respect to bone weight distribution only minor influences of the nutritional treatments were apparent. These results are in general agreement with those of RICHMOND and BERG (1972), as is the muscle to bone ratio (bone weight regressed on muscle weight) that remained unchanged after the treatments had been imposed.

The fat distribution again was influenced by the nutritional treatments in that the HEHP treatment decreased the growth (relative to total fat) of the subcutaneous fat, whereas that of intermuscular fat increased. Furthermore, the adjusted means for the body cavity fat and intramuscular fat were also higher on the high energy treatment. In the case of intramuscular fat the examination, however, was only based on three individual muscles.

A further experiment was carried out by GOENAGA and CARDEN (1978) to study muscle weight distribution in particular. They imposed greater differences in feed intake in that one group of pigs was fed *ad libitum*, while a second one was allowed to grow only less than one third of the *ad libitum* group. About similar results were found as in the earlier experiment. The differences were somewhat more pronounced. Moreover, the effect on the proximal muscles of the pelvic limb did not disappear when the group of muscles of the abdominal wall was excluded from the calculations. It further appeared that again the muscle to bone ratio was very stable, being not affected by the nutritional treatment even under these large differences in energy intake.

The results obtained in studies concerning relative growth pose a number of problems, because conflicting results appear to exist. On the other hand remarkably similar results can be found as well. Conflicting results may arise from non-comparability between experiments. Apart from the relatively minor importance of factors like breed and sex, the major factors that may influence the interpretations are the stage of development and the choice of the independent variate in regression techniques or the reference chosen when percentages are to be calculated. Within the group of farm animals the species may play a role in this respect as well.

The conclusion reached by MCMEEKAN (1940bc), as decribed earlier, in that the level of nutrition differentially affects the development of the parts of the muscle tissue, is directly related to the independent variate chosen. The reanalysis of his data (especially by ELSLEY et al. (1964)) showed that no differential effect was apparent when the most variable tissue – fat – was excluded from the calculations. In other cases, as demonstrated by COLE et al. (1976), different independent variates (i.c. carcass weight and muscle plus bone weight) were used, and although the growth coefficients differed somewhat, they did not lead to different interpretations as to the relative development of the tissues. In that case, however, the gross composition of the carcass was involved.

The choice of an appropriate independent variate is defined not only by the variability of components, but also by the object in view with which growth is evaluated. In comparing development of tissues or parts it is expedient to choose independent variates made up of components that are rather insensitive to environmental effects. The weight-dependent growth pattern of the tissues is better shown on the basis of muscle plus bone weight than on the basis of carcass weight.

Owing to the stable nature of bone tissue, muscle weight in many cases therefore is enlarged to muscle plus bone weight as the independent variate. But when muscle, bone or fat weight distribution is to be studied it is more reasonable, as also stated by SEEBECK (1968a), that the calculations are carried out on a within-tissue basis, so choosing the corresponding tissues as the independent variate. In the literature described in the preceding sections this approach has been applied by all authors studying distribution of tissues. Of course one may go into further detail in that parts of a tissue serve as independent variates. In these cases, however, it must be kept in mind that auto-correlation plays an increasing role and so do the findings of GUTTMAN and GUTTMAN (1965) who suggested that correlations between parts closely situated to each other are higher than between parts that are more remote.

Much insight is gained when certain functional entities are taken as independent variates as shown by the examples given by FOWLER (1968) and FOWLER and LIVINGSTONE (1972). In general it was demonstrated that for particular muscles or bones nutritional treatments were significant when the muscles or bones did not belong to selected functional groups which were chosen as independent variates. Significant results were also found for components of the fat-free carcass when the independent variate included fat. Changes in body composition and differential growth of groups of muscles in a number of cases may be explained by functional demands. Examples were described by HEAP and LODGE (1967), FOWLER (1968), BRYDEN (1969), LOHSE et al. (1971), FOWLER and LIVINGSTONE (1972), JOHNSON (1974) and BERG and BUTTERFIELD (1975, 1976abc). In other cases, however, differential growth could hardly be explained by functional adaptation (FOWLER and LIVINGSTONE, 1972; LOHSE et al., 1971), and in addition the latter showed that anatomical grouping does not automatically coincide with a functional grouping of muscles.

With regard to the growth coefficients of the main tissues relative to carcass weight the authors were very unanimous. Bone is growing slowest with *b*-values varying from 0.69 to 0.92. Muscle grows at about the same rate as total carcass (*b*-values vary from 0.92 to 1.07), whereas fat is the fastest growing tissue with *b*-values varying from 1.13 to 1.88. The range for fat would be 1.26–1.88 abandoning the data of pigs. These animals from the experiments of DAVIES (1974a) and COLE et al. (1976) had a live weight up to 65 kg, so that fat growth had not yet been fully in progress. Nevertheless, as COLE et al. (1976) concluded, the *b*-values for the tissues mentioned did not differ much between cattle, sheep and pigs, which is also valid when these tissues are related to empty body weight or to muscle plus bone weight.

Gross carcass composition is clearly influenced by breed, sex and nutritional treatments, which is especially seen in the ratio between muscle and fat. The increase of muscle relative to bone during growth is more difficult to alter. In almost all cases nutritional treatment did not influence this ratio, neither did sex in the cases reported. Breed, however, significantly influenced the muscle to bone ratio, at least in cattle. In pigs both cases reported did not result in a significant influence. The comparison by RICHMOND and BERG (1971a), however, did not involve pure breeds, only the breeds of sire; but on the other hand the ratio is calculated on the basis of equal carcass weight, whereas in most cases muscle plus bone weight is taken as the basis.

Treatment effects on a within tissue basis mostly are much smaller. The influence of breed on muscle weight distribution was found to be small in cattle (BERG and BUTTERFIELD, 1975, 1976ac; BERGSTRÖM, 1974b, 1978), although in more extreme breeds also significant differences were shown (KEMPSTER et al., 1976b; TRUSCOTT et al., 1976; ROBELIN et al., 1977; BERG et al., 1978b). Significant differences also appeared in sheep (SEEBECK, 1968b) and in pigs (DUMONT et al., 1969; RICHMOND and BERG, 1971b; DAVIES, 1974b). In general these differences are only limited to some muscle groups or some muscles, but on the other hand the more expensive groups of muscles were involved. The same holds true for the influence of sex on muscle weight distribution. Again small, but specific differences were found in cattle (BERG and MUKHOTY, 1970; BRÄNNÄNG, 1971; BERGSTRÖM, 1974b, 1978) and in rabbits (VEZINHET et al., 1972). In sheep (SEEBECK, 1968b) hardly any significant difference has been attained. As in cattle the females had a higher proportion of the group of muscles of the proximal pelvic limb in early periods of life, but castrated pigs (RICHMOND and BERG, 1971b) produced a higher proportion of this group in later stages. Contradictory results appeared from the work of WILSON (1966, 1968b).

In line with the calculations made by ELSLEY et al. (1964) the few experiments in which the influence of nutritional treatment was studied revealed almost similar results (in calves: BUTTERFIELD and BERG, 1966c; BUTTERFIELD and JOHNSON, 1968, 1971; in pigs: WILSON, 1968a) or only differences in some muscles (in cattle: ANDERSEN, 1975; in pigs: WILSON, 1968b) or differences in the relatively unimportant groups of distal muscles of the limbs (in sheep: MURRAY and SLEZACEK, 1975; in pigs; RICHMOND and BERG, 1971b; CARDEN and GOENAGA, 1977). The first and last-named workers, however, also noticed significant differences for the more expensive muscle groups, which were also found in the identical twin pairs of BERGSTRÖM'S (1978) experiment kept under extreme conditions. In the case of sheep and pigs the proportion of the more expensive muscle groups was in favour of lower energy levels in the diet, but in the case of cattle to the contrary, higher energy levels led to higher proportions of these groups. More distinct levels showed more pronounced differences (GOENAGA and CARDEN, 1978).

The differences in muscle weight distribution as influenced by breed, sex or nutritional treatment remained small and were often called commercially unimportant.

In their classification of individual muscles and muscle groups into impetus groups BUTTERFIELD and BERG (1966a and 1966b respectively) did not go further than diphasic growth patterns. Following the same procedure LOHSE et al. (1971) indicated that triphasic patterns might occur. In addition to mono or diphasic patterns others found or suggested curvilinear growth (in rabbits: CANTIER et al., 1974; in cattle: TRUSCOTT et al., 1976; ROBELIN et al., 1977; BERGSTRÖM, 1978). In pigs almost exclusively monophasic growth patterns have been reported

(RICHMOND and BERG, 1971b; DAVIES, 1974b; CARDEN and GOENAGA, 1977). The results of the experiment of CUTHBERTSON and POMEROY (1964) reasonably correspond with this, since changes in percentages between the two stages studied were of minor importance.

It was said that the main changes during growth take place in the early stages after birth, in cattle (BERG and BUTTERFIELD, 1975, 1976ac; BERGSTRÖM, 1978; BERG et al., 1978b) as well as in pigs (CUTHBERTSON and POMEROY, 1964; RICHMOND and BERG, 1971b). On the other hand, however, the curvilinear growth in cattle (ROBELIN et al., 1977) was calculated after 9 months of age and DAVIES (1974b) in pigs claimed monophasic growth in the most interesting period in this respect in that in his work already four dissection stages were involved before 25 kg live weight had been attained.

In many cases the individual muscles follow the pattern of the group to which they belong, but clear exceptions were noted as well.

CUTHBERTSON and POMEROY (1964) presented a number of examples in which relative growth of given muscles was closely related to that of parts of the skeleton to which they were attached. BERG et al. (1978d) rather had to conclude the reverse in cattle.

The growth coefficients of muscles and muscle groups given by the various authors partly approximate to each other. The correspondence, however, is rather dependent on the trajectories over which the coefficients have been calculated.

Furthermore, rate of growth (BERG and BUTTERFIELD, 1975, 1976ac) and degree of fatness (BERGSTRÖM, 1978) would not influence muscle weight distribution to a great extent, explained by the fact that JOHNSON et al. (1973) in cattle found that the distribution of intramuscular fat hardly changed when total dissectable fat increased. Also DAVIES and PRYOR (1977) in pigs showed that intramuscular fat did not disturb the muscle weight distribution.

With respect to bone weight distribution the influences of breed (RICHMOND and BERG, 1972; DAVIES, 1975), sex (RICHMOND and BERG, 1972) or nutritional treatment (RICHMOND and BERG, 1972; CARDEN and GOENAGA, 1977) were insignificant in pigs. In sheep SEEBECK (1968b) did not find significant differences for the influences of breed and sex either, but PRUD'HON et al. (1978) did. Nutritional treatment also had a significant influence (FOWLER, 1968, using the sheep data of PÁLSSON and VERGÉS, 1952b). In cattle differences were found in the growth pattern (BERG et al., 1978d; JONES et al., 1978). Significant, but small influences were shown for breed or breed-type (TRUSCOTT et al., 1976; KEMPSTER et al., 1977; BERG et al., 1978d; JONES et al., 1978; ROBELIN, 1978) as well as for sex (BERGSTRÖM, 1974b; JONES et al., 1978). Only ROBELIN (1978) stressed that the differences in bone weight distribution were commercially important.

The ratio between length and width of the bones was studied in pigs in particular. Contradictory results were reported. Thickening of bones would occur in later stages (MCMEEKAN, 1940a; CUTHBERTSON and POMEROY, 1962b), whereas WENHAM et al. (1973) rather found the reverse. RICHMOND and BERG (1972) also found that thickening relative to length growth had taken place on an earlier stage.

Fat weight distribution was not influenced by breed or sex in pigs (RICHMOND and BERG, 1971c); in sheep (SEEBECK, 1968b) sex also did not, but in the case of breed significant differences were noticed. In cattle for both breed (CHARLES and JOHNSON, 1976; KEMPSTER et al., 1976a; TRUSCOTT et al., 1976; BERG et al., 1978c) and sex (BERG and BUTTERFIELD, 1976c) significant but relatively small differences were found. The nutritional treatment affected the fat weight distribution as well, in that in pigs the higher energy level led to a higher proportion of intermuscular fat (RICHMOND and BERG, 1971c; CARDEN and GOENAGA, 1977). Besides, FOWLER and ROSS (1974) were able to differentially affect the fat depots via extreme compositional changes in the diet.

In general the distribution of fat is a function of total fatness (BERGSTRÖM, 1974b; BERG and BUTTERFIELD, 1976c).

The growth gradients as established by MCMEEKAN (1940abc) and PÁLSSON and VERGÉS (1952ab) were largely confirmed in the preceding sections, most clearly in the skeleton in pigs by CUTHBERTSON and POMEROY (1962b), RICHMOND and BERG (1972) and DAVIES (1975), in sheep by LOHSE et al. (1971) and PRUD'HON et al. (1978), in cattle by BUTTERFIELD and BERG (1966b), BERG et al., 1978d, JONES et al. (1978) and ROBELIN (1978) and in rabbits by DULOR et al. (1976). But the gradients in anterior-posterior direction and down the limbs were also found in muscle in pigs by CUTHBERTSON and POMEROY (1964), DAVIES (1974b) and DAVIES and PRYOR (1977), in rabbits by VEZINHET et al. (1972), and in cattle by BERG et al. (1978b) solely with respect to the limbs, because over the trunk a caudo-cephalically gradient was established. Furthermore, DAVIES and PRYOR (1977) noticed the gradients in intramuscular fat of individual muscles within total intramuscular fat. KEMPSTER et al. (1976) also found an opposite gradient in subcutaneous fat from the proximal pelvic limb via the dorsal joints. Gradients for total fat in the joints ran centripetally from the limbs and neck to the rib and loin area (BERG et al., 1978c).

In a number of cases the growth gradients were not perfectly arranged. It seems worth mentioning that especially the cervical vertebrae more than once did not fit in (CUTHBERTSON and POMEROY, 1962b; RICHMOND and BERG, 1972; PRUD'HON et al., 1978).

3. MATERIALS AND METHODS

3.1. GENERAL

The growth rhythm experiment was carried out at the Institute's (I.V.O.) experimental farm 'Bantham'. Offspring of the then Dutch Landrace herd, kept under minimal disease conditions, was designed for the experiment that ran from 1970 to 1974.

During the growing period from about 25 kg up till mature weight animals were slaughtered after certain intervals. The right carcass half was dissected by the I.V.O.-standard method and the left half by almost full anatomical dissection.

As the new-born stage was lacking it was decided in 1975 to complete the material with new-born piglets. These were offspring of sows of the same herd.

3.2. EXPERIMENTAL DESIGN

The experiment comprised four replicates. They partly ran alongside each other and were started within half a year intervals from each other. In the first three replicates the animals were housed in groups and also group fed. Because of circumstances at the experimental farm only the building for individual housing was available for the fourth replicate.

At weaning at an age of 7 weeks the dams were taken away from the piglets. So the latter stayed in the farrowing pen, where they were fed from dry feeders, until they were moved to the fattening house and placed on trial when they were 8 to 10 weeks old.

3.2.1. *Distribution of animals over the treatments*

Per replicate groups of 13 piglets were formed: boars, castrates and sows for the *ad libitum* as well as for the restricted feeding level. Castration had taken place at an age of 5 to 6 weeks. The two feeding levels were introduced at the actual start of the experiment when the animals were 10 to 12 weeks old. The distribution of the piglets over the treatments and the different dissection stages is shown in Table 3.1. According to this scheme the planned number of animals involved in the total experiment was 322.

Littermates were allotted to the six treatment groups according to their weight. Thus as the start the variation in age between the groups was very small, but also within groups the variation coefficient exceeded 10% only in a single case. The variation coefficient in weight within groups was somewhat greater (in general 10 to 15%), and between groups it was about 5%. Concerning the new-born piglets four weight groups were introduced, viz. 1100, 1300, 1500 and 1700 grams birth weight.

TABLE 3.1. Experimental scheme showing the distribution of the animals over the treatments sex and feeding level at the different dissection stages.

Dissection stages (age groups)	Sex					
	Boars		Castrates		Sows	
0 New-born	8				8	
I 12 weeks	6*		6		6	
	Feeding level		Feeding level		Feeding level	
	high	low	high	low	high	low
II 18 weeks	8	8	8	8	8	8
III 24 weeks	8	8	8	8	8	8
IV 30 weeks	8	8	8	8	8	8
V 36 weeks	8	8	8	8	8	8
VI 50 weeks	8	8	8	8	8	8
VII Mature	8	8	8	8	8	8

*Dissection stage I of the fourth replicate was abandoned.

With regard to the distribution of littermates over the different dissection stages it was stated that littermates should not be slaughtered at the same dissection stage if possible. Therefore the littermates were assigned by lot beforehand to the different dissection stages.

Dissection stage I took place at the start of the experiment, so that there had been no influence of the feeding level. The other dissection stages up till stage V proceeded each other at six week intervals. From stage V to VI a 14 week interval was taken. Some deviations occurred in this procedure in connection with holidays etc. The mature stage was considered to be reached when after a number of weighings the weights declined or fluctuated without any tendency towards increase.

From the start of the experiment on, the animals were weighed and the feed intake was assessed every fourteen days. Live weight was assessed to the nearest 0.5 kg. The amount of feed per pen over a fortnight period was measured to the nearest 0.1 kg.

3.2.2. *Genetic background*

In the first replicate the piglets were born from 16 dams; in the other three replicates 13 litters were involved. Because of the too limited number of dams and the sex distribution in their litters it was not always possible to apply exactly the desired distribution over the treatments. The surplus of piglets from some litters was randomized between the treatments to fill up the gaps. In the four replicates 10, 5, 3 and 3 sires were used respectively. The three boars from the third replicate also mated dams from the second replicate, while one boar from the fourth replicate was also used in the first replicate. So in total 17 sires were involved.

The dams and sires used belonged to a simultaneously running selection experiment. Second litters of dams could be used for the growth rhythm experiment. A selection index, which is comparable with that used by the herdbooks in their breeding schemes, is also known for 13 out of the 17 sires. These 13 boars had an average index of about 0.4 standard deviation above the average of the contemporaries from the selection experiment.

The dams and sires, except for two A.I. boars, of the new-born piglets were descendents from the same herd. From the litters of 8 dams, sired by five boars, one gilt piglet and one boar piglet of approximately the same weight were taken. From the five sires used, one boar mated three dams and another one mated two dams.

3.3. HOUSING

The pens for the animals in group housing as well as in individual housing had concrete partly slatted floors and timber partitions. No bedding was used. At the start of the experiment 13 animals were housed together. Because of the slaughterings after certain intervals the number of animals in the pens gradually decreased, so that the remaining animals could stay in their pens throughout the experiment. Moreover the fronts of the pens were movable. In this way the pen size was always adjusted to the space requirement of the animals. In the individual housing the pen size could also be adjusted to the size of the animals.

Nipple drinkers were present in all pens.

3.4. FEEDING

The animals were placed on trial when they were 8 to 10 weeks old. The piglets were given a week to acclimatize to their new environment, while in the meantime they gradually changed from the starter ration to the experimental grower ration. In this week all piglets were fed restrictedly according to their weight. All treatment groups then received the same amount of feed per day. A second week was needed to establish the *ad libitum* feeding level of the concerning treatment groups, because the restricted feeding level was made directly dependent on the *ad libitum* level. After that week when the piglets were 10 to 12 weeks old the experiment actually started. This procedure was followed in the first two replicates. In the third replicate all piglets were kept on the restricted feeding level, also in the second week. The *ad libitum* feeding level for the concerning groups then was introduced at the start of the experiment. In this case the treatment groups at start had about the same live weight, whereas the groups from the first two replicates at that moment already differed in weight. The procedure in the fourth replicate deviated from the others. Owing to circumstances of management the pens were not ready in time. Because the piglets in this replicate already had the desired weight comparable with the other piglets at start, they directly started at both feeding levels after moving from the farrowing pens.

TABLE 3.2. The composition and the (calculated) feeding value of the grower ration.

Percentage	Ingredients	Feeding value
3	fish meal	energy value 1.06
2	meat-and-bone meal	NE_F 9265 kJ
15	soy oil meal	digestible protein 15.0%
3	alfalfa meal 18%	crude fibre 3.6%
10	barley	lysine 0.84%
41.2	maize	Ca 1.03%
20	sorghum	P 0.64%
3	molasses	
2	minerals	
0.5	dicalcium phosphate	
0.3	vit. BAD_3 and B_{12}	

3.4.1. *Feed composition*

After placing the animals on trial a grower ration was introduced which was fed throughout the experiment. The composition and feeding value of this diet is shown in Table 3.2. During the first replicate we were confronted with leg weakness problems, mostly in the weight range 115–200 kg. Lowering the daily rate of gain might give improvement. Therefore it was decided to increase the amount of crude fibre in the ration; a percentage of more than 10 would then be needed (A.R.C., 1967). In the diet 30% oat hulls were incorporated, the amount of crude fibre raising to 11.3%. The dilution of the diet led to the following feeding value: energy value 0.82, NE_F 7243 kJ, digestible protein 10.7%, lysine 0.59%, Ca 1.10% and P 0.62%. Except the 30% dilution with oat hulls an extra 0.5% dicalcium phosphate was added. This new ration was given throughout the other three replicates.

3.4.2. *Feeding level and feeding procedure*

The amount of feed over a fortnight period for the restrictedly fed groups was related to the *ad libitum* (= free access to feed during the 24 hour period) fed groups. The restrictedly fed pigs received an amount of feed equal to their maintenance requirement plus half of the feed for production of the *ad libitum* fed groups of the same weight and sex.

For assessment of the maintenance requirement figures cited and calculated by VERSTEGEN (1971) were used. This means approximately 525 kJ *ME* per kg metabolic weight (i.e. $W^{0.75}$) for pigs below 50 kg live weight, approximately 480 kJ *ME* per kg $W^{0.75}$ beyond 50 kg and approximately 420 kJ *ME* per kg $W^{0.75}$ for older animals. So maintenance requirement is $x \times W^{0.75}$, in which x runs from 525 to 420. The efficiency of *ME* for production being 70% (VERSTEGEN, 1971) the normal and diluted diet contain 9265/0.7 and 7243/0.7 kJ *ME* respectively. Thus the average daily amount of feed for maintenance can be calculated. Subtracting this from the known intake of the *ad libitum* fed animals the kg feed for production can be computed for these groups and hence that for the restrictedly fed groups. For practical use a line was constructed (Fig. 3.1), so

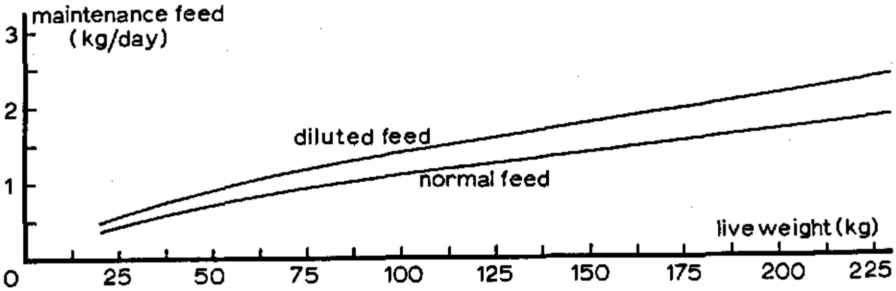

FIG. 3.1. Estimation of kg feed for maintenance requirement.

that an estimation of the kg feed for maintenance could be made at different live weights.

Beyond about 150 kg live weight the feed intake pattern of the *ad libitum* fed groups rather fluctuated. Therefore it was decided that the level used as reference for the restrictedly fed groups was fixed at 3.2 kg per day. Beyond 225 kg the feeding levels were no longer related and the restrictedly fed groups were given the same amount of feed of 3.1 kg per day up till maturity.

Animals of all treatment groups had access to the nipple drinkers throughout the 24 hours. Automatic dry feeders were placed in the pens of the *ad libitum* fed groups. The restrictedly fed groups received their feed in dry form also, from troughs and, except on Sunday, twice daily. Therefore the total amount of feed over the fourteen day period was divided into 26 parts. To all groups the feed was given as pellets.

3.5. SLAUGHTER PROCEDURE

The experimental pigs were slaughtered on the day of their fourteen days weighing or the day thereafter. These weights were used in calculating weight gain and feed conversion. At the day of slaughter the live weight was measured at the slaughter-house and this weight was used for assessment of the dressing percentage. Before slaughter the pigs were fasted for approximately 18 hours, except for water.

After arrival at the slaughter-house the pigs went through the normal process of stunning, bleeding and removal of viscera. The carcasses were split as careful as possible leaving the tail on the right side. Besides the warm carcass weight some meat quality characteristics were measured in the slaughter-line 45 min. post-mortem. The pH_1 of *mm. semimembranosus* and *adductor* were assessed with a portable pH-meter (Electrofact), while the rigor value was measured at the surface of the *m. semimembranosus* with the rigormeter according to SYBESMA (1966).

Along with the IVO-standard method some other meat quality characteristics were measured. At a cross-section of the *m. longissimus lumborum* after one chop had been cut off from the cutlets, subjective scores were assessed for colour, firmness and overall impression, all at a scale from 4 (bad) to 8 (good). The most caudal chop was used for measurement of protein solubility by means of the transmission value according to HART (1962).

At slaughter the testes and the epididymes were collected and after preparation the left and right testis as well as the left and right epididymis were weighed separately.

After slaughter both sides were brought to the institute where they were stored overnight (20–24 h) in a chill-room at approximately 4°C. On the following day from both sides the cold carcass weight (to the nearest 100 grams) was assessed. From the sum of these weights, and the live weight the dressing percentage was calculated. The right carcass halves were immediately dissected according to the I.V.O.-standard method, whereas the left carcass halves were wrapped in polythene bags and deepfrozen at −18°C. The latter sides were anatomically dissected at appropriate times.

In general similar procedures were applied to the new-born piglets. They were slaughtered at the institute when they were 10–12 hours old and also chilled overnight. During chilling the carcasses were hung in polythene bags to protect them against desiccation. Both dissection methods were carried out the following day or in some cases the day thereafter. The meat quality measurements and the backfat measurement were omitted.

3.6. CARCASS MEASUREMENTS

In addition to the weights of the carcass halves a number of carcass measurements was taken as shown in Fig. 3.2.

Carcass length is measured from the middle of the cranial side of the first rib to the anterior edge of the pubic symphysis. Furthermore the inner thorax depth was assessed (as measured) from the ventral side of the spinal cord half-way the fifth thoracic vertebra in a straight line horizontally to the ventral side of the sternum. The same characteristic was measured starting from the same point also in a straight line to the ventral side of the sternum but then at the juncture of the fifth rib.

The backfat thickness is measured at five locations, viz. (1) at the thickest place above the shoulder, (2) at the thinnest place on the back, (3) at the back 10 cm cranial of the implantation of the last rib, (4) at the thickest place on the loin and (5) at the thinnest place above the *m. gluteus medius*.

All these measurements were taken in the slaughter-line at the right carcass half. At the anatomical dissection the leg length was measured with a tape from the distal end of the tibia to the anterior edge of the pubic symphysis.

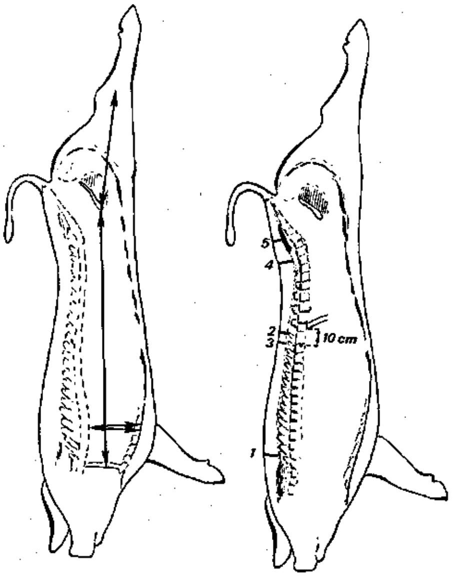

FIG. 3.2. Carcass measurements taken before dissection (for description see text).

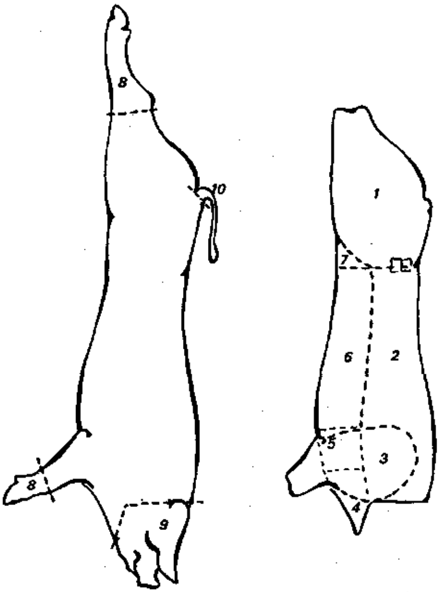

FIG. 3.3. The wholesale cuts as jointed according to the I.V.O.-standard method (for description see text).

3.7. CARCASS DISSECTIONS

3.7.1. *The I.V.O.-standard method*

This dissection method has been in use from 1965 and was described by BERGSTRÖM and KROESKE (1968). The right side was used to divide into wholesale lean and fat cuts. None of these cuts are deboned.

After removing the flare fat and the kidney, the tail, feet and head are separated from the carcass. The tail is cut off between the 3rd and 4th coccygeal vertebra. The separation of the fore foot is done between the proximal and distal carpal bones, while the hind foot is sawn just proximal to the tarsal joint. This is the reason why the leg length could not be measured like the other carcass measurements at the right carcass half. For splitting off the head a cut is made from the groove in the lower jaw to the mandible. The cut closely follows this bone around the angle and then proceeds in a straight line cranial to the first cervical vertebra and further just behind the ears as shown in Fig. 3.3. The figures in parenthesis in the text refer to those in Fig. 3.3. The three parts head (9), feet (8) and tail (10) together form the percentage offal.

The ham (1) is separated with a cut at 1/3 (cranial) of the last lumbar vertebra in a straight line down to the belly. From the ham the 'broek' (7) is trimmed off containing lean and fatty parts. Then a cut is made at the middle of the last ribs and thus going in cranial direction following the vertebral column a separation is made between cutlets (2) and belly (6). From the belly the 'krabbetje' (5) is removed, a part with the 1st to 4th rib. After that the cutlets are separated from the subcutaneous fat, the lower jaw fat (4) is removed and the shoulder (3) comes free. Finally the subcutaneous fat is trimmed off from the shoulder and the ham.

The meat percentage by this method is formed by ham, cutlets, shoulder and meat scraps. The latter includes in addition to the meaty parts of the 'broek' (parts of cutaneous and rectus abdominis muscle), the dorsal part of the latissimus dorsi and trapezius muscle, parts of the cervical cutaneous muscle, remnants of the diaphragm, some parts of the cranial serratus dorsalis muscle, and some parts of the dorsal and ventral muscles of the neck. The remainder of the carcass is calculated as fat percentage which can be divided in a more streaky part (belly and 'krabbetje') and a real fat part (subcutaneous fat from ham, loin, back and shoulder, lower jaw fat, and flare and kidney fat).

All parts were weighed on a balance to the nearest 5 g, except for the new-born piglets of which the parts were weighed on another balance to the nearest 0.05 g.

3.7.2. *Anatomical carcass dissection*

The left side of the carcass was used for the anatomical dissection. It is not possible to give a comprehensive description now of all actions and cuts done by applying this technique. The reader is referred to the relevant textbooks (e.g. NICKEL, SCHUMMER and SEIFERLE, 1961). A brief description is given here and is confined to a list of the single muscles and bones. The nomenclature used is adopted from Nomina Anatomica Veterinaria (1973).

After trimming off the flare fat and the kidney, the feet and head are removed. The head is separated from the carcass according to the standard method as shown in Fig. 3.3 and the feet with again a cut between the proximal and distal carpal bones, and between the tarsal bones and the tibia for the fore and hind foot respectively. No further dissections were done on these parts. The head and feet together with the kidney are calculated as the portion carcass offals. The subcutaneous fat and skin together were then removed from the whole carcass and these two were separated next after trimming off the *mm. cutanei trunci* and *colli*. After the muscles had become free they were trimmed off individually and weighed on a balance to the nearest gram. The same was done to the individual bones. The muscles and bones of the new-born piglets were weighed to the nearest 0.05 g.

3.7.2.1. Dissection of muscles

About 65 muscles were separated and weighed individually. Some muscles, however, were weighed together. In Table 3.3 is shown which muscles were separated and to which topographic groups they are assigned. The classification of the muscles into groups is arbitrary. It is also possible to advocate a division into strict anatomical groups or into functional groups. In this study there is chosen for grouping the muscles to certain topographic regions to have associations with commercial jointing as much as possible.

At dissection two or three men were working simultaneously on the same carcass, except for the new-born piglets where the dissection work was done by

TABLE 3.3. List of dissected muscles or combinations of muscles as they were weighed and grouped on a topographic basis. The meaning of the braces is explained in the text.

A. Muscles of the proximal pelvic limb
m. biceps femoris
m. gluteus superficialis
m. gluteus medius
m. gluteus accessorius
m. gluteus profundus
m. semitendinosus
m. semimembranosus
m. quadriceps femoris
m. tensor fasciae latae
mm. gemelli }
m. quadratus femoris }
m. gracilis
m. sartorius
m. pectineus
m. adductor
m. obturatorius externus

B. Muscles of the distal pelvic limb
m. soleus
m. gastrocnemius
m. flexor digitorum superficialis
mm. flexores and *extensores*

C. Muscles of the proximal
thoracic limb
m. deltoideus
m. subscapularis
m. infraspinatus
m. supraspinatus
m. teres major
m. teres minor
m. coracobrachialis
m. tensor fasciae antebrachii
m. triceps brachii
m. biceps brachii
m. brachialis

D. Muscles of the distal
thoracic limb
mm. flexores and *extensores*

E. Muscles of the neck region
mm. recti and *obliqui capitis*
m. omotransversarius
m. splenius
*m. longissimus capitis et atlantis**
m. semispinalis capitis
m. brachiocephalicus
m. scalenus dorsalis }
m. scalenus ventralis }
m. omohyoideus
m. sternocephalicus
mm. longus capitis, longus colli, etc.

F. Muscles of the back and loin
m. serratus dorsalis cranialis }
m. serratus dorsalis caudalis }
m. iliocostalis
m. longissimus cervicis
m. longissimus thoracis et lumborum
mm. multifidi

G. Sublumbar muscles
mm. iliopsoas and *psoas minor*
m. quadratus lumborum

H. Muscles of the thoracic and
abdominal wall
m. transversus thoracis
m. rectus thoracis
diaphragma
partes costalis and *sternalis*
m. obliquus externus abdominis
m. obliquus internus abdominis
m. transversus abdominis
m. rectus abdominis
mm. intercostales

I. Muscles of the shoulder girdle region
m. trapezius
m. rhomboideus
m. latissimus dorsi
mm. serrati ventrales cervicis
and *thoracis*
mm. pectorales superficiales
m. pectoralis produndus

J. Cutaneous muscles
mm. cutanei trunci and *colli*

K. Muscle remnants

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* When *et* is used the concerning parts are considered as one muscle.

one man. First the shoulder was separated from the carcass and laid aside for later dissection. The muscles were trimmed off in the same order and of course from the outside inwards, starting with the muscles from the neck and shoulder girdle region, and the superficial abdominal muscles. The muscles from the limbs were dissected from proximal to distal. The last muscles to be dissected were those from the thoracic limb on the one hand and the *mm. intercostales* on the other.

Special care was given to the dissection of the carcasses of the new-born piglets. After separating the shoulder it was wrapped in damp polythene bags to minimize the loss of moisture as the water content of these piglets is high and as they have a greater relative surface area. The same procedure was followed when breaks in the dessection work occurred.

There are more muscles in carcasses than listed in Table 3.3. Some small muscles were not dissected, while other muscles could not be accurately separated. The braces in the table mean that although the concerning muscles were weighed separately, they were taken together because these muscles are of vestigial size or of secondary importance. And in the case of the scalenus muscles it was not clear afterwards whether the *m. scalenus medius* was turned up in the *ventralis* or *dorsalis* or alternately in both, so that it was decided to take these muscles together to avoid misunderstanding.

The weights of some muscles are subject to variation due to errors in dividing the carcass into its sides and in the removal of the head at the atlas. The following muscles can be affected particularly: *mm. recti* and *obliqui capitis, m. semispinalis capitis, m. sternocephalicus, m. pectoralis profundus* and occasionally the deep muscles located at the vertebral column. In some cases the *m. sternocephalicus* was not present at all. Another cause of variation is the fact that some muscles cannot be accurately separated. The distinction between *m. soleus* and *m. gastrocnemius* gave some difficulties in the new-born animals.

Some other remarks have to be made about the listed combinations of muscles. The combination *mm. longus capitis* and *longus colli* etc. actually includes the deep muscles situated ventrally along the cervical vertebral column and transversal processes, including the *mm. intertransversarii ventrales cervicis.* The combination *mm. multifidi* contains not solely the *mm. multifidi,* but also *mm. spinalis* and *semispinalis cervicis* and *thoracis, mm. intertransversarii thoracis* and *lumborum,* and the *mm. rotatores.* An accurate separation between *m. iliacus* and *m. psoas major* could not be made, so these two were weighed together and for commercial reasons the *m. psoas minor* was included in this combination. Because of its small size the *m. quadratus lumborum* was also incorporated in this combination. Finally the *m. triceps brachii* includes the *m. anconeus.*

The group muscle remnants mostly only contains the *diaphragma pars lumbalis* in the new-born piglets. In the elder animals the muscle remnants contain parts of the *diaphragma pars lumbalis* (the remainder is included in the loss at slaughter), possibly parts of muscles of the urogenital apparatus, possibly parts of muscles of the tail and furthermore parts of muscles of the right side as a result of inaccurate splitting of the carcass. The muscles involved were already mentioned above when the variability was under discussion.

With regard to the dissection of muscles from the new-born piglets it appeared that all listed muscles could be separated. Only the *m. omohyoideus* was difficult to find, not only because of its size but also because in general the muscles of new-born piglets are pale-coloured and resemble fatty tissue. In 50% of these animals this muscle was not found and turned up in the intermuscular fatty tissue. Occasionally, however, the *m. omohyoideus* is also not found in older animals either. In that case the muscle is presumably weighed together with the *m. longus colli.*

The tendons and aponeuroses were removed from the muscles as much as possible, but the connective tissue covers were generally left on the muscles.

3.7.2.2. Dissection of bones

The dissected bones are listed in Table 3.4. As much as possible muscle, tendon and fatty tissue were removed from the bones. All cartilage, however, was left on the bones.

Because of inaccurate splitting of the carcass particularly the sternum is affected. This can be very pronounced in a single case.

In addition to the recording of the weight of the individual bones, some bone measurements were determined. The greatest length of the scapula, the greatest length and smallest width of humerus, radius, ulna and *os femoris* were assessed.

3.7.2.3. Dissection of fatty tissues

The fatty tissue is subdivided into perinephric fat, subcutaneous fat and intermuscular fat. Intramuscular fat was not established. The perinephric fat includes the flare fat and kidney fat. They could not be separated and were therefore weighed together, and named flare fat.

The separation between subcutaneous and intermuscular fat is arbitrary in some places. At the start of the dissection procedure, however, the layer of subcutaneous fat is removed from the carcass. It also includes the lower jaw fat in which glandular tissue is embedded. Later on no other fatty tissue was added any more, so that this originally trimmed off layer is defined as subcutaneous fat. All

TABLE 3.4. List of dissected bones or combinations of bones as they were weighed and grouped together.

Vertebral column	Thoracic limb
vertebrae cervicales	*scapula*
vertebrae thoracicae	*humerus*
vertebrae lumbales	**radius* and *ulna*
vertebrae sacrales	Pelvic limb
	os coxae
Sternum	*os femoris*
Costae and *cartilagines costales*	*patella*
	tibia and *fibula*

*including the upper row of carpal bones other fatty tissue is called intermuscular fat. This intermuscular fat not only includes the adhering fat of the various muscles, but in addition to connective tissue that could not be separated from the intermuscular tissue, also includes other tissues such as possible remnants of nerves, blood vessels, lymph nodes, glandular tissue, tendons and aponeuroses. To minimize loss of water this intermuscular fat was weighed in parts each time a suitable quantity was obtained.

A slightly different procedure was followed with regard to the new-born piglets. The amount of subcutaneous fat in these neonates is small and because of the high moisture content this subcutaneous fat could not be separated accurately from the skin. Therefore it was included in the weight of the skin. As a consequence the glandular tissue from the neck region in the new-born piglets is included in the intermuscular tissue.

3.8. CALCULATIONS AND STATISTICAL METHODS

3.8.1. *General*

Experiments carried out involving complete anatomical dissections furnish an enourmous amount of figures. Apart from tabulation, calculation of means as percentages and graphic presentation, one of the major tasks was to find a formulation that describes the material in a conceptive and yet surveyable way.

3.8.2. *Primary attempts*

With some hesitation for reasons discussed in section 2.3.2 it was decided to base a regression model on the allometric equation $y = ax^b$ in its logarithmic form $ln\ y = ln\ a + b\ ln\ x$ in order to relate the parts y to the entities x as independent variates. The slope of the regression line, represented by b, then estimates the growth coefficient.

The experiment was carried out according to a cross-sectional design in which the animals to be slaughtered at the various successive dissection stages were predetermined. The data from these dissection stages were considered to be statistically independent. The least-squares method was applied to calculate estimates of the intercept and the slope of the regression lines and their standard errors.

As might be expected from the literature that the allometric equation would not always hold over the whole trajectory, this procedure was also applied within any single dissection stage and within each successive pair of dissection stages, every time for the different treatment groups separately. In this way multiphasic patterns would be verified. Statistical tests on the growth coefficients, however, showed that differences were hardly demonstrable. In many cases the growth coefficients found did not seem to be very accurate owing to the limited number of animals and the relatively small trajectories, especially within dissection stages. But also the growth coefficients of the pairs of successive dissection stages had relatively large standard deviations. Moreover it was hardly possible to compare systematically feeding level and sex because of the large amount of data.

On the other hand differences in the growth coefficients could be detected by the results of another attempt, viz. introducing a quadratic term into the allometric equation $ln\ y = ln\ a + b\ ln x + c\ ln^2 x$ to allow for curvilinearity. Counting the significant quadratic terms for the treatment groups separately, it appeared that they were needed more than had been assumed. Although their number diminished, this still held true when dissection stages 0 and I were excluded from the calculations. At that moment no systematic pattern could be ascertained in the treatment groups nor in the various (groups of) characteristics that did have a quadratic term and those that did not. An effort was made therefore to gain insight in the material in other ways.

3.8.3. *Attempts of ordering the material*

Groups of muscles with a similar growth pattern were formed first according to the magnitude of the coefficient c from the formula of the preceding section. One group with c not significantly different from zero, another with high positive values for c, and a third one with high negative values for c. For each of these groups thus formed, an analysis of variance was carried out on the growth coefficients. The growth coefficients used were those calculated over the periods of each consecutive and not overlapping dyad of the original dissection stages. Thus four or three periods were formed dependent on the feeding level. Moreover in the analysis the effect of the periods was subdivided into a linear, quadratic and cubic component.

Again it was found that the growth coefficients of the periods did differ. Evidence was found that third and even fourth degree terms may occur as well.

The latter result and the desirability of grouping beforehand parts of tissues to some clusters with regard to their growth pattern led to the use of a canonical analysis as a means (SEAL, 1966) of illustration of differences between the levels of the major classifications feeding level, sex and dissection stages. The canonical analysis searches for linear combinations of the original variables that maximize the differences between the levels of the classifications. An effort was made to discover some pattern in the contribution of the original variables to each of the canonical variates separately or to combinations of them, in order to assign a meaningful characterization to them. The differences between the levels of the classifications may be studied with regard to the calculated mean values of the canonical variates for each level, whatever the variates may represent.

It is to be expected that in the canonical analysis for the weights of the muscles the first canonical variate will describe size differences between the dissection stages in particular. The weights of the individual muscles therefore were transformed to a measure for size x (e.g. total muscle weight) on the one hand, and measures for shape y/x (portion of each muscle from total muscle weight) on the other hand. The canonical analysis thus has been limited to the measures for shape on a logarithmic scale, $ln(y/x)$.

This analysis, however, presented difficulties in interpretation of the results.

Although some distinct findings were achieved, in this study as well the calculated first three canonical variates could not be interpreted in terms of nameable combinations of the original variables. Likewise it was not possible to efform understandable groups of muscles with comparable behaviour with respect to relative growth.

Since there seemed to be no procedure for grouping (the muscles) beforehand it was decided to calculate regressions for the various individual variables.

3.8.4. *High power polynomials*

Based on the results in the preceding sections it appeared to be necessary to include high power terms in the regression equation. The ultimate formula used in this study now became

$$ln(y/x) = ln\,a + b\,ln\,x + c\,ln^2x + d\,ln^3x + e\,ln^4x,$$

so up to and including a fourth power term, where it is to be understood that power terms in $ln\,x$ are orthogonalized on all preceding terms. It thus means that when e.g. a second degree term would be needed the formula actually should be written as

$$ln\,(y/x) = ln\,a^* + b^* ln\,x + c\,ln^2x.$$

The coefficients b presented in tables of the next chapter, however, denote the growth coefficient b of the linear part of the equation (so not the b^*) even when a second degree or higher power term would be needed. The b has been given in order to compare different parts of the same entity and for comparability with the literature.

The meaning of b was outlined in section 2.3.2. Furthermore, parts having the same b grow at the same rate with respect to the entity x, but may differ in their constant terms $ln\,a$; the ratio of their proportions remains constant. When parts differ in slope ($b_1 > b_2$), then part y_1 will diverge from part y_2 ever more if $ln\,a_1 \geqslant ln\,a_2$, or regression lines (may) cross if $ln\,a_1 < ln\,a_2$.

Analogous to differences in slope in case of a linear growth pattern, high power polynomials may differ in what will be called shape. If e.g. $c_1 > c_2$ the curves in any case will diverge from each other ever more when $ln\,a_1^* \geqslant ln\,a_2^*$ and $b_1^* \geqslant b_2^*$, but curves may still diverge when $b_1^* < b_2^*$. Parts having the same curvilinear pattern with respect to the entity x may differ in the constant terms ($ln\,a_1^* - ln\,a_2^*$). Over the trajectory studied regression lines may cross once or twice when two curvilinear patterns are compared or when a linear pattern is compared with a curvilinear one, depending on the height and sign of each of the terms involved.

The regressions were calculated for the six treatment groups separately as well as for the various combinations of feeding level and/or sex. In order to determine the degree of polynomial needed for describing the growth pattern of the sets of variables concerned, t-tests were carried out both at the 5 and 1% level. For each of the linear, quadratic, cubic and quartic polynomials F-tests were carried out to establish whether differences existed between the treatment groups. The regressions were compared both for the growth pattern represented by the shape of the regression (at $\alpha = 0.10$ and $\alpha = 0.05$) and the difference in constant terms of the regression (at $\alpha = 0.05$ and $\alpha = 0.01$). The latter test of course has been ignored when a significant difference in shape could be shown.

The variables in the left hand side of the formula have been taken to be logarithms of shape measures, e.g. ratios of muscle weights to total muscle weight. Therefore the regression formula describes the relationship between shape and size. Significance of regression coefficients means that shape is not independent of size. The degree of polynomial indicates the type of dependency between shape and size. The definition of shape measures is straightforward if weights of parts are considered. On the other hand if linear measurements are considered, shape measures have been arbitrarily defined as ratios between these measurements and the third root of the weight that is taken to be the size measure.

The term $- ln\ x$ in the left hand side of the formula leads to the testing of regression coefficients against zero. However, to the values of b presented in tables or in the text unity has been added in order to make the results easier comparable to literature. This procedure was followed when in the left hand side as well as in the right hand side of the formula either gravimetric or linear measurements occurred. In a number of cases, however, terms of a different kind were introduced in the left hand side of the formula instead of $ln y - ln x$:

(1) $ln y_1 - ln y_2$, being the ratio of two parts; e.g. the muscle to bone ratio or the ratio between the left and right kidney.

(2) $ln y - 1/3\ ln x$ in the cases when a linear measurement was regressed on the third root of a weight measurement; e.g. bone lengths regressed on total bone weight or backfat thickness regressed on total fat weight.

(3) $1/3\ ln y_1 - ln y_1^*$, in the special case where the ratio of the third root of the weight and the length of a particular bone was regressed on total bone weight.

In all three cases again the regression coefficients were tested against zero. But there is no sense in adding unity anymore to the b-value. On the other hand the classification regarding the linear pattern as described in the scheme on p. 69 and p. 70 is maintained. It means that the classes of 0.05 unit running from $L^=$ to H^* remain unchanged. In the same way as they scatter around unity they do around zero now.

The regressions were calculated for all dissection stages, but an indicator variable for the data of dissection stage 0 was incorporated in the model in case of the *ad libitum* fed boars and sows in order to remove a possible effect of stage 0 on the regressions. Dissection stage 0 was thus treated because a preliminary canonical analysis had shown that this stage deviated markedly from the other stages. Moreover all three *ad libitum* fed groups now comprised the same stages. Tests were done to establish ($\alpha = 0.05$) whether the mean of dissection stage 0 fitted to the regression calculated for stages I through VII.

Besides testing for the degree of polynomial required for an adequate description, the contribution to the total variance of each of the linear, quadratic, cubic and quartic components was calculated. These proportions were also used as a means in classifying the growth pattern of the various variables.

3.8.5. *The way of classification*

But for a single exception the quartic component was only found significant in isolated cases. It was therefore decided that the quartic component was kept out of attempts in classifying the results of the regressions.

It seemed reasonable to base the classification of the various characteristics on the results of the regressions of the six treatment groups. In order to establish whether a particular variable had a linear, quadratic or cubic growth pattern, a number of rules had to be regarded. They concern the test whether or not a high power term is significant on the one hand and its proportion of the residual variance (after taking into account the linear term) on the other hand. Thus the possibility of forming a sex group (the combination of the treatment groups of the same sex) having a deviating growth pattern was examined. Also a feeding level group (the combination of the treatment groups with the three different sexes of the same feeding level) might be formed.

The rules maintained say:

- when all 6 treatment groups or 5 out of the 6 treatment groups had a significant term in the quadratic or cubic polynomial the growth pattern was considered as quadratic or cubic respectively, irrespective of the proportion of the residual variance;
- the preceding rule had an exception when (as in a single case) beside the only non-significant term, the same sex at the other feeding level had a proportion much smaller than 10%; in that case this sex group was considered as distinctly different from the other 4 significant groups;
- when a significant term was found 4 times or less, sex or feeding level groups might be formed, but under the condition that within these groups this term for each of the treatment groups accounted for a proportion of the residual variance of 10% at least;
- the preceding rule also had an exception, because a proportion of the residual variance of 9% has also been accepted, but only if the average of the sex or feeding level group was 10% at least.

It was thus possible to distinguish between linear growth patterns on the one hand and quadratic or cubic on the other. If required the sex groups or feeding level groups of the higher degree growth patterns are denoted in the right hand column(s) of the respective tables. However, also within the linear growth pattern a partition between isometric and allometric growth can be made. This may be based on the growth coefficient being significantly different from 1, or in our model whether *b* differs from zero. It may mean that allometric growth is found, while the growth coefficient is near to 1. In this study therefore priority is given to absolute limits for the growth coefficients. The main classification was into low (L), average (A) or high (H), each of them subdivided into three classes as follows:

$L^{=} < 0.825$
$0.825 \leqslant L^{-} < 0.875$
$0.875 \leqslant L < 0.925$
$0.925 \leqslant A^{-} < 0.975$

$0.975 \leqslant A \leqslant 1.025$
$1.025 < A^{+} \leqslant 1.075$
$1.075 < H \leqslant 1.125$
$1.125 < H^{+} \leqslant 1.175$
$1.175 < H^{*}$.

As for the degree of polynomials established, sex or feeding level groups may be formed. Whether or not they were formed has been based on the result of the test for significant differences in slope between treatment groups ($\alpha = 0.05$). The sex or feeding level groups were given in the various tables with their common *b*-value. If the test allowed the bringing together of treatment groups, but the *b*-value would fall into a different class, the concerning pooled regression was decisive for the classification.

Decisive prior to looking at the combination of treatment groups was the test result for the pooled regression over the 6 treatment groups for $\alpha = 0.10$.

The part to whole relationships were calculated in three steps. As a first step carcass weight was regressed on live weight. Then the weight of the carcass components (bone, muscle, fat, skin and offal) were related to the carcass weight. As a last step the tissue components (muscle groups and individual muscles, bone groups and individual bones, and fat depots) were regressed on their respective tissue weights. Where other independent variates were chosen this is indicated in the text.

4. RESULTS

4.1. GENERAL

The animals in this study were generally in a good state of health. The pigs grew well untill they reached a live weight of about 115 kg when a number of animals developed, in one form or another, leg weakness. Ultimately 283 animals were dissected and they were distributed over the treatments as shown in Table 4.1. Three times 9 animals were dissected at a given stage. In one case a castrate appeared to be a boar. In the other two cases animals of a wrong treatment group were delivered at the slaughter-house at a too early stage erroneously.

Animals showing clear signs of leg weakness were withdrawn from the experiment before they reached the intended slaughter weight. On the other hand six animals were slaughtered and dissected in between dissection stages (marked with an asterix in Table 4.1), because signs of leg weakness also were impending in these pigs. They, however, could be used in the regression analyses but were excluded from the means presented in the Text-figures and the various tables where percentages were calculated for the different dissection stages.

The intended improvement in the incidence of leg weakness by lowering the daily gain by means of increase of the crude fibre content to more than 11% was ineffective. The addition of oat hulls to the diet resulted in a higher intake. The increase in general amounted to 20–35%, with a tendency of the castrates compensating most and the sows the least.

TABLE 4.1. Distribution of the dissected number of animals over the treatments and the various dissection stages.

Dissection stages	*Ad libitum* feeding level			Restricted feeding level		
	Sex			Sex		
	Boars	Castrates	Sows	Boars	Castrates	Sows
0	8		8			
I	6	6	6			
II	8	6	7	8	8	8
III	9	7	5	7	8	9
IV	4	7	7	6	9	7
V	6	7	7	8	8	8
Va*	2	1				
VI	4	5	7	7	8	6
VIa*		1			1	1
VII	4	4	6	8	6	4
Total	51	44	53	44	48	43

* see text

Some animals died. Only a few were autopsied, so in most cases the cause of death was not known. Some other animals could not be dissected for different reasons: one had serious damages because of tail biting, one died during transport, one was not released by the meat inspection service because of endocarditis, and (only) one boar was not released because of strong boar taint.

4.2. LIVE WEIGHT GROWTH

4.2.1. *Growth rate and feed conversion ratio related to feed intake*

The time course of growth in pigs is largely dependent on the pattern of feed intake. The differences in feeding level as imposed in this study were such that the restrictedly fed animals received, beyond the feed for maintenance, half of the feed for production of the *ad libitum* fed animals of the same weight and sex, as described in section 3.4.2. Following this system until about 150 kg live weight (i.e. around dissection stage V for the *ad libitum* level) it turned out that the actual intake for the restrictedly fed pigs in average had been about 55% of the feed for production.

Including the feed for maintenance the mean intake of the restrictedly fed pigs was about 70% of the *ad libitum* fed animals. It varied over the growing period between 66 and 74% in boars, between 65 and 79% in castrates and between 66 and 72% in sows. The deviations in the percentages mentioned may occur because the amount of feed to be supplied to pigs on the restricted level had to be computed according to the estimated weight gain in the subsequent fortnight period. The average feed intake between stages as well as the cumulative feed intake is given in Appendix 1 separately for the different treatment groups. The intake was calculated for the diminishing number of animals mentioned in Tables 4.2–4.4.

The mean *ad libitum* feed intake between each of the stages increased from 2.90 to about 4.95 kg/day in boars. Castrates and sows started with about 3.10 kg/day and ended up with about 4.15 kg/day. The sows reached this level in the intermediate stages, whereas the castrates had the highest intake (about 4.20 kg/day) between stages II and III. It then steadily decreased in the intermediate stages to below the ultimate level. The mean cumulative feed intake in boars steadily increased to 4.55 kg/day. The other sexes had a cumulative intake higher than boars unto stage V, but ended up with about 4.00 kg/day.

The mean intake at the restricted level between the stages increased from about 1.35 kg/day to about 2.85 kg/day up to stage V and ended up with about 3.00 kg/day. The cumulative feed intake steadily increased via about 2.20 kg/day at stage V to about 2.85 kg/day at the end.

The different feeding levels evoked different daily gains. The growth rates between the various stages as well as the cumulative growth rates are presented in Tables 4.2–4.4 for boars, castrates and sows respectively. The results were calculated for the diminishing number of animals. As long as animals were not slaughtered at a given stage or were not otherwise withdrawn from the experi-

TABLE 4.2. Growth rate between dissection stages, cumulative growth rate and feed conversion ratios of boars on the *ad libitum* and restricted feeding level.

Dis-section stage	*Ad libitum*						Restricted					
	Live weight	n	Growth between dissection stages	Cumulative growth from dissection stage I onwards	Corresponding feed conversion ratios		n	Growth between dissection stages	Cumulative growth from dissection stage I onwards	Corresponding feed conversion ratios		Live weight
	kg		g/day	g/day	kg feed/kg growth			g/day	g/day	kg feed/kg growth		kg
0												
		52	314				50	293				
I	26											25
		49	794		3.66		47	408		3.20		
II	66			794		3.66			408		3.20	45
		40	824		4.66		39	653		3.07		
III	98			806		4.08			526		3.09	72
		26	752		5.24		31	745		3.52		
IV	133			789		4.39			599		3.29	105
		18	662		5.95		24	716		3.90		
V	163			747		4.85			642		3.42	140
		10	490		8.44		15	509		5.57		
VI	208			659		5.85			604		3.97	187
		5	208		23.71		8	168		17.83		
VII	300			394		11.50			285		9.93	311

TABLE 4.3. Growth rate between dissection stages, cumulative growth rate and feed conversion ratios of castrates on the *ad libitum* and restricted feeding level.

Dissection stage	*Ad libitum*						Restricted					
	Live weight kg	n	Growth between dissection stages g/day	Cumulative growth from dissection stage I onwards g/day	Corresponding feed conversion ratios kg feed/kg growth		n	Growth between dissection stages g/day	Cumulative growth from dissection stage I onwards g/day	Corresponding feed conversion ratios kg feed/kg growth		Live weight kg
0												
		50	305				51	304				
I	26											25
		45	844		3.68		49	389		3.38		
II	67			844		3.68			389		3.38	45
		38	825		5.07		41	636		3.20		
III	100			840		4.26			501		3.29	71
		31	667		5.92		33	617		4.33		
IV	129			773		4.75			541		3.74	98
		23	601		6.01		24	606		4.63		
V	157			732		5.02			557		3.99	126
		11	342		9.42		16	467		5.81		
VI	186			592		6.09			532		4.49	170
		7	182		22.86		8	169		17.92		
VII	269			333		11.89			269		10.62	309

TABLE 4.4. Growth rate between dissection stages, cumulative growth rate and feed conversion ratios of sows on the *ad libitum* and restricted feeding level.

Dis-section stage	*Ad libitum*						Restricted					
	Live weight kg	n	Growth between dissection stages g/day	Cumulative growth from dissection stage I onwards g/day	Corresponding feed conversion ratios kg feed/kg growth		n	Growth between dissection stages g/day	Cumulative growth from dissection stage I onwards g/day	Corresponding feed conversion ratios kg feed/kg growth		Live weight kg
0												
		48	320				51	300				
I	27											25
		46	758		4.13		47	415		3.21		
II	65			758		4.13			415		3.21	46
		35	777		4.89		40	653		3.11		
III	94			769		4.53			522		3.17	72
		29	691		6.02		31	662		3.98		
IV	125			741		5.03			565		3.53	101
		21	588		6.99		23	595		4.70		
V	152			710		5.44			580		3.85	129
		15	386		9.40		12	411		6.99		
VI	186			596		6.36			515		4.68	166
		8	168		24.71		8	163		18.01		
VII	269			331		12.04			315		8.62	235

ment, their data were utilized in computing the growth rates and corresponding feed conversion ratios. The latter are also shown in the tables just mentioned.

At the *ad libitum* feeding level the growth rate between the various stages reached a maximum beteween stages II and III for boars and sows, while for castrates the maximum fell one stage earlier. With respect to the growth rate at the restricted feeding level the pattern described consistently shifted to a subsequent stage. The live weights reached at the restricted feeding level also were about one stage behind those at the *ad libitum* level. Unto stage V the pigs grew well, but then the growth swiftly diminished. The growth rates between the stages were echoed in the cumulative growth rates, more directly at the *ad libitum* level, while at the restricted level the carry-over proceeded slower, the maximum leaping to stage V with an additional step in the castrates.

The growth rates at the restricted level outpaced those of the *ad libitum* level between stages IV and V for all sexes. The cumulative growth rates at the restricted level did not overtake those at the *ad libitum* level.

The feed conversion ratios increased from stage to stage, very consistently for the sexes, especially in case of those corresponding to the cumulative growth rates. The only decrease in the feed conversion ratio is exhibited in the restricted feeding level between stages II and III (repeated cumulatively unto stage III), owing to the favourable jump in growth rate in this trajectory. In all cases the feed conversion ratios were lower in favour of the restricted level.

As to the differences between the sexes on different feeding levels the results of these live weight performances are in line (at least up to the commercial slaughter weights) with our former experiments in investigating the effect of castration (WALSTRA, 1969). Later on the effects were comprehensively discussed and compared with the existing literature in the light of feed intake and compositional differences among the sexes (WALSTRA et al., 1977). It was then stated that an interaction is apparent between sex and feeding method. Castrates grow faster at an *ad libitum* level by virtue of their higher intake, while boars grow faster at a restricted level owing to a lower deposition of fat. Sows will rank in between. Furthermore, the feed conversion ratio is always more favourable in boars than in castrates, while again sows hold a position in between. In the present study these findings were confirmed largely including the faster growth of castrates as compared to boars especially in the first period. At the *ad libitum* level, however, the growth of sows lagged behind and as a consequence the feed conversion ratio was more unfavourable. The effect may partly be explained by a somewhat lower feed intake.

After the stage of commercial slaughter weight no information could be found with respect to differences in growth rate and feed conversion in relation to feeding level. As can be seen from the Tables 4.2–4.4 the growth rate of boars at the *ad libitum* feeding level surpassed that of castrates. This has to be ascribed to a combined effect of a higher intake and a more favourable lean meat deposition in boars, which will be shown in section 4.4. Because of a higher intake than in castrates, the sows grew faster in the last stages resulting in the same cumulative growth rate up to maturity as in castrates. At the restricted feeding level the boars easily maintained their leading position. The sows were not able to keep their intermediate position between stages V and VI, in spite of a higher feed intake than castrates in the later stages.

With respect to the feed conversion ratio the boars had the most favourable feed conversion practically in all cases. That of the sows mostly held a position in between, at least at the restricted feeding level. But because of the lagging behind of the growth rates at the *ad libitum* level the feed conversion ratios there mostly remained more unfavourable than in the other sexes.

The variation coefficients in many cases varied between 10 and 20%. In general they were lower for the cumulative growth rates and their corresponding feed conversion ratios than for rates of growth and feed conversion ratios between the various stages. Mainly between these stages in a number of cases coefficients higher than 20% could be calculated. Except in some single cases, only the variation coefficients for the cumulative feed conversion ratios in the restricted fed sows were (all but one) below 10%. Differences between feeding levels were hardly further discernible.

4.2.2. *Growth curves*

Since the main objective of this investigation was to describe relative growth, comprehensive descriptions of live weight growth as a function of age were considered out of the scope of this study. No further attempts therefore were made to examine whether a given derivative of the Richards function (or any other equation or model) fitted the data to a satisfactory extent, nor to compare the various equations in order to denote the one that fitted best.

Clinging to TAYLOR (1978) – 'even in the age of computers, there is nothing unsophisticated about a graph' – only a graphical method was chosen to elucidate the results as described in the preceding section. Such a graph may give a good picture of the course of growth if a reasonable number of animals is involved and measurements are regularly taken without too great a distance from each other. The sigmoid pattern for example is also neatly depicted in those graphs.

The weight-age relationships are presented in Figs. 4.1abc and 4.2ab. Fig. 4.1abc shows the differences brought about by feeding level in boars, castrates and sows respectively, whereas in Fig. 4.2ab the differences among sexes are illustrated for the *ad libitum* and restricted feeding level separately respectively.

The figures beside the curves indicate the number of animals that were still present at that given instant and thus also are related to the points representing the weights of the fortnight periods in the preceding trajectory. At each dissection stage, and likewise after stage VI at any time when animals were slaughtered for dissection or otherwise were withdrawn form the experiment, the standard deviations for weight as well as age were designated.

The standard deviations for age fluctuated around a week or a little more. Up till stage II the variation coefficients lay below 10%; after that below 5% ever decreasing unto maturity. The variation coefficients for weight amounted to over 20% before stage I; after that they (with some exceptions) at first lay

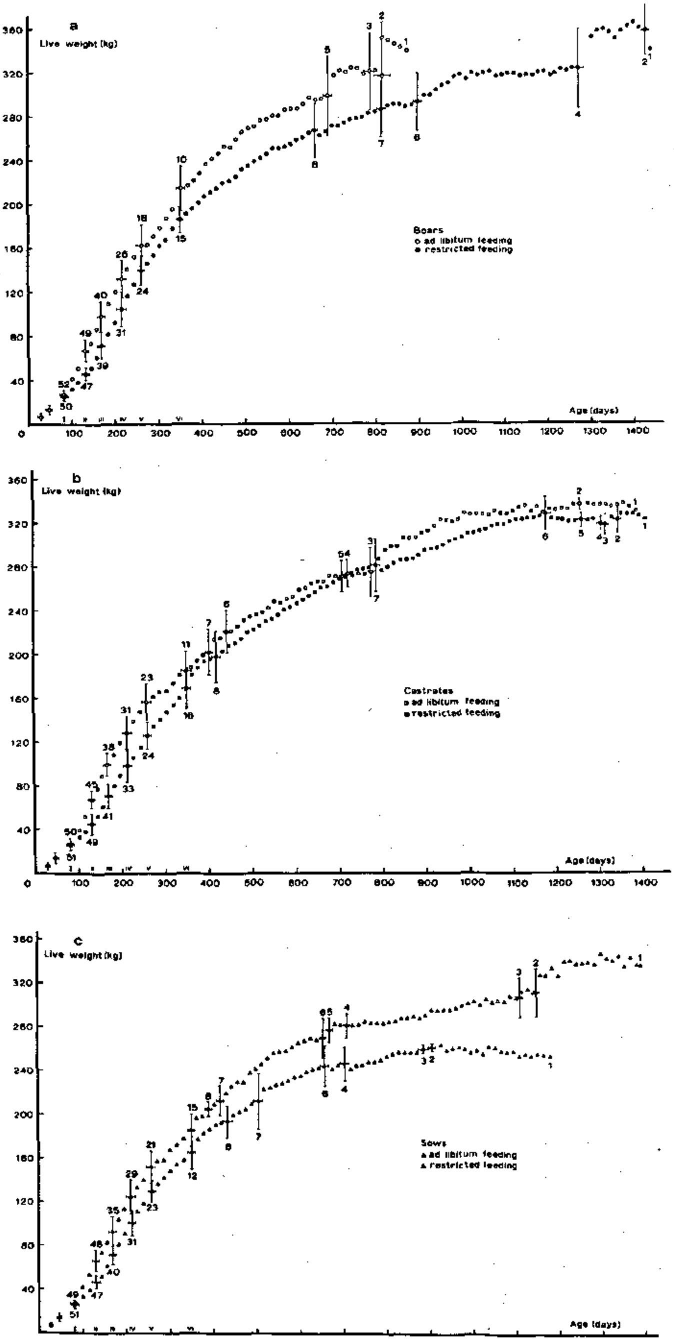

FIG. 4.1abc. Live weight growth of boars (a), castrates (b) and sows (c), each compared at *ad libitum* and restricted feeding level with standard deviations for age and weight at the various dissection stages (see text for explanation of the number of animals).

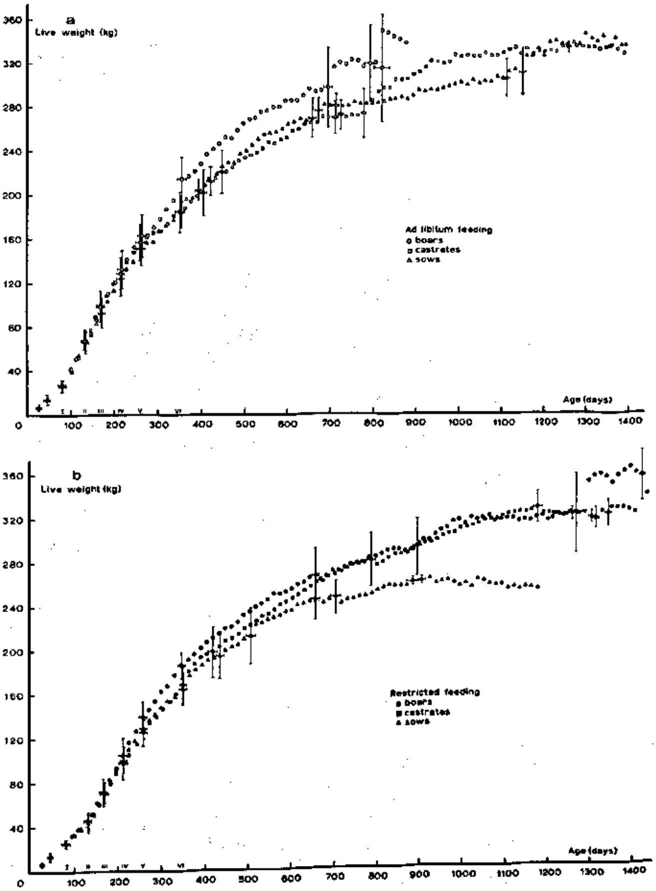

FIG. 4.2ab. Live weight growth of boars, castrates and sows compared at *ad libitum* (a) and restricted feeding level (b) with standard deviations for age and weight at the various dissection stages.

between 10 and 15% and later on below 10%. In Appendix 2 the weights and ages and the standard deviations are given for the relevant stages from birth to 'maturity'.

Immediately after the different feeding levels had been exposed, the difference in growth curves became clear for all three sexes (Fig. 4.1abc). The effect of overtaking growth rates starting between stages IV and V is reflected in the curves between stages V and VI, most pronounced in castrates. Since after 150 kg live weight the feed supplied to the restrictedly fed animals was no longer related to the *ad libitum* fed animals, the difference between the curves thus is largely dependent on the feed intake of the *ad libitum* fed animals. The difference between the curves within the sexes up to maturity was smaller in castrates than in the other sexes.

Except for a short period in castrates (during a few weeks the intake of the *ad libitum* fed castrates had decreased considerably), the *ad libitum* fed animals

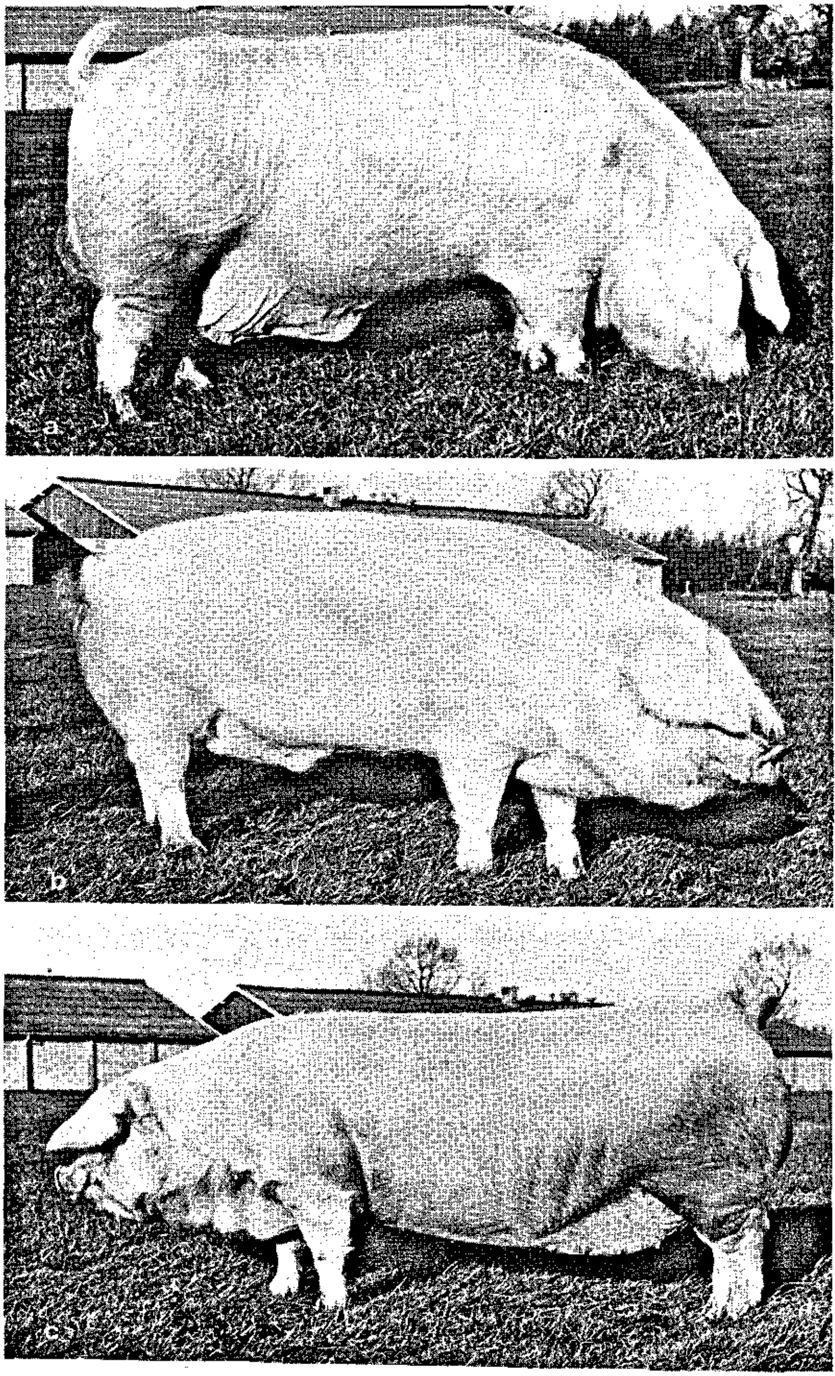

FIG. 4.3abc. Examples of an almost mature boar (a) (0X517–362 kg), castrate (b) (0X681–321 kg) and sow (c) (0X588–328 kg).

TABLE 4.5. Live weight and age with their standard deviations from the animals dissected at the different stages.

Dissection stage and Feeding level*	Boars					Castrates					Sows				
	n	weight kg	s.d.	age days	s.d.	n	weight kg	s.d.	age days	s.d.	n	weight kg	s.d.	age days	s.d.
0	8	1.4	0.2								8	1.4	0.2		
I	6	25.8	5.0	84.7	8.0	6	25.6	4.5	81.3	6.4	6	26.6	4.4	86.7	6.8
II A	8	66.6	8.7	130.6	5.7	6	66.0	4.5	134.2	6.2	7	69.0	12.5	135.9	5.8
R	8	43.1	4.5	129.0	9.5	8	46.1	9.2	129.9	9.0	8	46.6	10.5	129.9	7.7
III A	9	97.2	13.1	165.9	7.5	7	102.9	9.2	168.7	5.4	5	87.8	12.2	172.2	9.5
R	7	75.9	14.3	170.3	7.5	8	71.4	13.5	174.4	12.7	9	74.1	8.6	172.4	9.0
IV A	4	122.9	22.8	215.8	13.7	7	126.3	17.7	212.9	11.7	7	124.4	27.1	211.7	10.2
R	6	100.1	14.9	215.2	9.7	9	99.9	16.5	215.4	9.9	7	98.3	11.1	211.6	7.7
V A	6	164.0	24.7	260.8	6.5	7	158.4	17.0	257.4	8.2	7	147.4	23.9	256.1	8.8
R	8	136.1	21.4	260.1	8.6	8	122.1	11.0	258.1	9.4	8	126.9	8.0	257.5	6.5
VI A	4	202.5	30.0	351.8	13.6	5	189.8	17.4	353.4	13.1	7	177.1	14.6	348.6	8.4
R	7	185.4	13.8	348.3	7.0	8	161.3	12.1	351.5	7.1	6	157.3	10.5	349.3	5.1
VII A	4	296.5	46.2	799.3	81.4	4	295.8	47.6	1046.3	332.4	6	295.8	31.3	945.0	310.8
R	8	308.0	33.8	1089.0	302.8	6	320.5	10.5	1207.7	212.1	4	252.5	15.8	907.5	214.8

* A = *ad libitum* R = restricted

always had a higher weight at a given age. The curves in boars for both levels seem to flatten at about 320 kg live weight, but single boars from both levels reached a final live weight of 350–360 kg. The final weights in castrates were reached at 320–335 kg. So in these 'male' animals those on the restricted feeding level ultimately attained the same end weights. In sows, however, the restrictedly fed animals were not capable of attaining asymptotic weights higher than about 260 kg. The *ad libitum* fed sows seem to approximate end weights of 320 kg. One animal ultimately reached 340 kg live weight. The highest weight established in this study was 385 kg in a restrictedly fed boar. Examples of an almost mature boar, castrate and sow are exhibited in Fig. 4.3abc respectively.

The differences between the sexes at the *ad libitum* feeding level (Fig. 4.2a) show that boars reached their final live weight first; but ultimately the remaining animals of all three sexes attained the same final weight. At the restricted level at first the boars also lead, but in the self-inhibiting phase, they hardly are distinguishable from castrates, except for the very last remaining animals. The curve of the restrictedly fed sows already bends much earlier to an asymptotic weight.

Animals in this study were considered mature when after a number of weighings no increase in weight could be measured any more. This criterion may not be exact, because the actual final weight might have been higher when animals would have had the opportunity to grow over a still longer period. Furthermore, only a few animals were involved in the very last phase. On the other hand there is a paucity of information about mature weights in literature. As cited by THOMAS (1970), German Landrace boars and sows reached 360 and 290 kg respectively. CÖP (1971) also cited weights for boars and sows somewhat higher than those in the present study. It must be taken into account that in these cases instead of animals that were fattened, breeding sows and A.I.-boars were involved. The latter reached their highest weights at about 4 years of age, so in reasonable agreement with those in this study.

4.2.3. *Weight and age at the different dissection stages*

The number of animals involved in the dissections and how the animals were distributed over the different stages was already listed in Table 4.1. The means for weight and age for these pigs are given in Table 4.5. The results do not differ much from those to be seen in Appendix 1 for the diminishing number of animals.

The standard deviation for age is around a week or a little more. The variation coefficient in average amounts to 4.6% up to and including stage VI. At the mature stage the variation coefficient is much higher; raising to 33%. The variation coefficient for weight in average is about 13.4% including the mature stage.

As stated earlier six animals referred to as belonging to stage Va and VI a (see Table 4.1) were dissected in between. Their weight and age at slaughter were as follows:

stage Va

ad libitum fed boar	158 kg live weight and 322 days of age
ad libitum fed boar	177 kg live weight and 325 days of age
ad libitum fed castrate	154 kg live weight and 314 days of age

stage VIa

ad libitum fed castrate	258 kg live weight and 736 days of age
restrictedly fed castrate	185 kg live weight and 415 days of age
restrictedly fed sow	183 kg live weight and 436 days of age

The data of these six animals for the various variables were utilized in the regression analyses if required. Data of these animals were excluded from computations of the means at the different dissection stages which were used in tables and Text-figures in following sections.

4.3. CARCASS GROWTH

4.3.1. *General*

The two carcass halves were dissected, the left half by almost complete anatomical dissection and the right half into joints by the IVO-standard method. The objective was to examine whether and to what extend the actual carcass composition may be estimated from a simpler dissection method. Since a standard method, however, is not a universal method as is the anatomical dissection, and therefore is of more local importance, the results of the standard method are not dealt with here, but will be reported separately later on.

In order to avoid the term 'significantly different' as often as possible in this chapter, the use of it will be limited. When the results do indicate significant differences, terms like 'a difference existed' or 'a differential pattern was found' etc. will be used to describe the effects.

Furthermore, tissues or parts may grow linearly relative to a given entity or may have a linear growth pattern. The ever-recurring term 'linear' means that the relationship between two variables on the double logarithmic scale may be described by a straight line, so in the cases where no significant high power terms were discernible.

4.3.2. *Carcass growth and dressing percentage*

The calculation of percentages and regressions of the main components of the body have been based on the total side weights. The increase in weight of the half carcass for the dissection stages is given in Table 4.6. The average variation coefficient amounted to 14.7%. It can be seen that for the dissection stages II–VI the restrictedly fed groups follow the *ad libitum* fed groups with a delay of one stage.

From the regressions it appeared that the carcass side weight grew linearly relative to live weight. Since no differences in slope for the influence of feeding

TABLE 4.6. The carcass side weight of the treatment groups for the different dissection stages (in kg).

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	0.527	8.42	23.72	36.17	47.49	62.38	81.68	118.99
Castrates		8.42	24.70	38.52	49.88	63.41	77.12	121.56
Sows	0.522	8.99	24.84	34.41	48.57	57.89	71.88	122.83
Restricted								
Boars			14.47	26.19	36.35	49.03	70.62	124.46
Castrates			15.94	24.86	36.72	45.84	63.34	133.64
Sows			16.01	24.44	36.48	47.27	61.45	102.11

level or sex were discernible, the average pooled growth coefficient can be taken, being 1.10 (class H). This is near to the value given by SEEBECK and TULLOH (1966) calculated from various other investigations on sheep that also included the heavier weights. The data given by DAVIES (1974a) in pigs are lower (about 1.00), but they were calculated for quite a different trajectory with the lower weights. Those of ROBELIN et al. (1974, 1977) in cattle lay in between, also for a trajectory in between.

Differences in constant terms of the regression were clearly in favour of the *ad libitum* fed animals in all three sexes. The sexes also differed, viz. the boars from castrates and sows at *ad libitum* feeding and the boars from castrates at the restricted feeding level.

The linear growth pattern found would be transformed into a curvilinear one if the new-born piglets were included. The carcass weight at birth was relatively higher than had to be predicted from the regression over the trajectory I–VII in both sexes. This can also be read in Table 4.7 where the dressing percentages are given for the different dissection stages. The dressing percentage at birth did not return until the animals had reached a live weight of about 100–125 kg.

TABLE 4.7. The dressing percentage of the treatment groups for the different dissection stages.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	76.9	67.8	72.8	75.5	78.1	77.8	80.7	81.0
Castrates		67.8	76.2	76.1	80.2	80.6	82.2	82.9
Sows	76.3	70.6	73.7	80.5	79.2	79.3	81.8	83.5
Restricted								
Boars			68.9	71.5	74.0	73.8	77.2	81.3
Castrates			70.2	71.1	74.6	76.5	80.0	84.4
Sows			70.0	67.6	75.7	76.5	79.3	81.6

The dressing percentages (with an average variation coefficient of 3.5%) in general are higher for the fatter animals. It means a higher dressing percentage for the *ad libitum* groups, for castrates and to a much lesser extent for sows. This may also be found in castration experiments for animals slaughtered at the commercial weights (WALSTRA et al., 1977). The increase in the dressing percentage (excluding stage 0) during growth was also found by others as described in section 2.4.2.1 and in the experiments of RICHMOND and BERG (1971a). The increase of 5% mentioned there for the trajectory 70/80 to 120 kg is in agreement with that in Table 4.7 for the dissection stages II–IV on the *ad libitum* and stages III–V on the restricted feeding level. In the present study the increase is more than 10% for the whole trajectory.

4.3.3. *Carcass length*

The differences in length of the carcass of the treatment groups for the consecutive dissection stages is given in Table 4.8. The average variation coefficient was 21.8%. At maturity the male animals seemed to be longer than the female ones. Especially between the first stages the increase in length was more than in later stages taking into account the interval between the stages. The regressions showed that the new-born stage did deviate from the others in that new-born piglets were relatively shorter.

An illustration is also presented in Fig. 4.4 where carcass length is related to carcass side weight as well as to side muscle + bone weight. Under the assumption of a linear relationship no differences in slope were found based on the muscle + bone weight. A *b*-value therefore of −0.01 (class A) was computed. Based on carcass weight the only difference was between boars and sows at the *ad libitum* feeding level, the *b*-values being −0.04 and −0.06 respectively. The restrictedly fed groups and also the castrates had a common *b*-value of −0.06 (class A^-).

Several differences, however, in constant terms of the regressions were discernible. Castrates and sows were longer at the *ad libitum* than at the restricted feeding level when based on muscle + bone weight, but sows were shorter based

TABLE 4.8. The carcass length of the treatment groups for the different dissection stages (in cm).

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	18.0	54.1	75.1	83.7	91.1	99.1	106.9	115.4
Castrates		54.8	73.8	84.1	90.8	96.8	103.7	117.6
Sows	18.5	56.4	74.0	82.3	91.6	95.4	100.9	112.8
Restricted								
Boars			65.5	75.9	85.8	95.1	103.1	117.0
Castrates			66.3	75.3	83.5	88.6	97.9	116.3
Sows			67.1	77.3	84.4	91.2	97.4	110.6

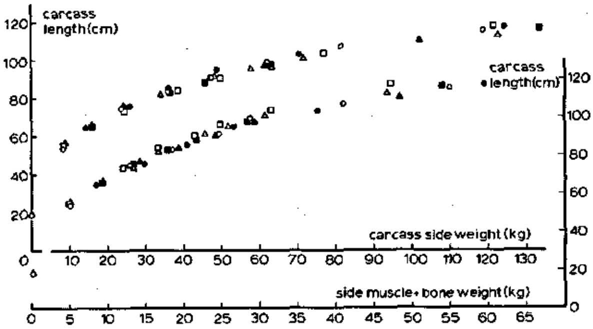

FIG. 4.4. Carcass length in relation to carcass weight and muscle + bone weight for boars (○), castrates (□) and sows (△), both on *ad libitum* (open marks) and restricted feeding level (solid marks).

on carcass weight. The choice of the independent variate also influenced the sex differences. Boars were longer than castrates (at both feeding levels) based on carcass weight, but they were shorter at a given muscle + bone weight. Based on the latter weight also sows were shorter than castrates at the *ad libitum* feeding level. Furthermore, castrates were shorter than sows at the restricted feeding level when based on carcass weight.

The growth pattern A^-, at least based on carcass weight, means that carcass length lags behind ever more with increasing carcass weight. Since the actual growth pattern was not linear this is augmented, because when based on carcass weight at least for boars a cubic term was established also with a negative coefficient. And when based on muscle + bone weight boars as well as castrates had a cubic component. The test results then show that at both independent variates the shapes between *ad libitum* and restricted feeding level differed in boars. In addition a difference in shape between *ad libitum* fed boars and castrates and between restrictedly fed boars and sows was established based on carcass weight. No further differences in constant terms than those already mentioned above appeared.

4.3.4. *Other carcass measurements*

The results for leg length and inner thorax depth are tabulated in Appendix 3 and 4 respectively.

The development of the leg related to carcass side weight showed a linear pattern. The new-born animals, however, did deviate negatively. The common *b*-value amounted to −0.02 (class A). With regard to the constant terms it appeared that the restrictedly fed animals had a greater leg length than the *ad libitum* fed ones. Furthermore, the boars had a longer leg than castrates and sows at the *ad libitum* feeding level.

The leg length was also related to carcass length. Then a common *b*-value (0.99, class A) could be established as well. The linear pattern did not hold when the new-born piglets were included. They had a relatively longer leg length. Except for the difference between boars and sows, similar differences in constant terms of the regressions were recorded.

The inner thorax depth 1 (measured from the 5th thoracic vertebra horizontally to the sternum) grew linearly with the increase in carcass weight. The new-born stage was in accordance with this pattern. No differences in slope could be assessed, so the common *b*-value may be given, being -0.03 in class A^-. With respect to the constant terms it was shown that boars and sows restrictedly fed had a greater depth than those fed *ad libitum*. The boars were deeper than castrates and sows at the *ad libitum* feeding level and boars and sows were deeper than castrates at the restricted feeding level.

A quadratic term was needed to describe the growth of inner thorax depth 2 (measured to the juncture of the 5th rib at the sternum) for the *ad libitum* fed animals. A tendency towards this pattern already existed for depth 1. The animals would have had a common growth coefficient of -0.03 (class A^-) when they would have grown linearly. The pattern found resulted in a different shape in boars and castrates between the feeding levels. In sows the feeding levels differed for the constant terms of the regression. The differences between the sexes were the same as for depth 1.

The thorax depth was also related to carcass length. Both for depth 1 and 2 a quadratic pattern was established for the *ad libitum* fed animals, and again for sows in the case of depth 2. The new-born piglets were less deep than was indicated by this pattern. A common *b*-value for the animals in case of a linear pattern amounted to 1.06 and 1.05 (both class A^+) for depth 1 and 2 respectively. So the animals' bodies deepen in relation to their carcass length during growth. Differences in shape could not be ascertained, but for the constant terms the feeding levels differed for castrates and sows in case of depth 2 and for all three sexes in case of depth 1. No differences between sexes were found in this respect.

Results of measurements of backfat thickness will be dealt with when describing the growth of the fatty tissue components.

4.4. GROSS CARCASS COMPOSITION

4.4.1. *The main carcass components as percentages of carcass weight*

The weight of the main components of the body have been expressed as percentages of carcass weight. The partition into bone, muscle, fat, skin and offal is illustrated in Fig. 4.5abc. The average percentages of the components at the various dissection stages on which the figure was based to build up the carcass to 100% are given in Tables 4.9–4.11. The average variation coefficients for bone, muscle, fat, skin and offal were 6.4, 7.8, 12.7, 11.2 and 9.9% respectively.

From the figure and the tables it can be seen that the general trend is a decrease in the percentages of bone and muscle, and an increase in the percentage of fat. This pattern is generally found as was described in several sections of chapter 2. Furthermore, the percentages of offal and of skin decrease; the latter, however, increased in boars.

It is also easily seen that the major effect of feeding level on the carcass composition is on the amount of fat which is compensated for most in the

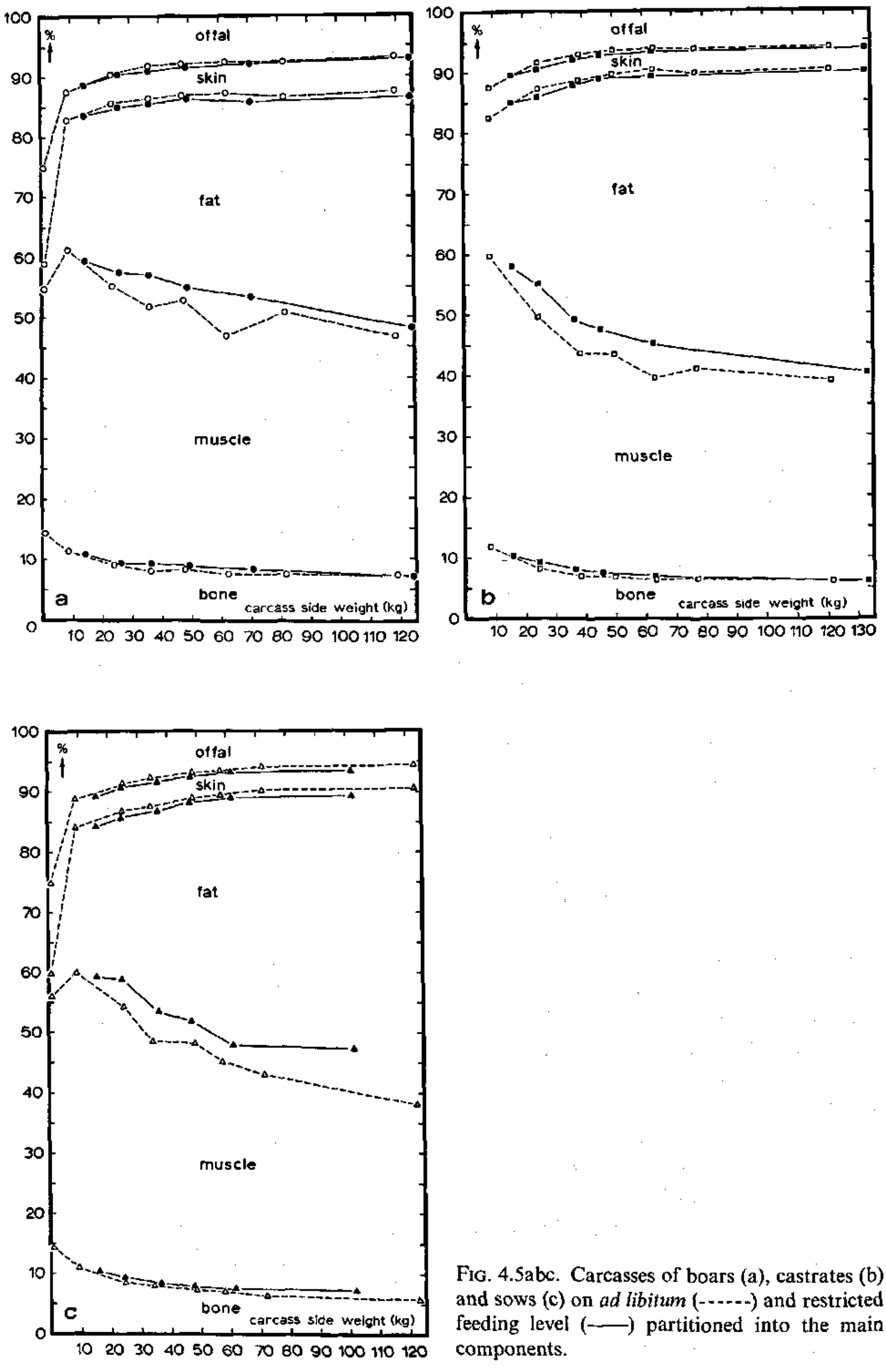

FIG. 4.5abc. Carcasses of boars (a), castrates (b) and sows (c) on *ad libitum* (------) and restricted feeding level (——) partitioned into the main components.

TABLE 4.9. The main carcass components of boars at the *ad libitum* and restricted feeding level for the different dissection stages expressed as a percentage of carcass weight.

Feeding level and Sex	Dissection stage							
	0*	I	II	III	IV	V	VI	VII
Ad libitum								
Offal	24.81	12.37	9.32	7.98	7.81	7.46	7.56	6.77
Skin	16.09	4.84	4.96	5.60	5.27	5.26	5.76	5.72
Fat	4.18	21.49	30.29	34.50	34.03	40.27	35.81	40.59
Muscle	40.50	49.85	46.23	43.77	44.55	39.41	43.19	39.48
Bone	14.42	11.46	9.20	8.15	8.34	7.60	7.69	7.43
Restricted								
Offal			11.20	9.33	8.84	8.30	7.77	7.00
Skin			5.02	5.58	5.48	5.33	6.38	6.52
Fat			24.34	27.56	28.50	31.37	32.23	38.23
Muscle			48.51	48.15	47.72	45.97	45.15	41.16
Bone			10.93	9.38	9.46	9.03	8.47	7.10

* Subcutaneous fat is included in the skin.

TABLE 4.10. The main carcass components of castrates at the *ad libitum* and restricted feeding level for the different dissection stages expressed as a percentage of carcass weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Offal		12.50	8.41	7.08	6.45	6.17	6.27	5.93
Skin		4.99	4.30	4.25	4.02	3.46	4.01	3.80
Fat		22.81	37.69	44.97	46.13	50.80	48.53	51.16
Muscle		47.86	41.32	36.56	36.54	33.20	34.53	32.91
Bone		11.83	8.28	7.15	6.86	6.36	6.66	6.21
Restricted								
Offal			10.44	9.45	7.91	7.26	6.61	6.24
Skin			4.60	4.73	4.29	3.87	4.13	3.78
Fat			26.91	30.75	38.61	41.26	44.14	49.58
Muscle			47.75	45.73	41.01	40.03	38.15	34.24
Bone			10.30	9.34	8.19	7.59	6.97	6.16

amount of muscle. Remarkable was the high fat content of the *ad libitum* fed sows upon reaching the mature stage.

The percentage of skin in the new-born piglets is not justifiable because the subcutaneous fat was not separated from the skin. The positive deviation in skin and the negative deviation in fat from the regression line in the new-born piglets therefore may be (partly) due to this. A negative deviation, however, did occur in bone, while in muscle only the sow piglets had less muscle than predicted from the regression line.

TABLE 4.11. The main carcass components of sows at the *ad libitum* and restricted feeding level for the different dissection stages expressed as a percentage of carcass weight.

Feeding level and Sex	Dissection stage							
	0*	I	II	III	IV	V	VI	VII
Ad libitum								
Offal	25.18	11.18	8.68	7.73	6.89	6.48	5.82	5.41
Skin	15.01	4.69	4.51	4.72	4.25	3.99	3.91	3.96
Fat	3.78	24.11	32.46	38.89	40.65	44.26	47.21	52.47
Muscle	41.81	49.10	45.78	40.65	40.92	38.12	36.68	32.40
Bone	14.24	10.91	8.57	8.02	7.29	7.15	6.38	5.76
Restricted								
Offal			10.73	9.27	8.38	7.44	6.75	6.52
Skin			5.00	5.01	4.84	4.29	4.29	4.16
Fat			24.92	26.83	33.23	36.45	40.97	41.97
Muscle			48.91	49.43	45.05	43.94	40.44	40.09
Bone			10.45	9.45	8.51	7.88	7.55	7.26

* Subcutaneous fat is included in the skin.

A likely explanation for the *ad libitum* fed boars standing out with respect to the percentage of muscle at dissection stage V could not be found. The deviation was mainly due to one particular animal. A closer examination revealed that the deviation only returned in the proximal muscle group of the thigh. Since in the other half carcass (standard dissection method) the ham percentage within the total lean meat was found to be low as well in this animal in comparison to members of its group, we had to accept that on occasion one may discover such animals. Excluding, however, the animal from the computations learned that the group as such still (to a much lesser extent) seemed to stand out. Moreover, since there were no irregularities (e.g. illness) in its history the animal was maintained.

The development of the main body constituents is more clearly shown by the regressions. In none of the five components differences in slope, or in shape in the quadratic case, between the feeding levels could be ascertained, not even the diverging of the *ad libitum* fed sows in fat growth (see Fig. 4.6c). The impact of feeding level, however, was obvious in the constant terms for all five components and in all three sexes, except for skin in castrates. During carcass growth *ad libitum* feeding renders more fat, but less muscle, bone, skin and offal. It is illustrated in Fig. 4.6abc for the major tissues.

A common growth coefficient for each of the sexes, at least as far as linear growth was involved, thus was allowed. In Table 4.12 the growth coefficients and the growth pattern is given. The *b*-values in italics indicate those cases in which a significant quadratic term was established. Whether a positive or negative coefficient of the quadratic term for the concerning sex group was found is symbolized in the last column of the table.

Bone and offal (of which the major part is bone) are the slowest growing tissues, muscle tissue grows faster than bone, but still slower than the carcass

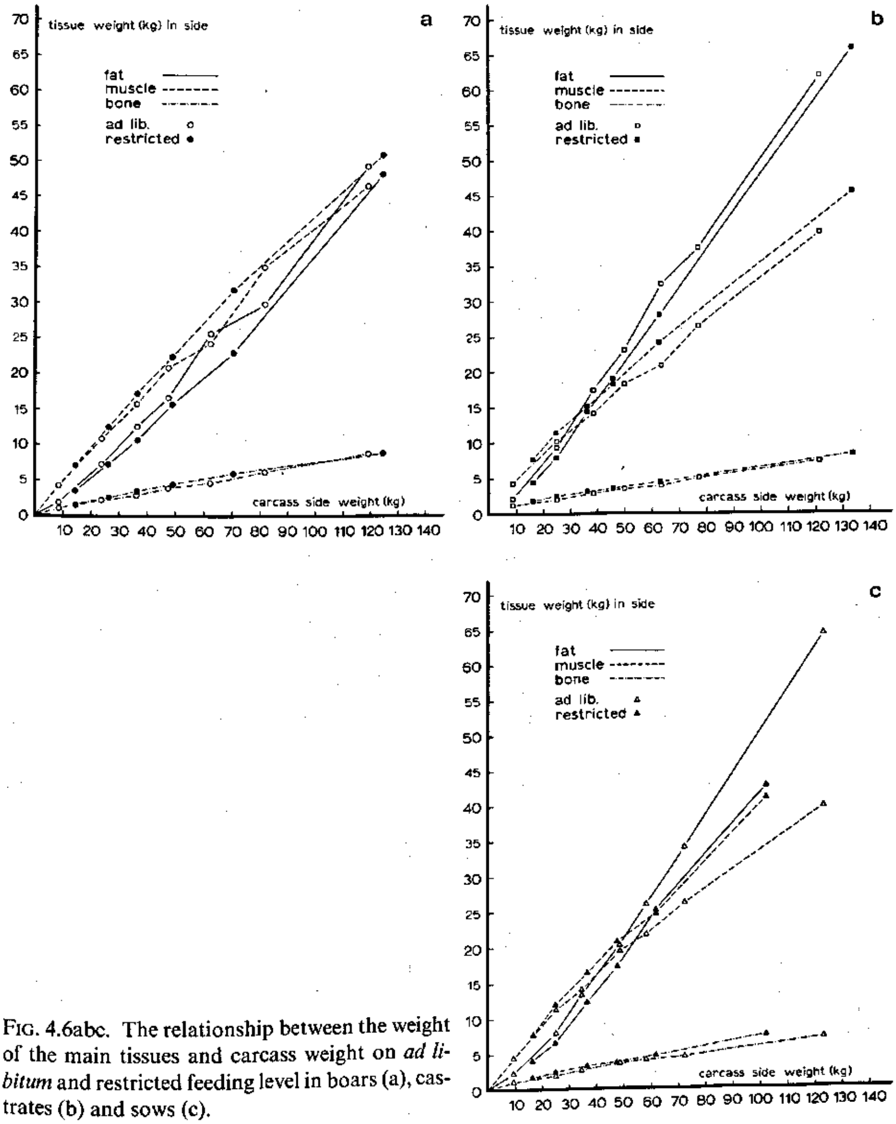

FIG. 4.6abc. The relationship between the weight of the main tissues and carcass weight on *ad libitum* and restricted feeding level in boars (a), castrates (b) and sows (c).

itself. Fat is the fastest growing tissue, much faster than the carcass. The skin grows at about the same rate as muscle, but not in boars where it has a high growth pattern.

It is clear from Table 4.12 that in linear growth boars behave different from both other sexes. The positive coefficients of the quadratic terms in castrates for offal and bone mean a tendency upwards to the growth of bone and offal in boars in the later stages. On the other hand the negative quadratic term in boars implies a tendency in muscle growth downwards to that of the other sexes in the later

TABLE 4.12. The classification of the growth pattern and the growth coefficients of the main carcass components in the three sexes.

Component	Linear growth									Quadratic growth
	boars			castrates			sows			
	b	s_b	class	b	s_b	class	b	s_b	class	
Offal	0.77	0.01	$L^=$	*0.71*	0.01	$L^=$	0.70	0.01	$L^=$	⚦ +
Skin	1.09	0.02	H	0.89	0.02	L	0.90	0.02	L	
Fat	1.24	0.02	H*	*1.32*	0.02	H*	1.33	0.02	H*	⚦ –
Muscle	*0.91*	0.01	L	0.85	0.01	L^-	0.85	0.01	L^-	♂ –
Bone	*0.81*	*0.01*	$L^=$	*0.75*	*0.01*	$L^=$	*0.76*	*0.01*	$L^=$	⚦ +

stages. And the negative quadratic term in castrates indicates that fat growth in these animals diverges less from boars than supposed by linear growth.

In Fig. 4.7ab the differences between sexes are presented for the three major tissues. At the *ad libitum* feeding level the differences in slope between boars and the other sexes were found to be significant for the three major tissues as well as for skin and offal, except for the difference between boars and castrates in fat. The difference, however, did exist when tested quadraticly, as it should be done as soon as a quadratic term is involved. It then also appeared that castrates and sows differed in shape, except in muscle. With respect to the constant terms further differences were found between castrates and sows in skin, muscle and fat.

At the restricted feeding level (Fig. 4.7b) differences in slope were found

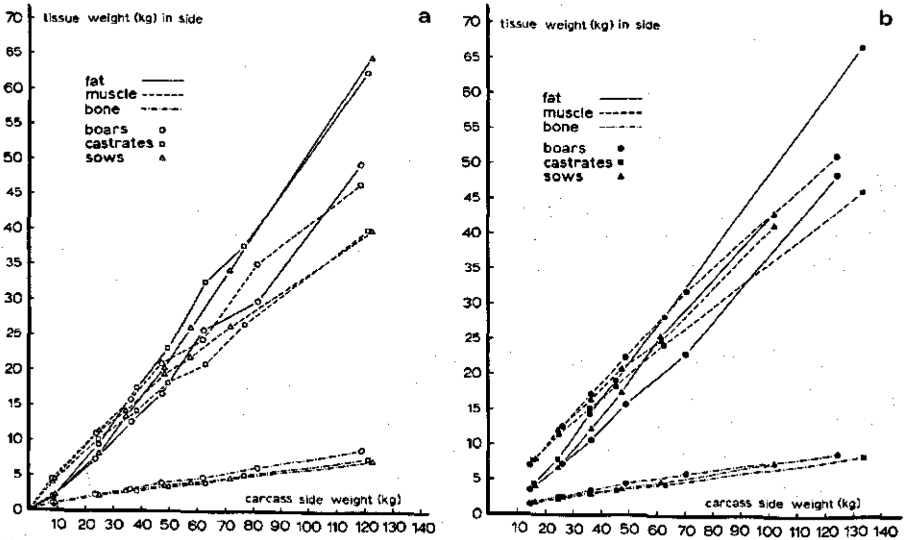

FIG 4.7ab. The relationship between the weight of the main tissues and carcass weight in boars, castrates and sows on *ad libitum* (a) and restricted feeding level (b).

between boars and both other sexes in skin and fat, between boars and castrates in bone and muscle, and between boars and sows in offal. Where no differences in slope could be established all other differences in constant terms of the regressions were significant, except for the difference between castrates and sows in offal. When tested quadraticly the results did not change.

4.4.2. *The main carcass components as percentages of other entities*

The weights of the three major tissues were related to muscle + bone weight as the independent variate as well. In bone and muscle most differences disappeared. In bone no differences in slope and shape were established any more, while for the constant terms only the difference between boars and sows remained on both feeding levels, but a difference between castrates and sows arose at the *ad libitum* feeding level.

Common *b*-values of 0.90 (L) and 1.02 (A) were now calculated for bone and muscle respectively. For the latter tissue this only holds true as far as linear growth is considered. A quadratic term was still needed, but for castrates instead of boars. This only results in a difference in shape between castrates and sows at the *ad libitum* feeding level.

It further appeared that only the boar piglets of stage 0 deviated from the regression line in bone. Beside the sow piglets now also the boar piglets were not in line with the regression in muscle; they had less muscle than predicted from it.

In fat the most important change was towards a total linear pattern, including the new-born sows. The boar piglets still had less fat than estimated from the regression line. Growth coefficients of 1.35 for boars and 1.55 for both other sexes were achieved. Furthermore only the tendency (preceding section) to the difference in slope between boars and castrates at the *ad libitum* feeding level became significant.

When offal was regressed on muscle + bone weight a fully concave quadratic pattern was discernible. All sex differences in slope disappeared, while the differences in constant terms revealed a lower percentage of offal in sows with respect to the other sexes.

Finally the muscle + bone weight was regressed on carcass weight. All significant differences were the same as when muscle alone was the dependent variate. The growth pattern, however, changed in that the quadratic term disappeared, but the *b*-values only were 0.02 lower in all three sexes. New-born boars as well as the sow piglets had relatively less muscle + bone than was predicted from the regression line.

Exclusion of the amount of fat from the independent variate shifted the growth coefficients for muscle and bone towards average. The increase of the *b*-value in this study was somewhat higher in bone and about equal in muscle as compared to the value reported by COLE et al. (1976). In the only other example in the literature reviewed (DAVIES, 1974a) no increase in *b*-value was found.

The height of the *b*-values mentioned in this and in the preceding section was not always in accordance with that in the literature. The trajectory, however, over which the regressions were computed has to be taken into account.

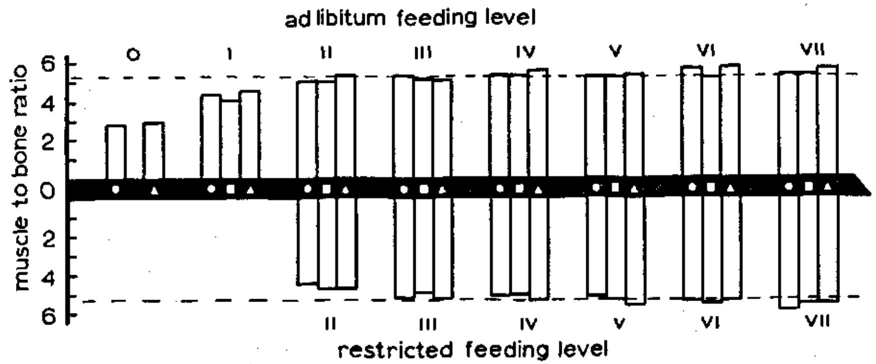

FIG. 4.8. Muscle to bone ratio at the different dissection stages (roman figures) for boars (○), castrates (□) and sows (△) on *ad libitum* and restricted feeding level; (------) weighted average 5.26 for stages II-VII.

4.4.3. *The muscle to bone ratio*

The decrease in the percentage of muscle and bone of the carcass does not proceed at the same rate as could already be concluded from the different *b*-values found for these tissues. The ratio of muscle to bone therefore increases, especially during the first stages. It appears from Fig. 4.8 that after stage III there only was a slight increase. The corresponding figures are given in Table 4.13. The average variation coefficient was 8.4%. The differences between the feeding levels are not very consistent as can be seen when the length of the bars is compared with the striped line that represents the weighted average (= 5.26) for stages II–VII. This can also be seen in Fig. 4.9abc and it resulted from the regressions of muscle to bone ratio on carcass weight, in that slope and shape as well as constant terms did not differ in all three sexes.

With respect to the growth pattern a quadratic pattern was established in castrates. The linear growth in boars and sows also disappears, when the newborn stage is taken into account. At birth the muscle to bone ratio is relatively

TABLE 4.13. The muscle to bone ratio of the treatment groups for the different dissection stages.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	2.81	4.36	5.06	5.37	5.36	5.23	5.65	5.36
Castrates		4.07	5.00	5.13	5.33	5.23	5.20	5.37
Sows	2.94	4.54	5.35	5.08	5.61	5.38	5.74	5.66
Restricted								
Boars			4.45	5.17	5.07	5.12	5.36	5.86
Castrates			4.72	4.92	5.01	5.28	5.50	5.57
Sows			4.74	5.26	5.30	5.59	5.36	5.56

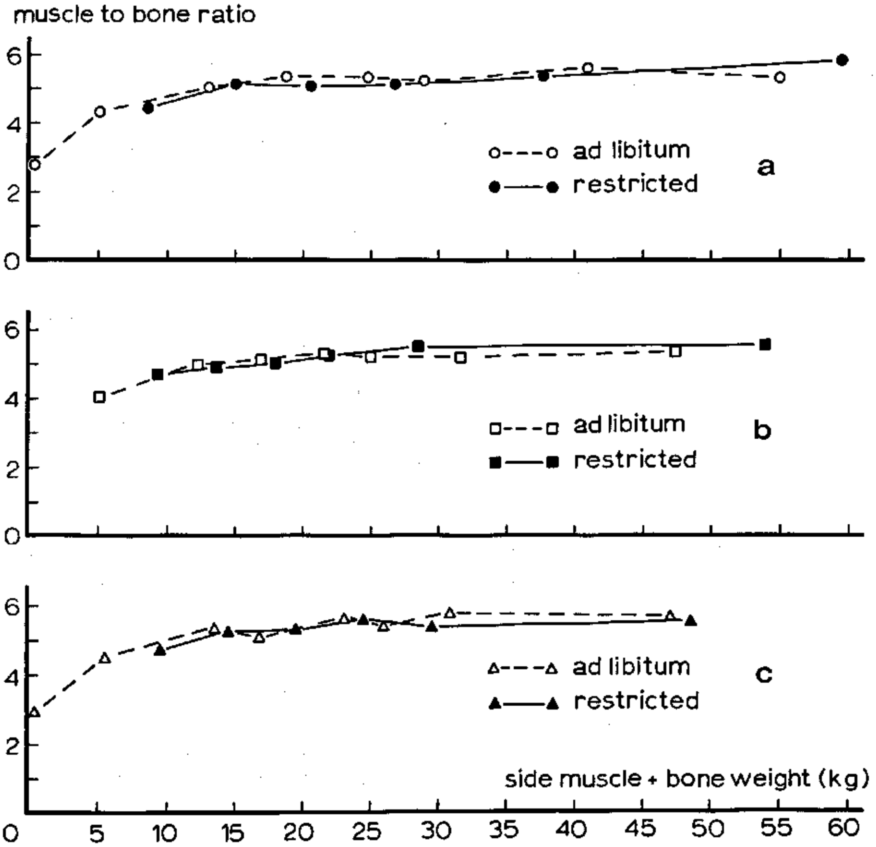

FIG. 4.9abc. Muscle to bone ratio in relation to muscle + bone weight on *ad libitum* and restricted feeding level in boars (a), castrates (b) and sows (c).

lower in comparison with later stages, indicating the skeleton as an early developing component in new-born animals.

The differences between sexes are illustrated in Fig. 4.10ab. From the tests on discrimination between the regressions it appeared that all sexes differed mutually for constant terms at the *ad libitum* feeding level. Boars and sows also differed for constant terms at the restricted feeding level. Sows had the most favourable muscle to bone ratio at both feeding levels. Boars followed at the *ad libitum* feeding level.

Ignoring the quadratic term in castrates a common *b*-value could be calculated, because the sexes did not differ in slope either. It amounted to 0.10 (class H). The muscle to bone ratio thus increases with increasing carcass weight. No essential alteration in interpretation was required when the ratio was based on muscle + bone weight as the independent variate. Only the difference between *ad libitum* fed boars and castrates disappeared, and the new-born sows now fitted to the regression line. The *b*-value only shifted to 0.12 (class H). The differences of

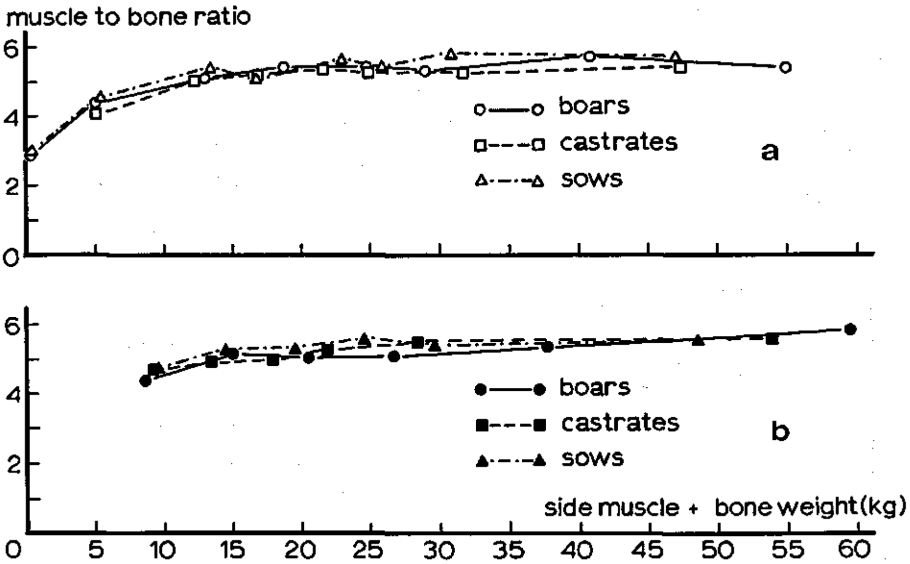

FIG. 4.10ab. Muscle to bone ratio in relation to muscle + bone weight in boars, castrates and sows on *ad libitum* (a) and restricted feeding level (b).

0.10 and 0.12 respectively with isometry were the differences in *b*-values between the tissues in the respective cases.

The finding that feeding level does not influence the muscle to bone ratio is in accordance with the literature (RICHMOND and BERG, 1971a; PEDERSEN, 1973; CARDEN and GOENAGA, 1977; GOENAGA and CARDEN, 1978). But the influence of sex was not found by RICHMOND and BERG (1971a) or in cattle by BERG and BUTTERFIELD (i.a. 1976c). PEDERSEN (1973), however, reported a difference between sows and castrates of 0.2 unit, which is in accordance with the difference in this study.

4.4.4. *The muscle to fat ratio*

As might be expected from the height of the *b*-values of muscle and fat and

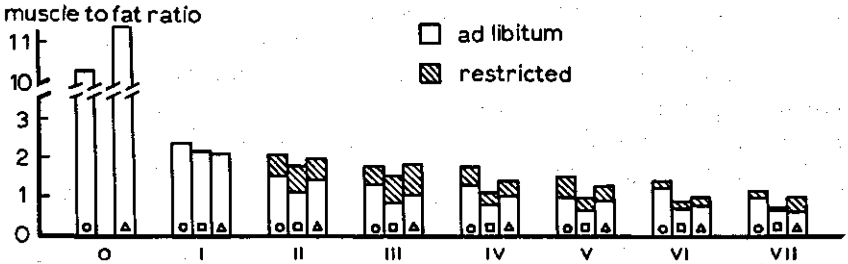

FIG. 4.11. Muscle to fat ratio at the different dissection stages (roman figures) for boars (O), castrates (□) and sows (△) and the difference between the *ad libitum* and restrictedly fed groups with respect to this ratio.

TABLE 4.14. The muscle to fat ratio of the treatment groups for the different dissection stages.

Feeding level and Sex	Dissection stage							
	0*	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	10.27	2.37	1.55	1.32	1.35	1.01	1.26	1.00
Castrates		2.14	1.13	0.83	0.80	0.67	0.72	0.65
Sows	11.45	2.09	1.44	1.05	1.06	0.88	0.79	0.62
Restricted								
Boars			2.08	1.77	1.74	1.53	1.42	1.14
Castrates			1.79	1.53	1.09	0.98	0.87	0.70
Sows			2.00	1.86	1.40	1.26	1.01	0.98

*Subcutaneous fat was excluded from total fat.

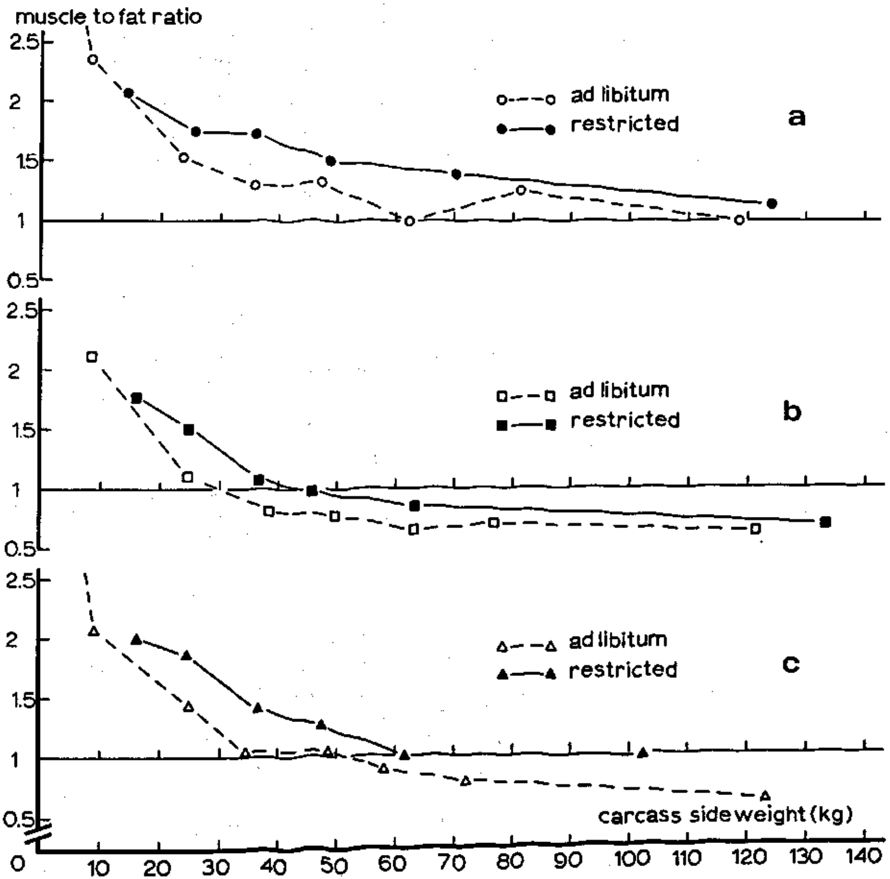

FIG. 4.12abc. Muscle to fat ratio in relation to carcass weight on *ad libitum* and restricted feeding level in boars (a), castrates (b) and sows (c).

the sex differences between them, the muscle to fat ratio decreases markedly during growth. Fig. 4.11 visualizes the decrease in the ratio, the differences between feeding levels and those between sexes. The most favourable ratio is seen in boars and the least in castrates. The difference between feeding levels is consistently in favour of the restricted feeding level, but it diminishes in older animals, except in sows. The corresponding figures are given in Table 4.14. The average variation coefficient of 20.4% is much higher than that of the muscle to bone ratio.

The ratio was regressed on carcass weight. There was a linear growth pattern, while the new-born sows fitted to the regression line as well, but the new-born boars did not. The latter had a ratio higher than estimated from the regression line. With regard to feeding level no differences in slope were descernible, but the constant terms did differ in all three sexes. It is demonstrated in Fig. 4.12abc. Likewise the differences between the sexes are shown in Fig. 4.13ab. It appeared that at both feeding levels differences in slope between boars and castrates and between boars and sows were found. The castrates and sows differed in constant terms at both feeding levels. Common *b*-values may thus be given combining the feeding levels. For boars, castrates and sows they were computed as –0.33, – 0.47 and –0.48 (all class L$^=$) respectively.

In Fig. 4.13ab the line drawn at unity reveals that castrates already in early stages produce more fat than muscle in contrast to boars. The latter showed ratios not descending below unity, even not the *ad libitum* fed ones. The restrictedly fed sows at later stages just remained around unity.

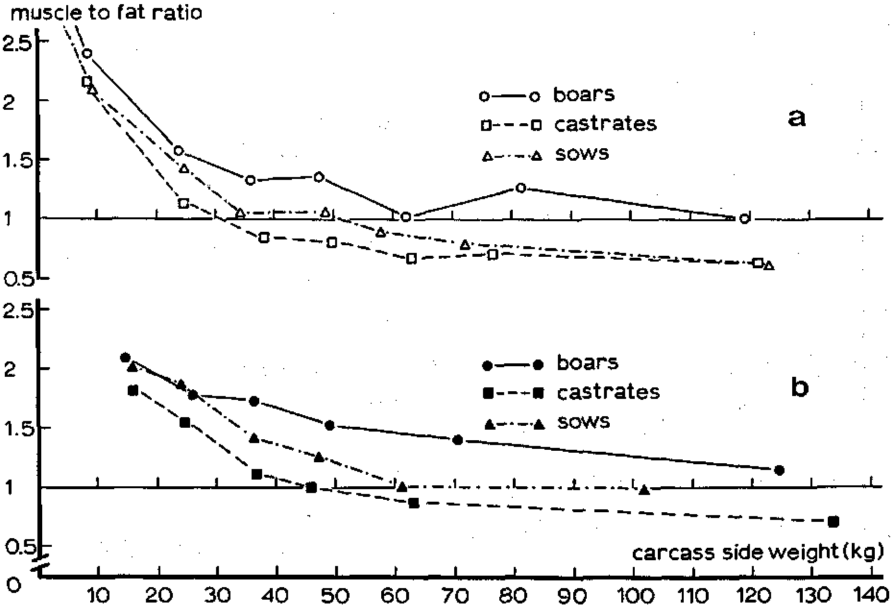

FIG. 4.13ab. Muscle to fat ratio in relation to carcass weight in boars, castrates and sows on *ad libitum* (a) and restricted feeding level (b).

4.5. GROWTH OF OFFAL COMPONENTS

4.5.1. *Growth of head and feet*

Like individual bones and muscles were compared within their respective tissues, the components of offal were regressed on total side offal weight.

The growth pattern showed a quadratic term for boars with a positive coefficient in head and a negative one in feet. The new-born boars grew in line with these patterns. The new-born sows, however, positively and negatively respectively differed from the linear pattern of the other stages. In case of the head there were also tendencies for quadratic growth in sows and in the *ad libitum* feeding level group.

When for the head only linear growth would be involved no differences in slope would be found, leading to a common *b*-value of 1.05 (class A^+). The constant terms differed between feeding levels in castrates and between sexes in that boars at the restricted feeding level had a relatively lighter head. Because of the positive quadratic term, however, the growth of the head in boars will diverge from that of the other sexes.

The percentage of the head within total offal in average slightly increased from about 60 to about 67. The average variation coefficient only amounted to 3.7%.

The test for linear growth and quadratic growth in feet show the same results. No differences in slope or shape were found. The common *b*-value amounted to 0.92 (class L). The constant terms differed between feeding levels in boars, while again boars differed (having heavier feet) from castrates and sows at the restricted feeding level.

In ontogeny much attention is paid to the development of the head. As a very early developing part it has a high proportion of the body at birth. from Table 4.15, where the head is expressed as a percentage of carcass side weight, it appears that it forms about 18% of the carcass at birth. The percentage then rapidly

TABLE 4.15. The weight of the head of the treatment groups for the different dissection stages expressed as a percentage of carcass side weight.

Feeding level and Sex	Dissection stage 0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	17.97	7.57	5.59	4.83	4.73	4.78	4.90	4.63
Castrates		7.66	5.05	4.40	4.02	3.85	3.95	3.85
Sows	18.29	6.79	5.16	4.78	4.24	4.10	3.71	3.64
Restricted								
Boars			6.76	5.55	5.46	5.05	4.83	4.80
Castrates			6.41	5.96	5.00	4.54	4.18	4.26
Sows			6.62	5.78	5.37	4.73	4.24	4.37

Average variation coefficient 11.9%.

becomes lower and ends up with about 4.0–4.5%. It can also be seen that the head of the boars is heavier than that of the other sexes.

Regressions were carried out with the weight of the sum of the heads of both carcass halves on the weight of the sum of these halves. They revealed a concave quadratic pattern over the treatment groups. The new-born boars did not follow this curvilinear pattern; they deviated from it by a negative term. A difference in shape was found between feeding levels in sows, furthermore between all sexes at the *ad libitum* feeding level and between boars and castrates at the restricted feeding level. The other possible differences were significant for the constant terms. Boars had a less concave pattern than castrates as had the latter with regard to sows.

In case of only linear growth the *b*-values would have varied from 0.73 to 0.83 which is the $L^{=}$-pattern and is in the range found by ROBELIN et al. (1974, 1977) in cattle.

Analogous to the procedure in the head the feet were treated. Their percentage of carcass side weight is given in Appendix 5. The regressions showed a linear pattern from which, however, the new-born piglets negatively deviated. Only the constant terms did differ between feeding levels, so the *b*-values for boars, castrates and sows may be given, being 0.71, 0.68 and 0.65 respectively, which is in agreement with the value in cattle given over a similar trajectory (ROBELIN, 1978). Furthermore, a difference in slope existed between boars and sows at the *ad libitum* feeding level, whereas the constant terms between sexes all differed, except for those between castrates and sows at the restricted feeding level. The percentage feet was lowest in the *ad libitum* fed animals, as it was in boars at the *ad libitum* feeding level, whereas the boars were intermediate at the restricted feeding level.

4.5.2. *Growth of some organs*

The only organs which were dissected in this study were the kidneys and the testes. The first ones as a component of offal, but the latter belonging to the loss at slaughter.

The left kidney was regressed on side offal weight. The growth pattern of the *ad libitum* feeding level group differed distinctly from the restricted feeding level group. The latter group only needed the linear term, but the first group grew according to a convex quadratic pattern from which the new-born animals did not deviate.

The restricted feeding level group did not show differences between the sexes; the common *b*-value amounted to 0.86 (class L^{-}). The constant terms differed between boars and the other sexes. Within offal boars had the heaviest kidney. In the *ad libitum* feeding level group there were differences in shape between boars and castrates. The former showed a less convex pattern resulting again in a heavier kidney of boars within offal.

Being a part of the carcass the weight of the kidney expressed as a percentage of carcass side weight is given in Appendix 5. Since in the literature organs are expressed as a proportional function of body weight, the sum of the weights of the kidneys was regressed on live weight. Again a quadratic term was found for the *ad libitum* feeding level group, while the new-born piglets also did not differ from this pattern. The boars differed from castrates and sows in shape in that they had a less convex pattern. In the restricted feeding level group there was a tendency to concave quadratic growth. However, we had to decide for linear growth. The only difference was found in constant terms between boars and the others. The kidneys were heaviest in boars. The common *b*-value for this feeding level group amounted to 0.71 (class $L^{=}$). This is in the range for growth of organs reported by BRODY (1945) and the same as found in young bulls (ROBELIN et al., 1977), but higher than reported by ROBELIN et al. (1974) also in young bulls and by CANTIER et al. (1969) in rabbits. The latter, however, gave also a similar result when other trajectories were taken.

A deviating growth pattern in comparison with other organs is reported for growth of gonads. Their S-shaped curve would deviate from the others because a spurt of growth preceding puberty has been found.

In this study the testes were carefully separated from the surrounding tissue. The sum of the weights of the left and right testis was expressed as a percentage of live weight (Table 4.16). The absolute weights are also given in this table. From the table it can be seen that the percentages remain low at the onset, but at stage III (which in fact is about puberty) they almost show their maximum, whereas in later stages the percentage tends to diminish.

As for the kidneys, the sum of the left and right testis was regressed on live weights. A clear quadratic pattern was found with high negative coefficients. The groups of boars, however, differed in shape; the restrictedly fed boars showed a more convex pattern. Because of the strong bending curve the neonates deviated from the pattern with a positive term. When the epididymes were added to the weights of the testes the same results were found.

Considering a linear pattern, a common *b*-value of 1.46 could be computed. Such high values may also be deducted from the results found in rabbits (CANTIER et al., 1969), where the trajectory was divided into two or three parts. A first part with a *b*-value of 0.89, but a second one with a value of about 3.00, while a third part was given a *b*-value of 1.38. These results confirm the S-shaped growth

TABLE 4.16. The weight of the testes at both feeding levels for the different dissection stages as absolute weights (in g) and expressed as a percentage of live weight.

	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Absolute weight								
Ad libitum	0.63	21	154	333	458	560	693	890
Restricted			58	227	391	511	641	881
% of live weight								
Ad libitum	0.04	0.09	0.23	0.34	0.38	0.34	0.34	0.30
Restricted			0.13	0.29	0.39	0.37	0.35	0.29

pattern of testes. ROBELIN et al. (1974) mentioned a *b*-value of 1.21 in the Friesian bulls over the trajectory of 9–15 month of age.

Furthermore the ratio of left and right testis as well as the ratio of the left and right epididymis were regressed on live weight. Since the *b*-value did not differ from zero the ratio remained unchanged with increasing live weight. As in addition the *ln a*-value did not differ from zero either (though less convincing in the epididymes than in the testes), thus the left and right organs were of the same weights.

4.6. GROWTH OF BONE

4.6.1. *General*

Bone growth as the increase of side bone weight (y) with regard to carcass side weight (x) can be given according to the following regression equations:

			S.E.^*_D	S.E.^*_L	S.E.^*_Q
boars	A	$\ln y = -1.787 + 0.812 \ln x$	0.019	0.012	
	R	$\ln y = -1.710 + 0.812 \ln x$			
castrates	A	$\ln y = -1.133 + 0.436 \ln x + 0.044 \ln^2 x$	0.016	0.080	0.011
	R	$\ln y = -1.056 + 0.436 \ln x + 0.044 \ln^2 x$			
sows	A	$\ln y = -1.703 + 0.762 \ln x$	0.016	0.012	
	R	$\ln y = -1.603 + 0.762 \ln x$			

$^*\text{S.E.}_D$ = the standard error of the difference between constant terms
$^*\text{S.E.}_L$ = the standard error of the slope of the linear term
$^*\text{S.E.}_Q$ = the standard error of the shape of the quadratic term.

Because of the differences in constant terms the equations had to be given for the *ad libitum* and the restricted feeding level separately, A and R respectively.

The growth of bone in comparison to other carcass components was described in section 4.4.1.

TABLE 4.17. The weight of total bone in side of the treatment groups for the different dissection stages (in kg).

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	0.076	0.96	2.18	2.93	3.88	4.65	6.18	8.66
Castrates		0.99	2.04	2.73	3.40	4.00	5.11	7.43
Sows	0.074	0.97	2.14	2.75	3.47	4.07	4.57	7.03
Restricted								
Boars			1.58	2.46	3.40	4.37	5.97	8.73
Castrates			1.60	2.30	3.00	3.47	4.41	8.23
Sows			1.64	2.30	3.10	3.72	4.63	7.41

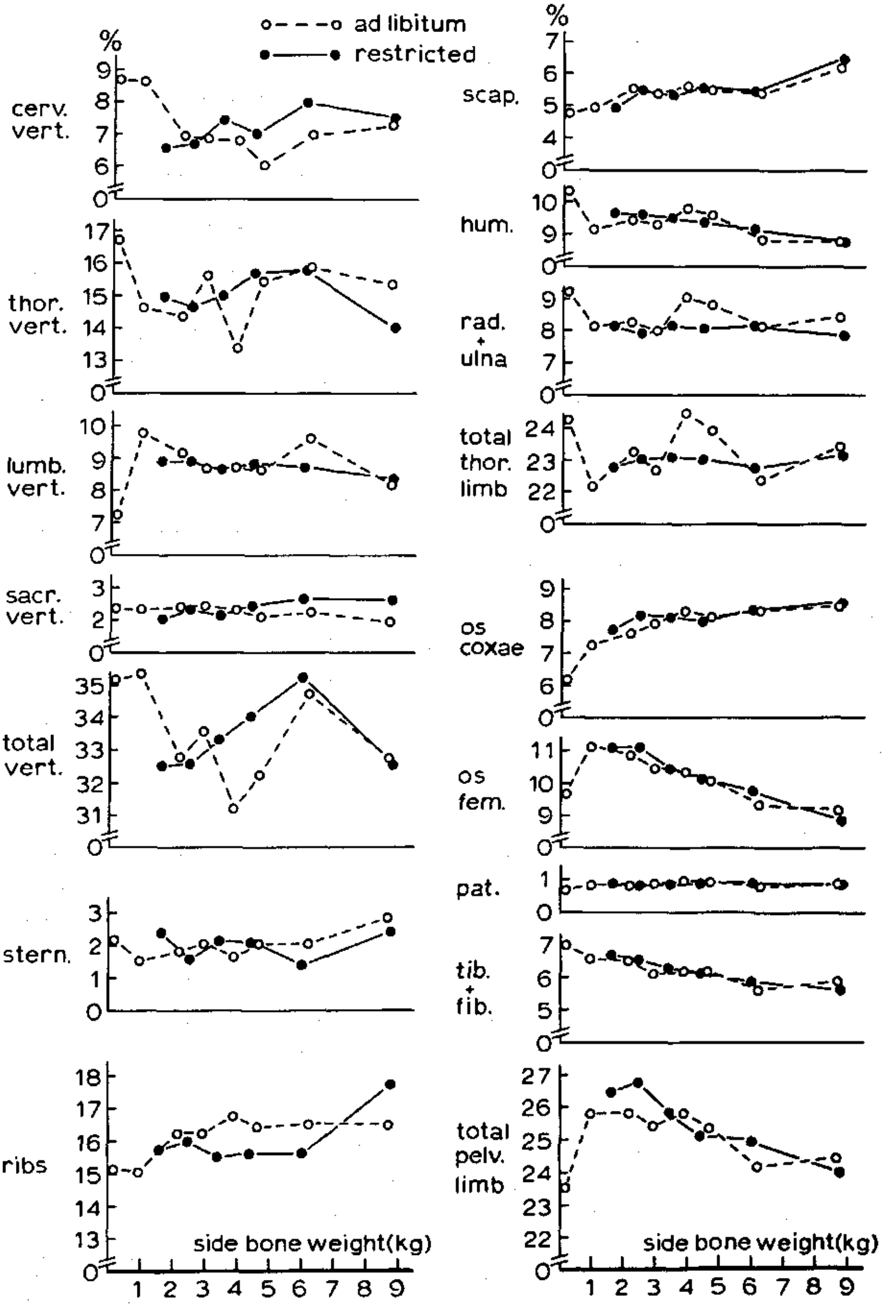

FIG. 4.14. Bone weight distribution of bones and bone groups within total bone of boars compared on *ad libitum* and restricted feeding level.

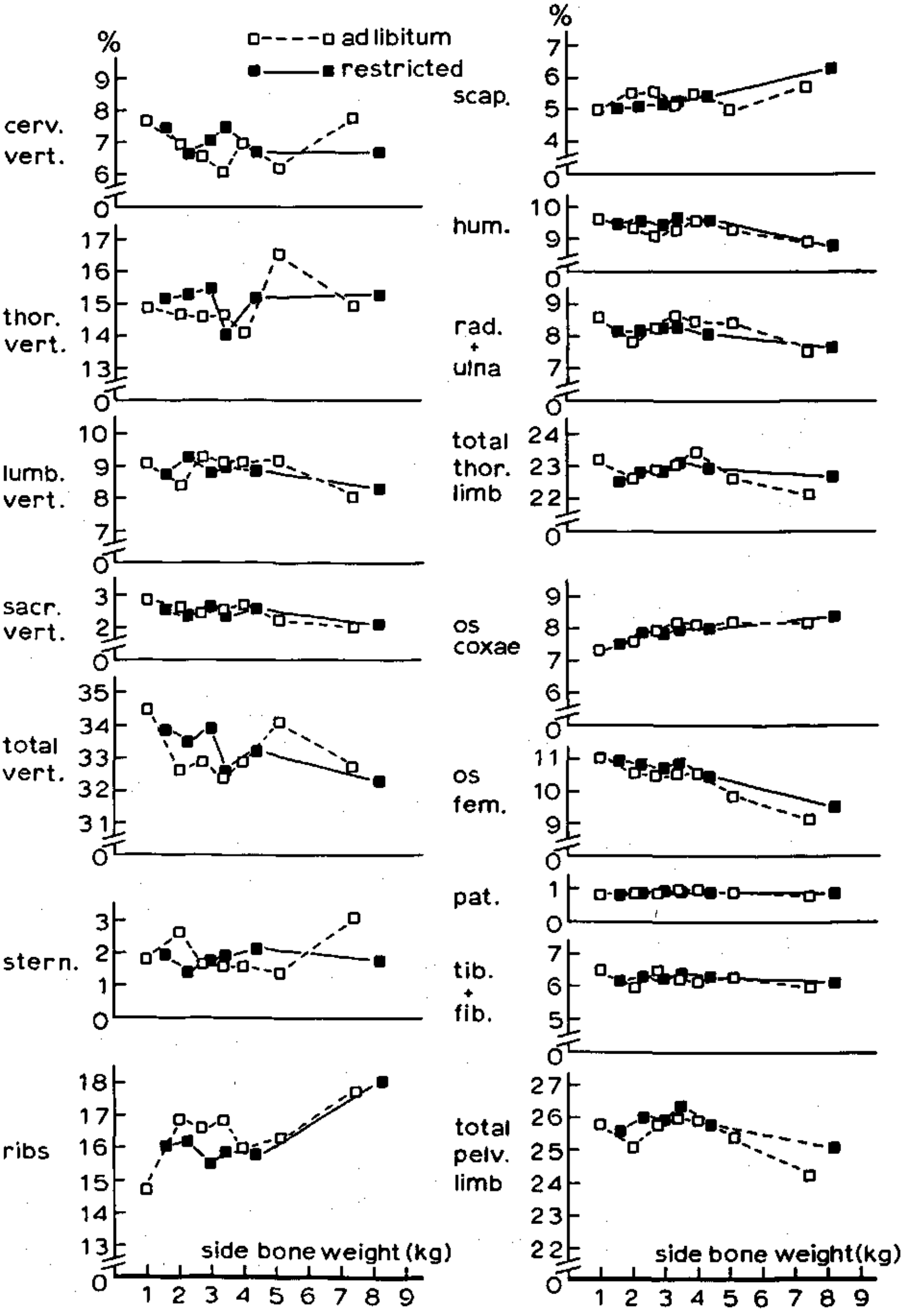

Fig. 4.15. Bone weight distribution of bones and bone groups within total bone of castrates compared on *ad libitum* and restricted feeding level.

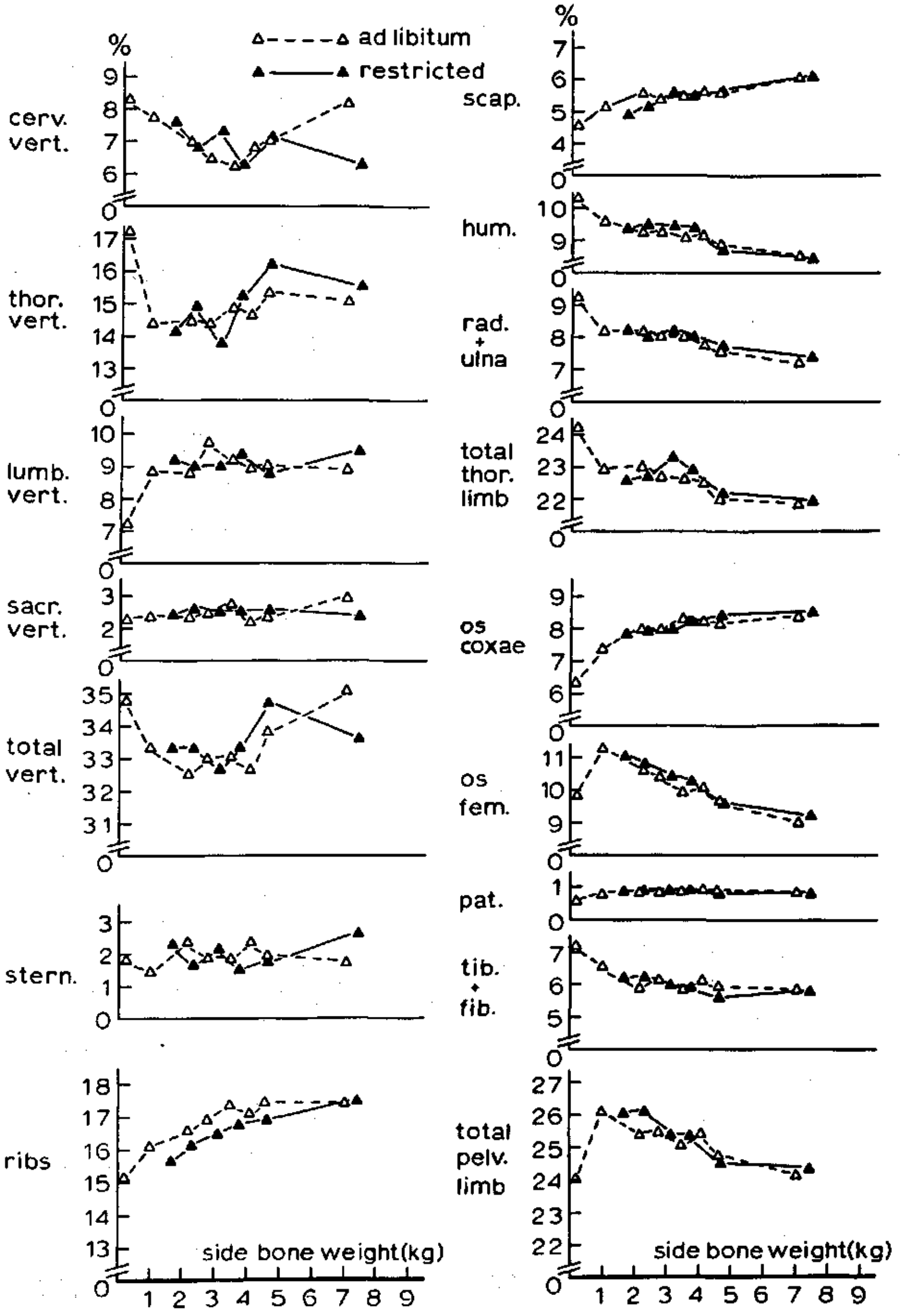

FIG. 4.16. Bone weight distribution of bones and bone groups within total bone of sows compared on *ad libitum* and restricted feeding level.

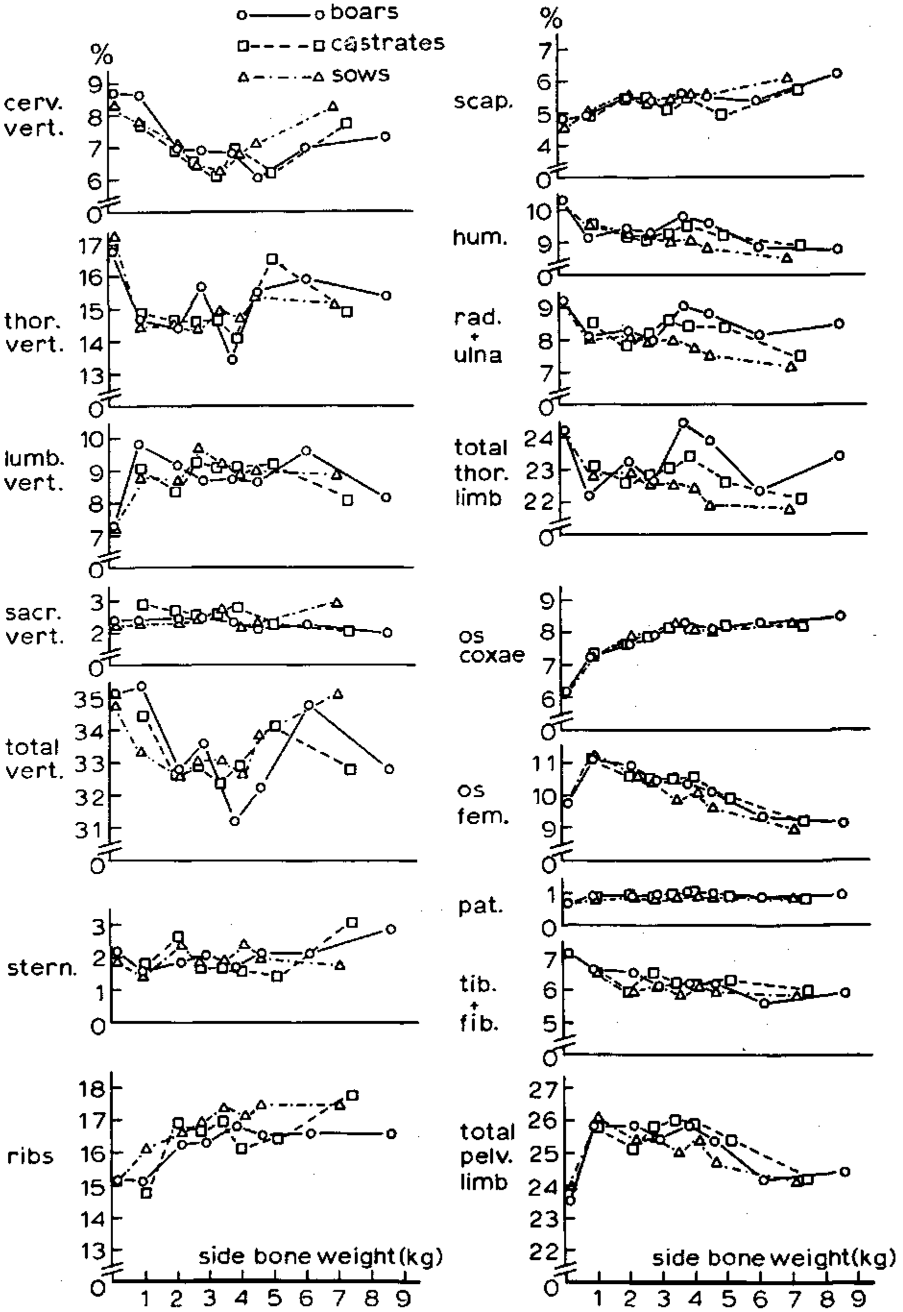

FIG. 4.17. Sex differences in bone weight distribution of bones and bone groups within total bone on *ad libitum* feeding level.

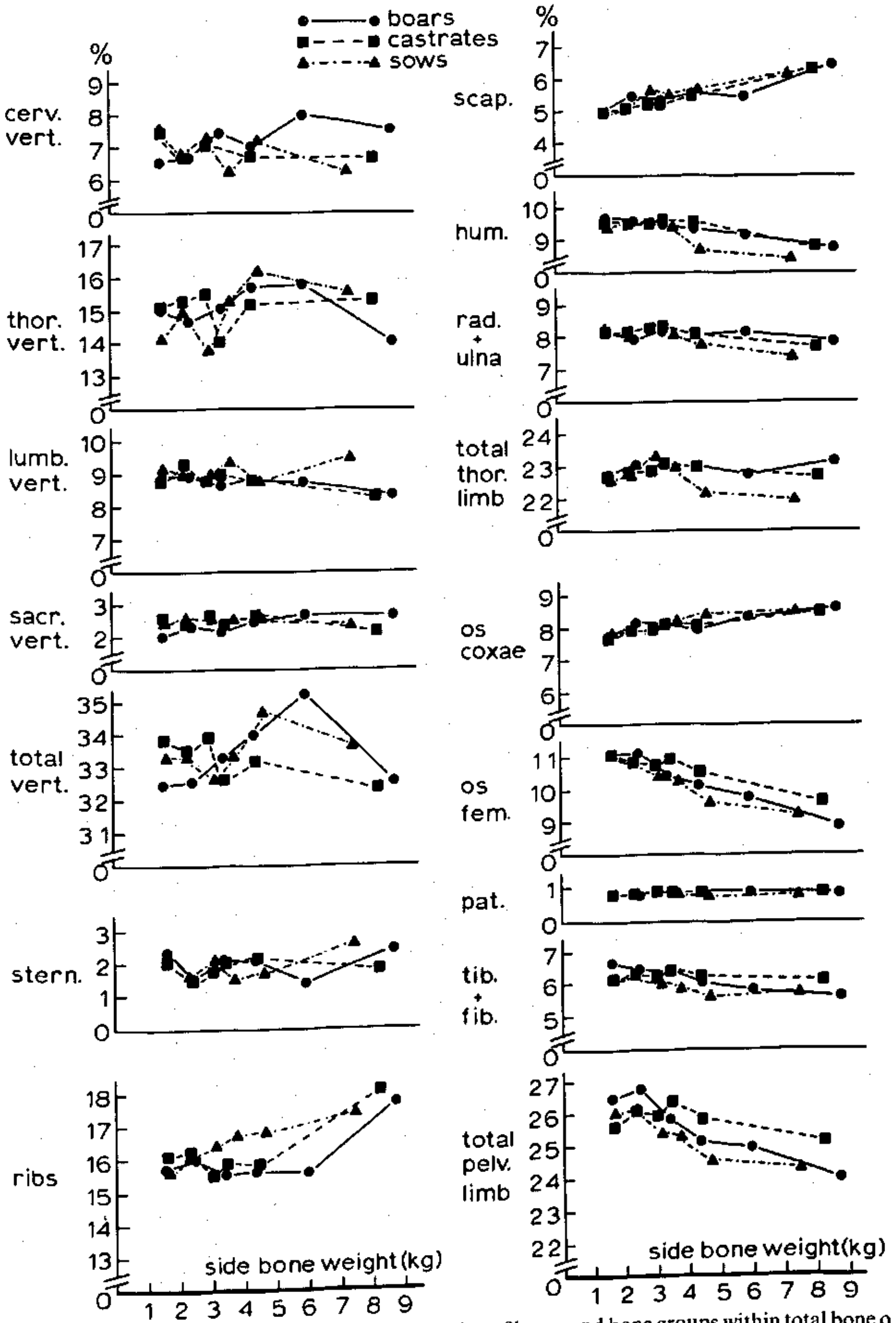

FIG. 4.18. Sex differences in bone weight distribution of bones and bone groups within total bone on restricted feeding level.

The total side bone weights as established during growth of the experimental pigs are presented in Table 4.17. The weights had an average variation coefficient of 11.8%. These weights served as the independent variates in the regressions of individual bones and bone groups.

4.6.2. *Bone weight distribution*

The weight of individual bones and bone groups was expressed as a percentage of total side bone weight. An illustration of the influence of feeding level on the bone weight distribution is given in Fig. 4.14–4.16 for each of the three sexes. In Fig. 4.17 and 4.18 the influence of the sexes on bone weight distribution is demonstrated for each of the feeding levels.

4.6.2.1. The vertebrae, ribs and sternum

With respect to the vertebrae and the sternum the regressions revealed that for the influence of feeding level as well as sex neither differences in slope nor in constant terms were found. The rather variable picture in these bones, as is easily seen in Fig. 4.14–4.18, may have contributed to this finding. A part of the variability at least is due to the procedure of splitting the carcasses. The average variation coefficients of the percentages over the treatment groups and the dissection stages in the cervical, thoracic, lumbar and sacral vertebrae were 18.0, 10.2, 11.6 and 26.7% respectively. In the sternum the variation coefficient was very high with 41.4%.

The percentages of total vertebrae to bone weight are given in Table 4.18. Due to the variability of the constituent parts the picture (Fig. 4.14–4.18) is rather variable, in spite of an average variation coefficient of 6.3%.

Since no differences at all were found, the overall regressions could be taken for the vertebrae and the sternum. The *b*-values are presented in Table 4.19. The difference between feeding levels in slope for the group of total vertebrae in boars (Fig. 4.14) was the only significant difference. This is the reason why boars were excluded from the presentation in the table for this character. They had a growth

TABLE 4.18. The weight of the total vertebrae of the treatment groups for the different dissection stages expressed as a percentage of side bone weight.

Feeding level and Sex	Dissection stage 0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	35.05	35.35	32.79	33.59	31.19	32.21	34.76	32.76
Castrates		34.48	32.66	32.91	32.37	32.92	34.14	32.74
Sows	34.79	33.35	32.55	33.02	33.07	32.57	33.82	35.11
Restricted								
Boars			32.53	32.59	33.33	34.04	35.24	32.59
Castrates			33.84	33.51	33.92	32.66	33.22	32.33
Sows			33.43	33.41	32.68	33.38	34.73	33.66

TABLE 4.19. The classification of the linear growth pattern of vertebrae, ribs and sternum.

Bones	b	s_b	Class	Bones	b	s_b	Class
Cervival vertebrae	0.97	0.02	A^-	Ribs	1.05	0.01	A^+
Thoracic vertebrae	1.03	0.01	A^+	Sternum	1.05	0.06	A^+
Lumbar vertebrae	0.98	0.01	A				
Sacral vertebrae	1.00	0.03	A				
Total vertebrae*	1.00	0.01	A				

*Without boars, see text.

coefficient of 0.97 and 1.02 (A^-/A) for the *ad libitum* and restricted feeding level respectively. The linear growth pattern did not alter for the cervical and sacral vertebrae when the new-born piglets were taken into consideration. New-born sows deviated from the regression line in the thoracic and total vertebrae with a positive term; the boar piglets deviated negatively in the lumbar vertebrae and positively in the sternum.

Although a difference was found between cervical and thoracic vertebrae with regard to their growth coefficients, no further growth gradient along the vertebral column in an anterior-posterior direction could be established. In the literature growth gradients are often reported. In some cases a 'second phase of active growth' (CUTHBERTSON and POMEROY, 1962b) is connected to the cervical vertebrae. It could not be ascertained in this study. On the other hand the faster growth of thoracic vertebrae with regard to lumbar vertebrae as found by CUTHBERTSON and POMEROY (1962b) was in agreement with the results as shown in Table 4.19.

The growth of the ribs together with that of the scapula and the *os coxae* mostly shows a higher b-value relative to other bones. As can be seen from Table 4.19, Table 4.21 and Table 4.23 this was confirmed. The linear growth pattern of ribs was adapted to that of the new-born piglets. The tendency towards the somewhat higher b-value in ribs, sternum and thoracic vertebrae, as bones that are attached to each other, seems to be in accordance with the findings of GUTTMAN and GUTTMAN (1965).

In Table 4.20 the percentages of the weight of the ribs to bone weight are given. The average variation coefficient amounted to 5.2%. The regressions showed some differences in constant terms. The *ad libitum* fed sows had a higher percentage of ribs than the restictedly fed ones (Fig. 4.16). Furthermore, the sows had a higher percentage than the other sexes at the *ad libitum* feeding level (Fig. 4.17), and a higher percentage than boars at the restricted feeding level (Fig. 4.18).

The height of the b-values of the vertebrae is lower than found by ROBELIN (1978) in cattle and PRUD'HON et al. (1978) in sheep, but higher (especially for the cervical vertebrae) than those reported by JONES et al. (1978) in cattle. The figures given by DAVIES (1975) in pigs for the combination of the cervical and thoracic vertebrae are in accordance with those in Table 4.19, but the combination of lumbar and sacral vertebrae was higher in DAVIES' experiment. The b-value for

TABLE 4.20. The weight of the ribs of the treatment groups for the different dissection stages expressed as a percentage of side bone weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	15.08	15.09	16.27	16.25	16.81	16.48	16.57	16.53
Castrates		14.74	16.92	16.69	16.94	16.09	16.40	17.76
Sows	15.14	16.12	16.62	16.91	17.38	17.11	17.45	17.41
Restricted								
Boars			15.78	15.99	15.56	15.63	15.62	17.77
Castrates			16.09	16.23	15.57	15.90	15.86	18.10
Sows			15.67	16.14	16.45	16.78	16.90	17.46

the ribs was rather low as compared to that found in the ruminants.

4.6.2.2. The bones of the thoracic limb

The results of the growth ratios of the bones of the thoracic limb are given in Table 4.21. The tests revealed more differences than in the vertebrae, so that in none of the bones a common *b*-value over all groups could be computed. Bringing together of bones to feeding level groups or sex groups was allowed in the cases mentioned in Table 4.21. In the scapula a difference between feeding levels in castrates was established (Fig. 4.15). The boar group is not represented in the case of the humerus. It means that there is an influence of the feeding level (Fig. 4.14); the *ad libitum* and restrictedly fed boars had a *b*-value of 0.99 and 0.94 (A/A$^-$) respectively. No differences were found between the sexes at the restricted feeding level in each of the bones. Hence the tendency in the decrasing

TABLE 4.21. The classification of the linear growth pattern of bones of the thoracic limb.

Bones	b	s_b	Class	Feeding level group or sex group
Scapula	1.06	0.01	A$^+$	*ad libitum* feeding level
	1.12	0.01	H	restricted feeding level
Humerus	0.94	0.01	A$^-$	restricted feeding level
	0.97	0.01	A$^-$	castrates
	0.93	0.01	A$^-$	sows
Radius + Ulna	0.97	0.01	A$^-$	restricted feeding level
	0.99	0.02	A	boars
	0.97	0.01	A$^-$	castrates
	0.94	0.01	A$^-$	sows
Total thoracic limb	1.00	0.01	A	restricted feeding level
	1.01	0.01	A	boars
	0.99	0.01	A	castrates
	0.97	0.01	A$^-$	sows

TABLE 4.22. The weight of the total of the thoracic limb bones of the treatment groups for the different dissection stages expressed as a percentage of total side bone weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	24.20	22.18	23.24	22.66	24.47	23.89	22.38	23.42
Castrates		23.13	22.62	22.88	23.04	23.46	22.62	22.13
Sows	24.18	22.91	23.00	22.66	22.63	22.50	22.00	21.86
Restricted								
Boars			22.79	23.04	23.09	23.00	22.75	23.16
Castrates			22.52	22.79	22.83	23.10	22.97	22.68
Sows			22.55	22.64	23.30	22.92	22.06	21.94

order of the *b*-values from boars to sows is mainly accounted for by the differences at the *ad libitum* feeding level. They were found significant between boars and sows in humerus and in radius + ulna, whereas in total thoracic limb boars differed from the two other sexes (Fig. 4.17).

Differences in constant terms remained for those between feeding levels in boars in the radius + ulna (Fig. 4.14), between castrates and sows in all bones including the total thoracic limb at the *ad libitum* feeding level (Fig. 4.17), and at the restricted feeding level between castrates and sows in scapula and humerus, and between boars and sows in humerus and total thoracic limb (Fig. 4.18).

The weight of the total thoracic limb bones expressed as a percentage of total weight is given in Table 4.22. The average variation coefficient (4.3%) was lower than that of the total vertebrae. The scapula, humerus and radius + ulna had coefficients of 6.9, 4.7 and 6.8% respectively.

The total of bones of the thoracic limb has a nearly average growth pattern. The long bones slightly decrease, whereas the scapula clearly increases. A growth gradient down the limb, as established in the ruminants by JONES et al. (1978), PRUD'HON et al. (1978) and ROBELIN (1978) is disturbed in that the *b*-values in the humerus are lower than in the radius + ulna. This, however, was also found in pigs by others (CUTHBERTSON and POMEROY, 1962b; DAVIES, 1975) and in rabbits by DULOR et al. (1976). The height of the *b*-values is similar to those found by DAVIES (1975). In comparison with the values in ruminants those in pigs seem to be less differentiated; the scapula had a lower value, whereas the long bones showed higher values.

The new-born stage did not deviate from the regression line in case of the scapula, nor did the new-born boars in the humerus and the new-born sows in radius + ulna and the total thoracic limb. The sow piglets deviated negatively in the humerus, while the boar piglets had relatively higher weights of radius + ulna and total thoracic limb than estimated from the regression line through the later stages.

4.6.2.3. The bones of the pelvic limb

The growth pattern of the total of the pelvic limb bones and of the bones from which this total is made up is given in Table 4.23. A negative quadratic term was ascertained for the boars in the *os femoris* and for the castrates in the patella. In contrast to the bones of the thoracic limb those of the hind limb did show differences in slope between the sexes at the restricted feeding level. The missing sex groups showed a difference in slope between the *ad libitum* and restricted feeding level, the *b*-values being: 0.92 and 0.87 (L/L^-) for boars in the *os femoris* (Fig. 4.14), 1.04 and 0.93 (A^+/A^-) for sows in the patella (Fig. 4.16), and 0.98 and 0.94 (A/A^-) for boars in total pelvic limb (Fig. 4.16) respectively. When tested quadraticly there was only a tendency to a difference in shape for boars in the *os femoris*, while in the patella the difference between feeding levels in castrates (Fig. 4.15) was then significant, as was a difference between castrates and sows at the *ad libitum* feeding level.

Independent of the degree of polynomial tested the sex differences in slope or shape at the restricted feeding level (Fig. 4.18) were significant for castrates with regard to both other sexes in all bones, except in *os coxae*, and in the total pelvic limb. The boars and sows only differed in the patella. The quadratic term for boars in the *os femoris* is additive to the linear term already deviating from unity, so that the boars will deviate from castrates most at the higher bone weights.

Further differences remain as to constant terms between feeding levels in the *os femoris* for castrates (Fig. 4.15) and sows (Fig. 4.16). At the *ad libitum* feeding level (Fig. 4.17) castrates and sows differ in the *os femoris* and the tibia + fibula. At the restricted feeding level a difference between boars and sows was found in the long bones as well as in the total bones of the hind limb.

TABLE 4.23. The classification of the linear and quadratic growth pattern of bones of the pelvic limb*.

Bones	b	s_b	Class	Feeding level group or sex group	Quadratic pattern
Os coxae	1.06	0.01	A^+		
Os femoris	*0.91*	0.01	L	*ad libitum* feeding level	
					♂ −
	0.93	0.01	A^-	castrates	
	0.89	0.01	L	sows	
Patella	*1.04*	0.01	A^+	*ad libitum* feeding level	
	1.02	0.02	A	boars	
	1.05	0.02	A^+	castrates	⚦ −
Tibia + fibula	0.95	0.01	A^-	*ad libitum* feeding level	
	0.93	0.01	A^-	boars	
	0.98	0.01	A	castrates	
	0.94	0.01	A^-	sows	
Total pelvic limb	0.97	0.01	A^-	*ad libitum* feeding level	
	0.99	0.01	A	castrates	
	0.96	0.01	A^-	sows	

*The numbers in italics are valid if the quadratic terms are ignored.

TABLE 4.24. The weight of the total of the pelvic limb bones of the treatment groups for the different dissection stages expressed as a percentage of total side bone weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	23.55	25.82	25.88	25.42	25.85	25.35	24.20	24.45
Castrates		25.82	25.15	25.84	26.01	25.94	25.42	24.25
Sows	24.01	26.14	25.43	25.52	25.07	25.41	24.76	24.16
Restricted								
Boars			26.48	26.79	25.88	25.19	24.98	24.01
Castrates			25.57	26.05	25.94	26.39	25.80	25.10
Sows			26.05	26.13	25.40	25.38	24.56	24.34

The bones of the pelvic limb also showed a lower variability than the vertebrae. The average variation coefficients of the weights of *os coxae*, *os femoris*, patella and tibia + fibula as a percentage of total bone weight were 5.5, 4.9, 8.2 and 6.4% respectively, similar to those of the thoracic limb. In table 4.24 the data of the total pelvic limb bones are presented. They had an average variation coefficient of 4.2%, also similar to that of the total of the bones of the thoracic limb.

From Fig. 4.14–4.18 it could be seen that with increasing bone weight the *os coxae* increases, whereas the long bones have a decreasing pattern, so that also the total decreases. The patella slightly increased. These patterns are analogous to those of the bones of the thoracic limb. The *b*-values of the corresponding bones, however, are somewhat lower (about 0.03) than in those of the thoracic limb, which would not be in agreement with the statement that the hind quarter is later developing than the fore quarter.

An orderly growth gradient could not be ascertained, because like the humerus, the *os femoris* had lower *b*-values than the more distal tibia + fibula. Moreover the patella did not fit in. The latter also had a higher value than the *os femoris* in the experiments of DAVIES (1975) and JONES et al. (1978). The *os femoris*, however, did range well in DAVIES' experiment, but CUTHBERTSON and POMEROY (1962b) and JONES et al. (1978) on the other hand found the *os femoris* deviating from the decreasing growth gradient down the limb.

As to the height of the *b*-values the same may be said, as mentioned earlier, for the thoracic limb bones. The values given by DAVIES (1975) are somewhat higher now than in this study.

The new-born animals did not deviate from the regressions through later stages in case of the *os coxae* and the tibia + fibula. They were also adapted to the curvilinear pattern of the boars in the *os femoris*. The new-born sows deviated negatively from the others in this bone. Both boar and sow piglets also deviated negatively in the patella.

4.6.2.4. The Feet

Further down the limb the metacarpal and metatarsal bones and the digits were not dissected. The feet as a whole were discussed in section 4.5.1 as a part of the offal component. However, because of their high percentage of bone they were also regressed on total bone weight. No differences in slope occurred; the common *b*-value amounted to 0.87 (L^-). Differences in constant terms were found between sows and both other sexes at both feeding levels.

The new-born animals had lighter feet than estimated from the regression line. According to the *b*-value of the radius + ulna and tibia + fibula a growth gradient continues further in distal direction.

4.6.2.5. Bone weight distribution within a total bone weight excluding total vertebrae and sternum

Because of the variability of the vertebrae and the sternum the question arises whether the picture of the bone weight distribution would alter when these bones would be excluded from total bone weight. The average variation coefficient of the absolute weights of the new total bone weight, however, only diminished from 11.8 to 11.4%.

The picture from figures analogous to that presented in Fig. 4.14–4.18 did not change essentially. The *b*-values, if required, only changed with a maximum of 0.01.

The negative quadratic term for boars in the *os femoris* disappeared, but returned in the humerus for the boars as well as for the *ad libitum* feeding level group. This resulted in that new-born boars like the sows deviated from the pattern in the *os femoris*. In the humerus the new-born sows did not deviate any more, but now the new-born boars did not follow the curvilinear pattern newly formed.

With regard to the significant differences it appeared that obviously more were discernible. However, the feeding level groups and sex groups formed needed not be changed, except that in the *os femoris* the *ad libitum* feeding level group changed into a restricted feeding level group. Both boar groups missing before in the pelvic limb could now be formed.

4.6.3. *Bone length*

The lengthening of the bones was related to total bone weight and carcass length. The lengths of the humerus and the *os femoris* are given in Table 4.25. At dissection stage VI the animals at the restricted feeding level about parallelled those of the *ad libitum* level in length of humerus and *os femoris*. The average variation coefficients for length of scapula, humerus, ulna, radius and *os femoris* were 5.0, 5.1, 5.5, 5.6 and 4.9% respectively.

The regressions on total side bone weight were carried out with the third root of weight. The growth patterns of the length of the scapula and the long bones as they were related to total bone weight and carcass length are demonstrated in Table 4.26. All bones in one way or another bear a quadratic term. In the scapula all groups had a concave quadratic pattern when related to carcass length.

TABLE 4.25. The length of *humerus* and *os femoris* of the treatment groups over the different dissection stages (in cm).

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
*Humerus**								
Ad libitum								
Boars	5.4	11.9	15.6	17.3	19.6	20.7	22.4	25.3
Castrates		12.2	15.2	16.8	18.3	19.7	21.4	23.7
Sows	5.4	12.1	15.2	17.0	18.0	19.6	20.3	23.2
Restricted								
Boars			14.3	16.6	18.8	20.2	22.4	24.3
Castrates			14.2	16.1	17.9	19.1	21.1	24.4
Sows			14.4	16.5	18.5	19.3	20.3	23.5
*Os femoris***								
Ad libitum								
Boars	5.1	12.9	17.0	19.0	21.1	22.7	24.5	27.9
Castrates		13.1	16.4	18.2	20.0	21.5	24.0	26.1
Sows	5.2	13.1	16.8	18.6	19.5	21.5	22.6	26.1
Restricted								
Boars			15.6	18.2	20.5	22.1	24.9	27.6
Castrates			15.4	17.7	19.7	21.0	23.4	28.4
Sows			15.7	18.0	19.2	21.4	22.5	27.2

*Average variation coefficient 5.1%

**Average variation coefficient 4.9%

Concave quadratic patterns were found for the *ad libitum* feeding level in the scapula when regressed on bone weight, and in the long bones of the thoracic limb when regressed on carcass length. A tendency to this pattern also existed in the radius and ulna when related to bone weight, and in the *os femoris* when related to carcass length. Further concave patterns were established for boars in the scapula when related to bone weight and for sows in the radius, ulna and *os femoris* when related to carcass length. A convex quadratic pattern was found for the restricted feeding level in the humerus when regressed on bone weight, while this bone also had a convex cubic pattern for castrates. A tendency for a cubic term in castrates also existed in the *os femoris*.

The new-born animals were well adapted to these patterns. Only in the humerus the boar piglets positively deviated when regressed on bone weight, and when regressed on carcass length the boar piglets showed a shorter scapula and a longer *os femoris* than was estimated from the regressions.

In Table 4.26 also the linear pattern with the corresponding b-values is described, even in cases where a high power term was found. At ignoring these terms the scapula increases most. The increase in length in radius and ulna is more than that in the humerus, which would be in accordance with the increase in weight of these bones relative to bone weight. The increase in length of the *os*

TABLE 4.26. The classification and growth pattern of length of bones with respect to total side bone weight and carcass length.*

Bone	b	s_b	Class	Feeding level group or sex group	Quadratic pattern**	Cubic pattern
On bone weight						
Scapula	*0.09*	0.01	H	*ad libitum* feeding level	A +	
	0.10	0.01	H	boars	♂ +	
	0.08	0.01	H	sows		
Humerus	*0.00*	0.01	A	*ad libitum* feeding level		
					R —	
	0.01	0.01	A	castrates		⚦ −
	−0.00	0.01	A	sows		
Ulna	0.01	0.00	A			
Radius	0.04	0.00	A^+			
Os femoris	0.02	0.01	A	*ad libitum* feeding level		
	0.01	0.01	A	boars		
	0.04	0.01	A^+	castrates		
	0.02	0.01	A	sows		
On carcass length						
Scapula					+	
	1.14	0.02	H^+	*ad libitum* feeding level		
	1.25	0.02	H*	restricted feeding level		
	1.21	0.03	H*	boars		
	1.14	0.03	H^+	sows		
Humerus	*0.92*	0.01	L		A +	⚦ −
Ulna	*0.95*	0.01	A^-		A +, ♀ +	
Radius	*0.98*	0.02	A	*ad libitum* feeding level	A +	
	1.09	0.02	H	restricted feeding level		
	1.03	0.03	A^+	boars		
	1.01	0.03	A	sows	♀ +	
Os femoris	*0.98*	0.01	A		♀ +	

*The numbers in italics are valid if the high power terms are ignored.
**A = *ad libitum*; R = restricted.

femoris relative to bone weight seems to be comparatively higher than would be expected from the increase in bone weight of this bone.

The increase in length of the scapula and the long bones related to total bone weight as well as to carcass length is illustrated in Fig. 4.19. It can be seen that at the higher total bone weights the length of the bones relatively diminishes, and correspondingly to the b-values the least in the scapula, less in the radius and most in the humerus. The opposite is seen with respect to carcass length. In the heavier animals the length of the limb bones will relatively increase more than the length of the carcass.

The results of the regressions revealed more differences than may be read from Fig. 4.19. Related to carcass length, however, it also appears from the figure that the feeding levels differed in all bones and for all sexes. They differed in shape for sows in the scapula and for boars in the humerus. All other differences were in the constant terms. Differences in shape were further established between castrates

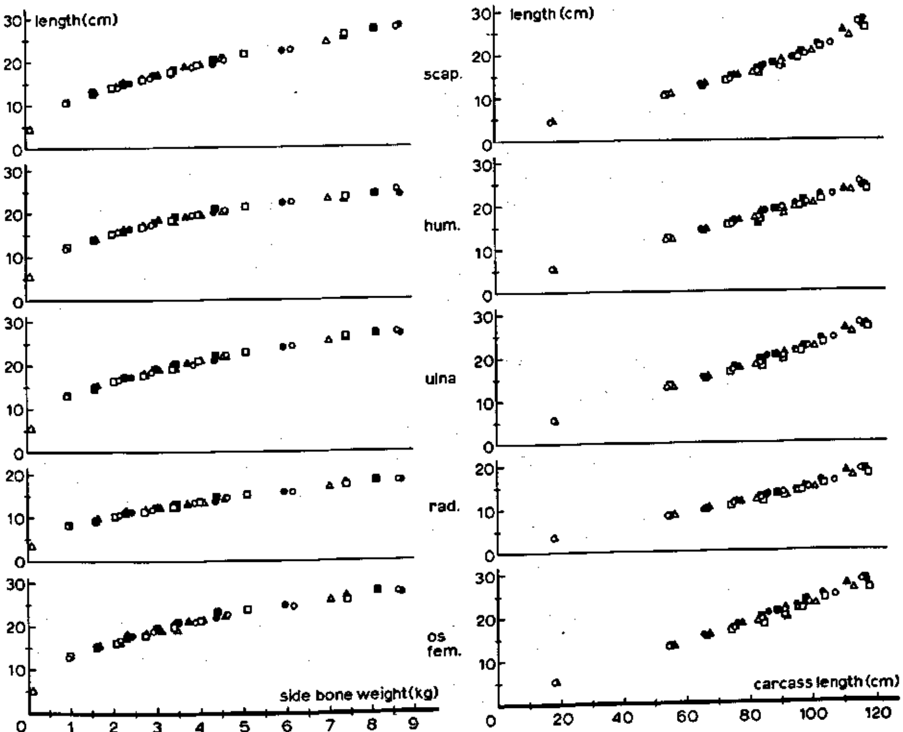

FIG. 4.19. Length of some bones in relation to bone weight and carcass length for boars (○), castrates (□) and sows (△), both on *ad libitum* (open marks) and restricted feeding level (solid marks).

and sows in the scapula, between boars and castrates in the humerus, both at the *ad libitum* feeding level, and between boars and sows in the *os femoris* at the restricted feeding level. Differences between sexes in constant terms were those between boars and sows in the humerus and those between boars and both other sexes in ulna, radius and *os femoris*, all at the *ad libitum* feeding level.

When related to total bone weight the feeding levels differed in shape for boars in the scapula and for boars and sows in the humerus. The feeding levels were different in constant terms for castrates in the humerus, for castrates and sows in the radius, and for all three sexes in the *os femoris*. The sexes differed in slope or shape for castrates with respect to both other sexes in the scapula, humerus and *os femoris* at the restricted feeding level and also in the humerus at the *ad libitum* feeding level. Furthermore, in constant terms there were differences between boars and sows in the scapula at both feeding levels, and between boars and castrates in the radius at the restricted feeding level.

The differences as listed in the two preceding paragraphs appeared in testing according to the growth pattern found. An impression of the differences, at least in slope, when tested solely for the linear pattern, may be gained from Table 4.26 observing which feeding level groups or sex groups could be formed and which groups are missing.

The main differences were those between castrates and both other sexes when related to total bone weight and those between boars and both other sexes when related to carcass length. Castrates had longer bones for a given total bone weight, especially at the restricted feeding level, while boars had longer bones for a given length of carcass, especially at the *ad libitum* feeding level. Furthermore the *ad libitum* fed pigs had shorter bones than restrictedly fed animals.

It is said that castration in farm animals would lead to longer bones at the mature stage. This could hardly be confirmed for pigs in this study. Boars seemed to have longer bones, at least when they were fed *ad libitum* (cf. Table 4.25). A tendency to longer bones (in the radius as well, but not in the ulna and the scapula) in castrates was found only when they were restrictedly fed, but they also had a somewhat higher live weight.

When the side bone weight excluding the vertebral column and sternum (see section 4.6.2.5) was taken as total bone weight some more differences were found, because in the scapula all groups then had a positive quadratic term, whereas in the *os femoris* a negative cubic term for castrates was established. The extra differences, therefore, were mainly connected with castrates.

4.6.4. *Bone thickness*

Bone thickness was established for the humerus, radius and *os femoris*. The average variation coefficients amounted to 6.2, 5.9 and 5.6% respectively, only a little higher than those of the length measures.

The regressions on total side bone weight showed that solely a linear pattern was present. Moreover there were no differences in slope at all, neither for feeding level nor for sex. Only differences in constant terms were discernible in the *os femoris* between castrates and sows at the *ad libitum* feeding level and between boars and castrates at the restricted level. This bone was thinner in castrates than in sows and thinner in boars than in castrates. The common *b*-values for humerus, radius and *os femoris* were calculated at 0.02 (A), –0.03 (A^-) and 0.02 (A) respectively. These values are in line with the increase in length in case of the humerus and *os femoris*, but the value for thickness of the radius seems to lag behind that of the length. The increase between the last stages was lowest in the radius, while on the other hand it had the greatest thickness at birth (0.7 cm) as compared to the other bones (0.6 cm). At stage I the thickness was doubled (about 1.5 cm). The thicknesses from stage II onwards increased regularly with 0.2 cm to stage VI, while upon maturing they (with respect to stage I) again had doubled (about 3.0 cm). The thickest bone is the *os femoris*, followed by the radius and then the humerus. The mutual differences between these three bones amounted to about 0.2 cm.

In the humerus the new-born animals were thicker than predicted from the regression line. The sow piglets had a thinner radius than estimated from later stages.

When the thicknesses of these bones were regressed on the bone weight excluding vertebrae and sternum, no further differences appeared.

4.6.5. *The bone length to bone thickness ratio*

The ratio of length to thickness for the humerus, the radius and the *os femoris* is given in Table 4.27. The average variation coefficients for humerus, radius and *os femoris* amounted to 5.7, 5.9 and 5.1% respectively.

The growth pattern of the ratio regressed on total side bone weight revealed a linear pattern for all three ratios. The new-born animals did not deviate from the others, except the sow piglets in the radius having a positive term.

In the humerus no differences in slope were found. It resulted in a common *b*-value of −0.02 (A) as might be expected knowing the values for the length and thickness increase, being about 0.00 and 0.02 respectively. So there is a decreasing tendency in the ratio.

There were some differences in the *os femoris*. The feeding levels differed in slope for castrates and in constant terms for both other sexes. For all three sexes the ratio was higher at the restricted feeding level. A further difference in slope was established between boars and castrates at the restricted feeding level with a

TABLE 4.27. The length to thickness ratio of some bones of the treatment groups for the different dissection stages.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Humerus								
Ad libitum								
Boars	8.53	8.84	9.12	9.10	8.71	8.86	8.85	8.95
Castrates		9.26	9.09	9.21	8.95	9.08	8.98	8.85
Sows	8.76	8.89	8.76	9.09	8.89	9.04	8.98	8.52
Restricted								
Boars			8.99	9.20	9.10	9.06	9.10	8.33
Castrates			8.87	9.09	8.19	9.13	9.37	8.29
Sows			9.30	9.49	8.82	9.21	8.65	8.68
Radius								
Ad libitum								
Boars	5.46	5.44	5.70	5.96	5.56	5.84	5.85	6.33
Castrates		5.34	5.46	5.72	5.72	5.78	6.27	6.30
Sows	5.57	5.50	5.54	5.68	5.81	5.88	6.20	6.27
Restricted								
Boars			5.43	5.68	6.04	5.70	6.08	6.28
Castrates			5.36	5.56	5.85	5.79	6.33	6.49
Sows			5.84	5.84	5.63	5.83	5.98	6.61
Os femoris								
Ad libitum								
Boars	8.03	8.15	7.99	8.21	8.06	8.43	8.14	8.21
Castrates		8.41	7.96	8.06	8.11	8.19	8.63	7.73
Sows	8.41	8.15	8.00	7.91	7.76	8.06	8.38	7.88
Restricted								
Boars			8.62	8.16	8.49	8.24	8.76	7.91
Castrates			7.93	8.08	8.35	8.49	8.79	8.02
Sows			8.15	8.28	8.41	8.55	7.87	8.38

higher *b*-value for the castrates. Since there were no sex differences at the *ad libitum* feeding level this feeding level group could be formed. It had a common *b*-value of −0.00 (A). Furthermore the sex groups boars and sows appeared, having *b*-values of −0.01 (A) and 0.00 (A) respectively. This means that there is no clear increasing or decreasing tendency in the ratio as could be seen from the figures in Table 4.27.

A dissimilar picture was ascertained for the ratio in the radius. The castrates differed from the sows for slope at the restricted feeding level in having a higher *b*-value. At this feeding level also the boars deviated from the sows in constant terms. The sows showed a higher ratio. The *ad libitum* feeding level group could thus be formed with a computed *b*-value of 0.07 (A^+). In addition all three sex

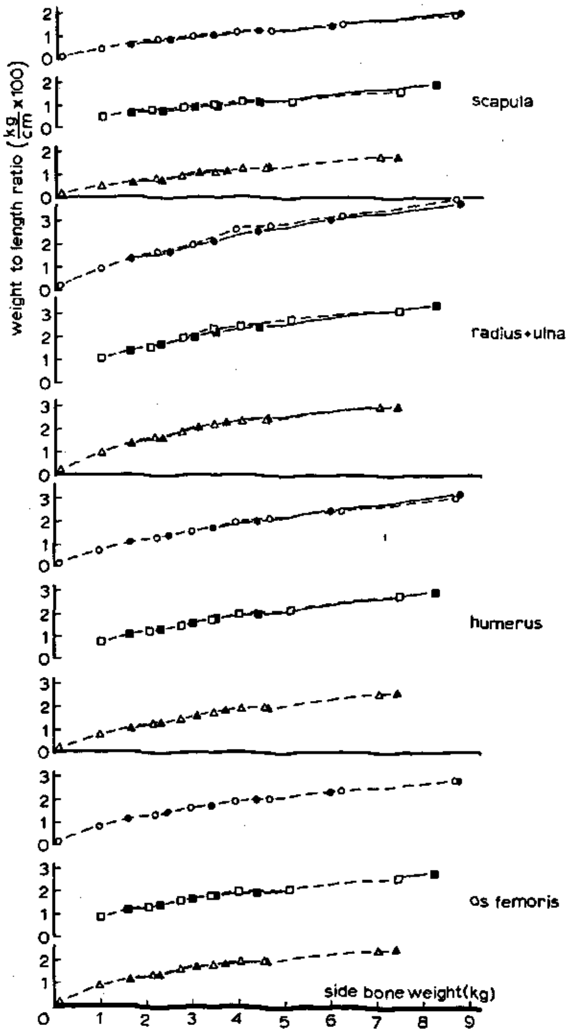

FIG. 4.20. Weight to length ratio of some bones in relation to bone weight for boars (○), castrates (□) and sows (△), both on *ad libitum* (open marks) and restricted feeding level (solid marks).

groups appeared, having b-values of 0.06 (A^+), 0.10 (H) and 0.07 (A^+) for boars, castrates and sows respectively. Hence an increasing length to thickness ratio which is also read from Table 4.27.

Taking bone weight excluding vertebrae and sternum as the independent variate no further insight is gained. The only change was that in the radius beside the sow piglets now also the boar piglets deviated from the regression line with a positive term.

The statement, sometimes formulated, that during development of the animal the bones will thicken comparatively more than lengthen, could not be confirmed for the bones examined in this study. The only indication was a very weak tendency in the humerus.

4.6.6. *The weight to length ratio of bones*

The measurement of the length of bones may be carried out over well-defined distances, whereas that of the width is more difficult to define. It was therefore decided to look after the ratio between weight and length as well.

An illustration of the weight to length ratio related to total side bone weight for some bones is given in Fig. 4.20. The ratio increases with increasing bone weight. The increase is highest in earlier stages. The variation coefficients of the ratios in the scapula, humerus, radius and *os femoris* were 11.3, 8.0, 9.5 and 7.8% respectively.

In the scapula the groups appeared to have a convex quadratic pattern. Differences between feeding levels in shape were only established for boars and castrates. The ratio was more convex for the restricted feeding level in boars and more convex for the *ad libitum* feeding level in castrates. In this bone a higher ratio at the *ad libitum* feeding level was also found for the difference between feeding levels in constant terms in sows.

Differences between feeding levels further appeared for castrates in the radius, humerus and *os femoris*, for sows in the humerus and for boars in the *os femoris*.

TABLE 4.28. The classification of the growth pattern of the weight to length ratio of some bones related to total side bone weight*.

Bones	b	s_b	Class	Sex group	Quadratic pattern	Cubic pattern
Scapula					—	
	−0.07	0.01	A^-	boars		
	−0.09	0.01	L	castrates		
	−0.05	0.01	A^-	sows		
Humerus	*−0.01*	0.00	A			⚦ +
*Radius***	−0.03	0.01	A^-	boars		
	−0.07	0.01	A^-	castrates		
	−0.05	0.01	A^-	sows		
Os femoris	−0.05	0.00	A^-			

*The numbers in italics are valid if the high power terms are ignored.

**The weight of *ulna* is included.

Although it is difficult to be seen from Fig. 4.20 the ratios were higher for the *ad libitum* feeding level.

In Table 4.28 the growth patterns of the weight to length ratio of the bones are shown. Beside the already mentioned convex quadratic growth pattern in the scapula, a concave cubic pattern was established for castrates in the humerus. There were also tendencies for quadratic terms with regard to the *ad libitum* feeding level in the long bones.

Considering the linear pattern it appears that there are only small differences in the b-values indicating that the increase in the ratio between the bones is rather small; it is somewhat less in the scapula and somewhat more in the humerus.

No feeding level groups could be formed in the scapula and the radius. It means that there were sex differences in shape or slope. However, sex differences were also ascertained in the humerus, because of the involvement of the cubic term in castrates; so the tests had to be carried out accordingly.

The differences in shape or slope were found between boars and castrates in scapula and radius at the restricted feeding level, between boars and castrates in radius and humerus at the *ad libitum* feeding level, and between castrates and sows in scapula and humerus at both feeding levels. These differences in shape or slope resulted in a higher b-value for boars in the radius and naturally in a more concave pattern in the humerus for the castrates. In the scapula the castrates had

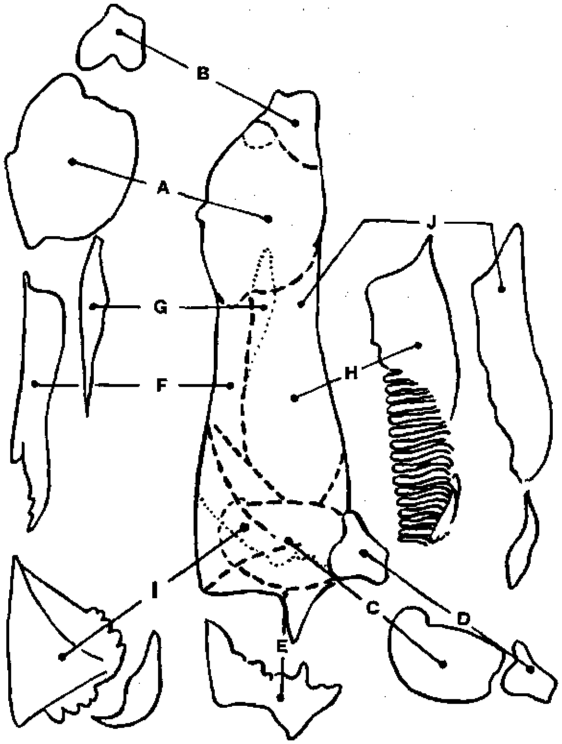

FIG. 4.21. The standard muscle groups.

A. proximal pelvic limb
B. distal pelvic limb
C. proximal thoracic limb
D. distal thoracic limb
E. neck region
F. back and loin
G. sublumbar muscles
H. thorax and abdomen
I. shoulder girdle region
J. cutaneous muscles

a more convex pattern than sows at the *ad libitum* feeding level, while boars and sows had a more convex pattern than castrates at the restricted level. Differences in constant terms were discernible between boars and castrates in scapula at the *ad libitum* feeding level, between boars and castrates in humerus and *os femoris* at the restricted feeding level, between boars and sows in scapula, radius and humerus at the restricted feeding level and between boars and sows in the radius at the *ad libitum* feeding level. In all these cases boars had the higher ratios.

The new-born animals neatly followed the curvilinear pattern in the scapula, while the boar piglets in the radius were adapted to the regression line as well. The sow piglets in the radius had a lower ratio than was estimated from the regression line. The same held true for the new-born boars and sows in the case of the humerus and the *os femoris*.

4.7. GROWTH OF MUSCLE

4.7.1. *General*

The growth of muscle as one of the carcass components was described in section 4.4.1. The treatment groups in shape or slope differed with regard to sexes. The *ad libitum* (A) and restricted (R) feeding level differed in constant terms. Therefore the regressions of the increase of side muscle weight (y) on carcass side weight (x) may be given as follows:

			$S.E._D^*$	$S.E._L^*$	$S.E._Q^*$
boars	A	$ln\,y = -0.814 + 1.097\,ln\,x - 0.027\,ln^2x$	0.017	0.073	0.010
	R	$ln\,y = -0.756 + 1.097\,ln\,x - 0.027\,ln^2x$			
castrates	A	$ln\,y = -0.417 + 0.846\,ln\,x$	0.016	0.011	
	R	$ln\,y = -0.323 + 0.846\,ln\,x$			
sows	A	$ln\,y = -0.347 + 0.847\,ln\,x$	0.017	0.012	
	R	$ln\,y = -0.253 + 0.847\,ln\,x$			

*$S.E._D$ = the standard error of the difference between constant terms
*$S.E._L$ = the standard error of the slope of the linear term
*$S.E._Q$ = the standard error of the shape of the quadratic term.

TABLE 4.29. The weight of total muscle in side of the treatment groups for the different dissection stages (in kg).

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	0.214	4.22	10.92	15.75	20.82	24.25	34.91	46.41
Castrates		4.03	10.16	14.08	18.21	20.91	26.51	39.87
Sows	0.219	4.41	11.33	13.98	19.45	21.81	26.20	39.77
Restricted								
Boars			7.01	12.57	17.17	22.36	31.77	50.85
Castrates			7.66	11.30	14.95	18.34	24.11	45.78
Sows			7.83	12.05	16.37	20.72	24.80	41.01

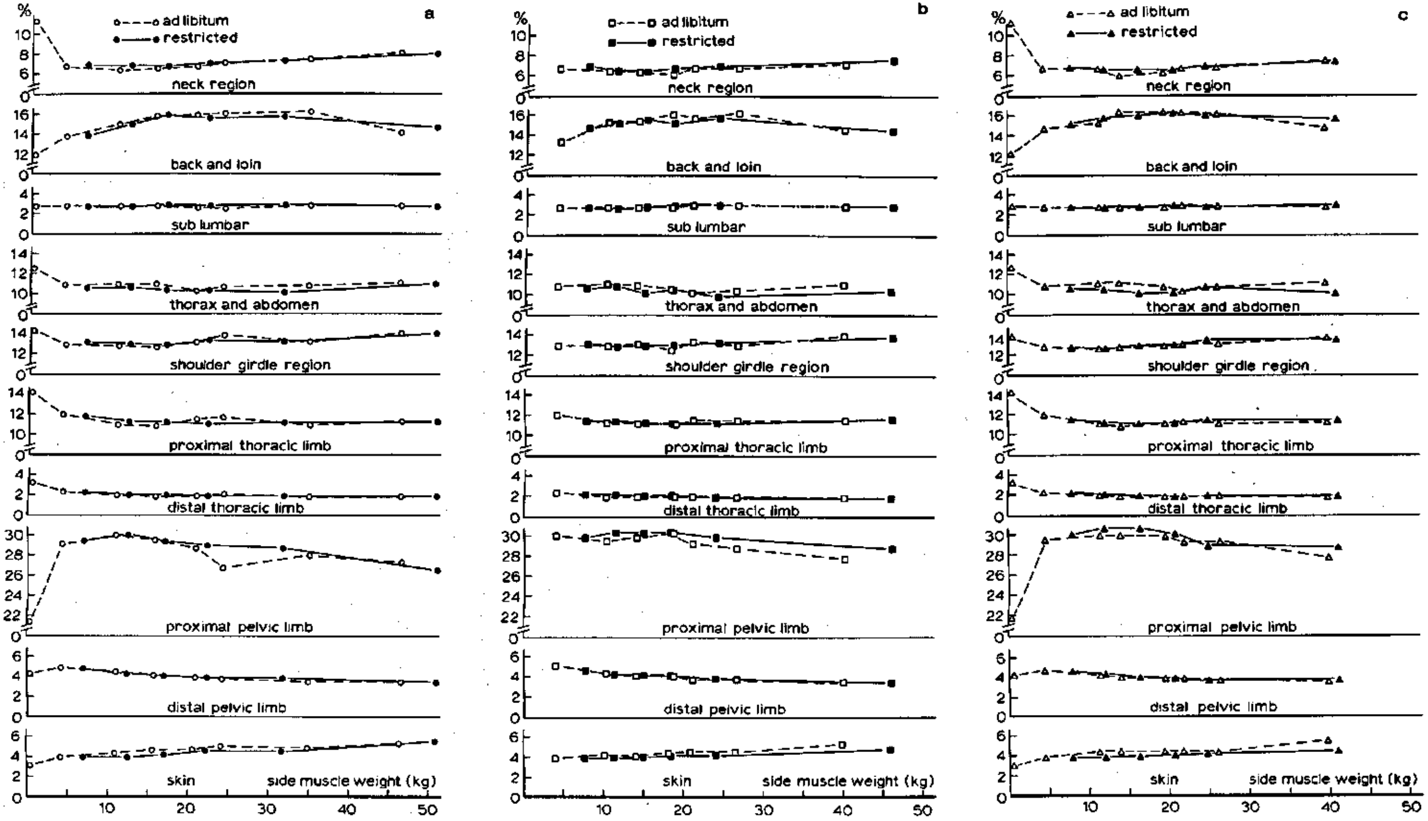

FIG. 4.22abc. Muscle weight distribution of standard muscle groups within total muscle on *ad libitum* and restricted feeding level in boars (a), castrates (b) and sows (c).

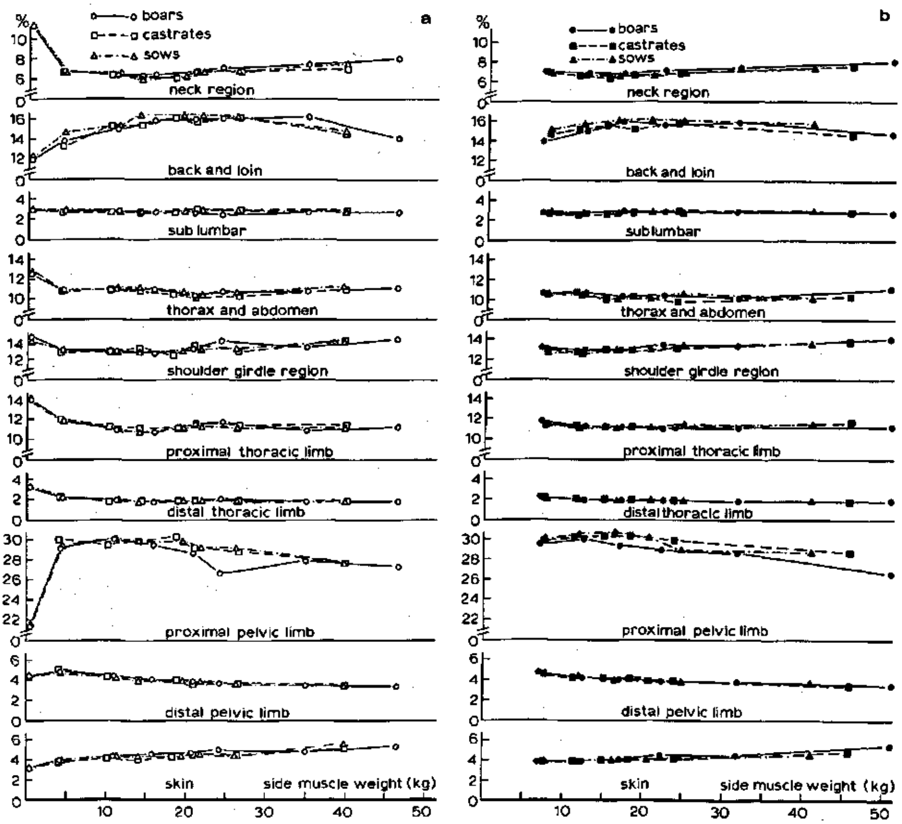

FIG. 4.23ab. Muscle weight distribution of standard muscle groups within total muscle in boars, castrates and sows on *ad libitum* (a) and restricted feeding level (b).

The results with regard to muscle weight distribution will be dealt with in the order of the muscle groups as listed in Table 3.3 on p. 62. An illustration of the alphabetical order of the anatomical groups is given in Fig. 4.21. This order is associated with that in the literature as far as our anatomical grouping does permit it.

The total side muscle weight is given in Table 4.29. The weights had an average variation coefficient of 13.7%. The total side muscle weight was the independent variate in the regressions for the anatomical groups as well as for all individual muscles.

4.7.2. *Muscle weight distribution*

The changes in the percentages during growth of the various standard muscle groups as related to total side muscle weight are demonstrated in Fig. 4.22abc and Fig. 4.23ab. In Fig. 4.22abc the influence of feeding level is depicted for boars, castrates and sows respectively, and in Fig. 4.23ab the influence of sex on the distribution is shown for the *ad libitum* and restricted feeding respectively.

The differences in each of the muscle groups will be described in the corresponding next sections in which the growth pattern of these groups with the individual muscles belonging to them will be outlined.

4.7.2.1. The muscles of the proximal pelvic limb

One of the most important group of muscles with regard to meat production is that of the proximal pelvic limb. The present group together with the group of sublumbar muscles furnishes the most valuable meat. It also comprises four of the heaviest ten muscles of the body. An impression of the size of each of the individual muscles dissected is given in Appendix 6, where they are expressed as a percentage of side muscle weight at the commercial slaughter weight.

The total weight of the muscles from which the group is made up is given in Table 4.30, expressed as a percentage of total muscle weight. At birth the percentage is comperatively low (cf. Fig. 4.22ac), it sharply increases to the first dissection stage, then there is a slight increase up to about 30% after which it steadily decreases, depending on feeding level and sex to about 28 % at maturity.

As mentioned earlier the *ad libitum* fed boars at dissection stage V showed a deviating percentage of total muscle with respect to carcass weight (cf. Fig. 4.5a). It can be seen in Fig. 4.22a that this aberration is almost totally accounted for by the deviating percentage of muscle of the proximal pelvic limb. A further explanation has been given in section 4.4.1.

The variation coefficient of the total group in average amounted to 3.9%. The average coefficients for the individual muscles varied from 6.2% in the *m. biceps femoris* to 16.9% in the *m. sartorius*. In general the coefficients were higher as the weight of the muscle was lower.

The growth pattern of the individual muscles of this group is set out in Table 4.31. A quadratic pattern in the restrictedly fed groups and in the sows was established for the *m. gluteus superficialis*. The test for this muscle on the second degree polynomial revealed differences in shape between feeding levels in boars

TABLE 4.30. The weight of the total of muscles of the proximal pelvic limb of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	21.31	29.08	29.99	29.41	28.70	26.71	27.91	27.30
Castrates		30.04	29.55	29.90	30.29	29.23	28.75	27.72
Sows	21.70	29.55	29.91	29.91	29.85	29.24	29.33	27.73
Restricted								
Boars			29.63	30.07	29.41	28.95	28.71	26.52
Castrates			29.80	30.23	30.35	30.17	29.87	28.75
Sows			29.99	30.60	30.65	30.16	28.88	28.68

TABLE 4.31. The classification and growth pattern of the muscles of the proximal pelvic limb.*

Muscle	b	s_b	Class	Feeding level group or sex group	Quadratic pattern**
M. biceps femoris	0.98	0.01	A		
M. gluteus superficialis	*1.01*	0.01	A		R−, ♀−
M. gluteus medius	0.98	0.01	A		
M. gluteus accessorius	1.01	0.02	A		
M. gluteus profundus	0.92	0.01	L		
M. semitendinosus	1.01	0.01	A		
M. semimembranosus	0.94	0.01	A$^-$		
M. quadriceps femoris	0.95	0.01	A$^-$	*ad libitum*	
	0.96	0.01	A$^-$	castrates	
	0.96	0.01	A$^-$	sows	
M. tensor fasciae latae	1.02	0.01	A		
Mm. gemelli + m. quadratus femoris	0.91	0.02	L		
M. gracilis	1.05	0.01	A$^+$		
M. sartorius	0.95	0.02	A$^-$		
M. pectineus	0.97	0.01	A$^-$		
M. adductor	0.94	0.01	A$^-$		
M. obturatorius externus	1.07	0.02	A$^+$	*ad libitum*	
	0.98	0.02	A	restricted	
	1.06	0.03	A$^+$	sows	
Total prox. pelvic limb	*0.97*	0.00	A$^-$		⚦−

* The numbers in italics are valid if the quadratic terms are ignored.

** R = restricted feeding level.

and castrates, while the sows differed in constant terms. The differences resulted in higher weights at the restricted feeding level.

All other muscles of the group exhibited a linear pattern. Considering the new-born animals, however, the linear pattern was disturbed in *mm. biceps femoris, gluteus medius, semimembranosus, quadriceps femoris, adductor* and *m. obturatorius externus,* in fact in the heaviest muscles. Furthermore the sow piglets in *m. semitendinosus* and the boar piglets in *m. gluteus superficialis* deviated from the regression line. Thus in the latter muscle the sow piglets followed the curvilinear pattern. In all cases mentioned the new-born piglets had lower weights than predicted from the regression line, except in *m. obturatorius externus,* where they positively deviated from the regression line.

In most muscles a common *b*-value for all groups could be computed. The differences in slope may be easily read from Table 4.31, because they are indicated by the missing groups in those cases where no common *b*-value was computed. Feeding level groups or sex groups that could be formed because of absence of significant differences in slope are listed in the table. Hence in the *m. obturatorius externus* slope differences were established between feeding levels in boars and castrates. Likewise in the *m. quadriceps femoris* sex differences were found at the restricted feeding level, i.e. boars had a lower *b*-value than both other sexes. A difference between feeding levels in boars existed as well, while in castrates and sows such a difference was in the constant terms. The relative weight of the muscle was higher at the restricted feeding level in the latter case, but was the reverse in the boars.

For the total group of muscles a convex quadratic pattern was ascertained in castrates. A tendency to such a pattern in castrates was only found in the *m. adductor*. Differences were only found in the constant terms, viz. between feeding levels in castrates and sows (Fig. 4.22bc) and between boars and the other sexes at both feeding levels (Fig. 4.23ab), resulting in lower percentages for the *ad libitum* feeding level and for boars respectively. The new-born boars and sows deviated clearly from the linear pattern with a negative term.

Because of these differences in constant terms and the appearance of the quadratic term the regression equations have to be given as follows:

			S.E.$^*_D$	S.E.$^*_L$	S.E.$^*_Q$
boars		$\ln y = -1.133 + 0.960 \ln x$	0.021	0.007	
castrates	A	$\ln y = -1.319 + 1.105 \ln x - 0.024 \ln^2 x$	0.007	0.036	0.007
	R	$\ln y = -1.306 + 1.105 \ln x - 0.024 \ln^2 x$			
sows	A	$\ln y = -1.173 + 0.981 \ln x$	0.011	0.009	
	R	$\ln y = -1.152 + 0.981 \ln x$			

* see section 4.7.1.

The only muscles in which no differences at all were found, were *mm. semitendinosus* and *gemelli + quadratus femoris*. The differences in constant terms for all individual muscles will not be given. The feeding levels differed in the gluteus muscles (except in *m. gluteus medius*), in *mm. quadriceps femoris, tensor fasciae latae, gracilis, sartorius, pectineus* and *adductor*. Mostly castrates were involved alone or in combination with one of the other sexes or both. In all cases the higher percentages were established at the restricted feeding level. The differences between sexes concern those between boars and the other sexes in *mm. biceps femoris, gluteus medius, semimembranosus, gracilis, pectineus* and *adductor*, appearing sometimes at both feeding levels, sometimes at one of them, mostly at the restricted feeding level. In all cases the boars exhibited the lower percentages. A difference between castrates and sows (in favour of the former) was only found in *m. adductor* at the restricted feeding level.

The slight decreasing growth pattern of the total group was followed by the majority of the constituent muscles. The deeper situated muscles *mm. gluteus profundus* and *gemelli + quadratus femoris* show a low (L) pattern, but also *mm. adductor* and *semimembranosus* show a tendency to such a pattern. On the other hand the more superficial *m. gracilis* demonstrated an A^+-pattern, while also *mm. tensor fasciae latae, semitendinosus* and *gluteus superficialis* have such a tendency. A faster growth was also found in the *m. obturatorius externus*, at least for the *ad libitum* fed groups and the sows. Since this muscle is firmly attached to the *os coxae* it may have the same relative pattern as the *os coxae* within total bone.

With regard to the literature the sex differences between sows and castrates in the leg muscles as found by WILSON (1968b) could not be confirmed, while the sex effect in the *m. adductor* was the reverse in this study. The nutritional effects on the *m. biceps femoris* (WILSON, 1968b) and *mm. semitendinosus* and *gracilis* (WILSON, 1968a), were not confirmed either. The effect on *m. tensor fasciae latae* found by the latter was in opposite direction.

The different proportions as a result of the nutritional treatment in various muscles of the group in the present study were not found by ANDERSEN (1975) in cattle, except that he did find a faster growth for the *m. obturatorius externus*. But MURRAY and SLEZACEK (1975) found a faster growth of the muscles of the total pelvic limb of sheep on a restricted feeding level. The lower energy ration also resulted in a higher proportion of this muscle group in pigs (CARDEN and GOENAGA, 1977), but in the experiments of RICHMOND and BERG (1971b) the effect was not discernible.

The faster growth of the *m. obturatorius externus* and the tendency to this in the *m. semitendinosus* as reported here, was also found by CUTHBERTSON and POMEROY (1964). Also DUMONT et al. (1973) found within the leg an increasing tendency to a faster growth for the semitendinosus muscle, but also for the *m. semimembranosus*. The latter muscle, however, rather showed a decreasing tendency in the present study. Our results with regard to *m. adductor* and *m. semimembranosus* are supported by COLE et al. (1976).

The slightly decreasing pattern of the group was also found by SEEBECK (1968b) in sheep and by BUTTERFIELD and BERG (1966b) and BERGSTRÖM (1978) in cattle, contrary to the findings of LOHSE et al. (1971) in sheep. In pigs WILSON (1968b) reported no change with total muscle weight, while in the experiment of DAVIES (1974b) the total of the group increased. The latter, however, examined the very first part of the whole trajectory leading to higher *b*-values. It might be in accordance with the present study taking into account the new-born piglets.

Although comparison with DAVIES' study may be questionable the higher *b*-value for the *mm. gluteus superficialis* and *obturatorius*, the tendency to a higher value for the *m. semitendinosus* and the lower value for the *m. quadratus femoris* relative to other muscles were also found. But on the other hand the *mm. semimembranosus* and *adductor* grew comparatively faster than in the present study.

In general the *b*-values from the present study agree well with those from BERGSTRÖM (1978) in cattle. In his experiment the *m. semimembranosus* and the *m. gluteus accessorius* seem to grow comparatively faster and slower respectively. A clear exception again is the obturator muscle. The same holds true for some other muscles, but there are striking similarities.

There is more differentiation in the values in case of ruminants than in case of pigs, especially as compared with the experiments of BUTTERFIELD and BERG (1966a) and LOHSE et al. (1971). The data in sheep reported by the latter do deviate markedly in the growth ratios of various muscles.

LOHSE et al. (1971) found a monophasic pattern for the total of the group. In the present study also considering the new-born animals, surely a diphasic pattern would be formulated in agreement with the high-average impetus as asserted by BUTTERFIELD and BERG (1966b) or with the impetus changed later on into high-low (BERG and BUTTERFIELD, 1976c). With regard to the individual muscles a high-average impetus was given to the heaviest muscles, neatly in accordance with those in the present study, except for the *m. quadriceps femoris* which was subdivided in their study into the four heads and from which two of them were too variable for classification. Furthermore the *m. obturatorius externus* was given a monophasic pattern. The classification in sheep showed more differences with the pattern just described.

4.7.2.2. The muscles of the distal pelvic limb

The weights of muscles together forming the group of muscles of the distal pelvic limb are given in Table 4.32 as a percentage of total muscle weight. They show a decreasing pattern from about 5% to about 3.5% as can also be concluded from Fig. 4.22abc. The average variation coefficient was 5.6%, while that of the individual muscles rated from 6.0% in *mm. flexores* and *extensores* to 13.9% in *m. soleus*.

In Table 4.33 the growth pattern is elucidated further. As far as the stages I to VII are involved only a linear pattern appeared to exist for the constituent muscles as well as for the total group. But the new-born animals, except the boar piglets in *m. soleus*, deviated from the regression line (cf. Fig. 4.22ac) in the same way as in the proximal muscles. It is in contrast to the results of BUTTERFIELD and BERG (1966a) and LOHSE et al. (1971) who only found a linear pattern, although as far as being comparable the latter also found a diphasic pattern for the extensor group of muscles and for two other distal muscles.

Differences in slope were established for *mm. flexores* and *extensores* between feeding levels in boars with a higher *b*-value when *ad libitum* fed, and between castrates and the other sexes at the *ad libitum* feeding level. The castrates grew slowest. The boars and sows also differed, but in constant terms at the same feeding level, while the feeding levels differed in sows in constant terms as well.

TABLE 4.32. The weights of the total of the muscles of the distal pelvic limb of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	4.29	4.84	4.45	4.15	3.90	3.78	3.53	3.40
Castrates		5.09	4.36	4.13	4.11	3.72	3.77	3.53
Sows	4.23	4.63	4.18	3.98	3.91	3.85	3.66	3.47
Restricted								
Boars			4.77	4.29	4.03	3.92	3.83	3.39
Castrates			4.58	4.26	4.20	4.11	3.87	3.41
Sows			4.50	4.26	3.98	3.81	3.75	3.64

TABLE 4.33. The classification of the linear growth pattern of the muscles of the distal pelvic limb.

Muscle	b	s_b	Class	Feeding level group or sex group
M. soleus	0.96	0.02	A^-	
M. gastrocnemius	0.81	0.01	$L^=$	
M. flexor digitorum superficialis	0.78	0.01	$L^=$	
Mm. flexores and *extensores*	0.87	0.01	L^-	restricted
	0.87	0.01	L^-	castrates
	0.90	0.01	L	sows
Total distal pelvic limb	0.85	0.01	L^-	

The sows had higher proportions at the restricted feeding level. Likewise had the boars in *m. flexor digitorum superficialis*. In the same muscle boars had higher proportions at the restricted feeding level than the other sexes. Further differences in constant terms were established in the *m. gastrocnemius* in that sows had lower percentages than the male sexes at both feeding levels.

The total distal pelvic limb only showed differences in constant terms for the sexes, in that sows had lower proportions than the other sexes.

The distal muscles as a group grew slower than the proximal ones, as is found by many others. The *m. soleus* as a more superficially situated muscle deviated most from the L^--pattern. As a more deeply situated muscle, the *m. flexor digitorum superficialis* embedded in the *m. gastrocnemius* may grow somewhat slower.

The comparison of the height of the *b*-values of the individual muscles poses problems because in this study the extensor and flexor muscles were not dissected any further. In comparison with the values reported by BERGSTRÖM (1978) in cattle the present data appear to be in good agreement. A clear exception, however, is that in his results the *m. soleus* to the contrary exhibits the lowest value.

An effect of nutritional treatment is barely found in this group of muscles. Only CARDEN and GOENAGA (1977) reported a faster growth at a low energy level for barrows, which is the opposite of the results found in boars in the present study, but only about 40% of the total group was involved. Castrates + sows, however, had a higher proportion at the higher energy level in the results of RICHMOND and BERG (1971b). Sex differences as found in the present study were not reported in the literature. The differences, however, were found mainly between boars and the other sexes, while in the literature almost always boars are left out from the experiments.

4.7.2.3. The muscles of the proximal thoracic limb

The percentages with respect to total muscle weight of the group of muscles of the proximal thoracic limb are given in Table 4.34. There is only a very slight decrease from about 12% in stage I to about 11.5% in stage VII, which may also

TABLE 4.34. The weights of the total of the muscles of the proximal thoracic limb of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	14.17	11.95	10.94	10.83	11.55	11.72	10.92	11.33
Castrates		11.96	11.24	11.13	11.10	11.47	11.47	11.49
Sows	14.17	11.92	11.05	10.74	11.07	11.26	11.11	11.19
Restricted								
Boars			11.80	11.30	11.22	11.06	11.19	11.26
Castrates			11.42	11.35	11.22	11.16	11.20	11.61
Sows			11.41	11.10	11.02	11.10	11.40	11.51

be seen in Fig. 4.22abc. The average variation coefficient amounted to 5.1%, while the coefficients for the individual muscles varied from 5.9% in *m. triceps brachii* to 15.3% in *m. tensor fasciae antebrachii*, again increasing as the muscle weight decreased.

The growth pattern of the individual muscles is outlined in Table 4.35. Considering first solely the linear pattern it appeared that the difference in slope between feeding levels was a faster growth of castrates at the restricted feeding level in *m. teres minor* and the reverse for boars in *m. biceps brachii*. The sex

TABLE 4.35. The classification and growth pattern of the muscles of the proximal thoracic limb.*

Muscle	b	s_b	Class	Feeding level group or sex group	Quadratic pattern**
M. deltoideus	*1.03*	0.01	A^+		♂+
M. subscapularis	*0.99*	0.01	A		⚦+
M. infraspinatus	*1.01*	0.01	A		+
M. supraspinatus	1.03	0.01	A^+		
M. teres major	1.01	0.01	A		
M. teres minor	*0.95*	0.02	A^-	*ad libitum*	
	0.93	0.03	A^-	boars	
					⚦+
	0.97	0.03	A^-	sows	
M. coracobrachialis	0.96	0.01	A^-		
M. tensor fasciae antebrachii	1.05	0.02	A^+		
M. triceps brachii	0.95	0.01	A^-		
M. biceps brachii	0.96	0.02	A^-	*ad libitum*	
	0.96	0.02	A^-	castrates	
	0.97	0.02	A^-	sows	
M. brachialis	0.89	0.01	L		
Total prox. thoracic limb	*0.98*	0.01	A		R+, ⚦+

*The numbers in italics are valid if the quadratic terms are ignored.

** R = restricted feeding level.

differences at the restricted feeding level were those between castrates and the other sexes in *m. teres minor*, and between boars and the other sexes in *m. biceps brachii*. The castrates grew faster and the boars slower than the others.

Differences between feeding levels were further found in constant terms for castrates and sows in *m. teres major* and for castrates in *m. tensor fasciae antebrachii*. The proportions were higher at the restricted feeding level in the former muscle, but were the reverse in the latter. In both muscles the boars differed from the other sexes at the restricted feeding level in the *m. teres major* and at the *ad libitum* level in *m. tensor fasciae antebrachii*. The boars had the highest percentages.

The group as a whole followed an almost average pattern. The deeply situated *m. brachialis* deviated from this with a L-pattern, while on the other hand more superficial muscles such as *mm. deltoideus*, *supraspinatus* and *tensor fasciae antebrachii* exhibited a higher *b*-value (A^+-pattern). Like some heavy muscles of the proximal pelvic limb the *m. triceps bracii* tended to have a slower growth. This tendency in the last-named muscle and the lower *b*-value for *m. brachialis* were also found by DAVIES (1974b). However, the muscles given the A^+-pattern were not conspicious in his results. Except for the tendency in the *m. triceps brachii* BERGSTRÖM (1978) found similar results in cattle.

Several muscles of this group demonstrated a curvilinear concave pattern. A quadratic pattern was found for boars in *m. deltoideus*, for castrates in *mm. subscapularis* and *teres minor* and in the group as a whole, while in this group also the restricted feeding level groups had a quadratic pattern. A fully quadratic pattern was ascertained for *m. infraspinatus*. It may be stated that such a pattern at least would demonstrate a diphasic pattern. This could be the reason that the muscle could not be classified by BUTTERFIELD and BERG (1966a), for the muscle is well-defined and is surely not of vestigial size.

A diphasic pattern was found for *m. deltoideus* by BUTTERFIELD and BERG (1966a); the low-average pattern seems in accordance with a concave pattern. Likewise LOHSE et al. (1971) found low-average patterns in sheep in *mm. teres minor* and *subscapularis*. The group as a whole also had a low-average pattern in the experiment of the former (1966b), which is in accordance with the present study, but LOHSE et al. (1971) found an average-low pattern. As far as the linear pattern was involved the heights of the *b*-values are in reasonable agreement with those listed by BUTTERFIELD and BERG (1966a) in cattle, except for the *m. supraspinatus* having a comparatively lower value. The *m. deltoideus* had a comparatively lower value in the results of LOHSE et al. (1971).

The picture as to the adaptation of the new-born animals to the regression lines was somewhat variable. The sow piglets were not adapted to the curvilinear pattern in *m. infraspinatus*; they had a deviating negative term. They also deviated from the linear pattern with a positive term in *mm. deltoideus*, *supraspinatus* and *teres major*. The same deviating pattern was established for the boar piglets in the two last-named muscles, and in *mm. coracobrachialis* and *tensor fasciae antebrachii*. The boar piglets also had a relatively higher percentage for the total group of muscles.

The quadratic patterns resulted in a number of differences. Shape differences were found between feeding levels in boars for *mm. deltoideus* and *infraspinatus*, and in castrates for the latter muscle. At the restricted feeding level a more concave pattern was calculated. Differences in shape between sexes were inconsistent. It resulted in higher percentages in castrates than in boars at the restricted feeding level for *m. deltoideus*, but the reverse was computed at the *ad libitum* feeding level for *m. infraspinatus*. In the latter muscle boars had a more concave pattern than sows at the restricted feeding level, while also castrates had a more concave pattern than sows at the *ad libitum* feeding level for *m. teres minor*.

Finally differences in constant terms between feeding levels were found in boars for *m. teres minor*, resulting in higher percentages for the restricted feeding level. Furthermore the sows had lower proportions than the other sexes at both feeding levels in *m. deltoideus*.

In a number of cases in ANDERSEN's (1975) results, muscles were combined, so that the results as to the influence of nutritional treatment were not comparable. Some of the differences found in the present study fell in ANDERSEN's combined groups in which he also found differences. On the other hand he did not find an influence of feeding level in *mm. deltoideus* and *biceps brachii*.

The suggested relationships between a relatively fast growing scapula and a relatively fast growing *m. subscapularis* (CUTHBERTSON and POMEROY, 1964) could not be supported based on the results of the present study.

Although a number of individual muscles was affected by the nutritional treatment and sex, the total group of muscles of the thoracic limb was not, which is in accordance with the literature.

4.7.2.4. The muscles of the distal thoracic limb

The *mm. flexores* and *extensores* were not further dissected and thus treated as a group. The weights as a percentage of muscle weight are presented in Table 4.36. There is a slight decrease in weights from just beyond 2% to just below 2%. The average variation coefficient amounted to 7.5%.

TABLE 4.36. The weights of the total of the muscles of the distal thoracic limb of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	3.26	2.28	1.97	1.84	1.92	2.05	1.83	1.87
Castrates		2.33	1.86	1.95	1.89	1.89	1.87	1.86
Sows	3.18	2.19	1.94	1.85	1.90	1.89	1.89	1.81
Restricted								
Boars			2.24	2.02	1.98	1.91	1.87	1.84
Castrates			2.14	2.15	2.05	1.98	1.86	1.79
Sows			2.14	2.05	1.95	1.86	1.91	1.88

The decrease is affirmed by a b-value of 0.91 ± 0.01 (L) for this group. It was a linear pattern from which the new-born animals did not deviate. A monophasic pattern was also found by LOHSE et al. (1971), but BUTTERFIELD and BERG (1966b) inclined to a low-average pattern. The value of 0.91 is comparatively higher than found in the results of the just mentioned workers and in those of DAVIES (1974b) and BERGSTRÖM (1978).

Differences in this group appeared to be limited to differences in constant terms between feeding levels in boars and sows. The higher proportions were calculated for the restricted feeding level. This was also found by MURRAY and SLEZACEK (1975) in sheep, but not by RICHMOND and BERG (1971b) in pigs. CARDEN and GOENAGA (1977) did find differences in slope after nutritional treatment, but a faster growth was achieved by restriction of protein concentrations in the diet.

4.7.2.5. The muscles of the neck region

In Table 4.37 the percentages of the total of the muscles belonging to this group is presented with respect to total muscle weight. The percentages decrease slightly first from just below 7% to just below 6.5% and then increase to about 7.5%, except in boars where the ultimate percentage rises to more than 8% (cf. Fig. 4.22abc). The average variation coefficient was 7.0%. The variation coefficients of the individual muscles rated from 6.4% in *m. brachiocephalicus* to 23.2% in *mm. recti* and *obliqui capitis*, while exceptional coefficients were calculated for *m. omohyoideus* and *m. sternocephalicus*, viz. 31.7 and 43.3% respectively. The relationship between the height of the variation coefficients and the weights of the muscles was largely disturbed in this group of muscles, because of errors introduced by splitting of the carcass. The muscles that are most affected have been listed in section 3.7.2.1.

The classification and growth pattern of the individual muscles are given in Table 4.3.8. Absence of differences in some muscles may also be caused by the high variation coefficients, e.g. the differences between sows and the other sexes

TABLE 4.37. The weights of the total of the muscles of the neck region of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	11.34	6.79	6.40	6.48	6.80	7.10	7.46	8.10
Castrates		6.70	6.42	6.34	6.12	6.71	6.76	7.11
Sows	11.28	6.68	6.59	5.86	6.15	6.67	6.70	7.44
Restricted								
Boars			6.89	6.78	6.73	7.01	7.35	8.01
Castrates			6.92	6.50	6.39	6.63	6.90	7.54
Sows			6.77	6.51	6.50	6.47	6.86	7.29

in *m. sternocephalicus*. On the other hand in *m. omohyoideus* differences between feeding levels in boars and sows in constant terms were ascertained. The higher percentages were found for the restricted feeding level.

A fully quadratic concave pattern was established for *mm. splenius* and *longus capitis, longus colli* etc., and in the group as a whole. In addition in *m. splenius* a positive cubic term was present for boars. Furthermore tendencies were found towards concave quadratic patterns for the *ad libitum* feeding level group in *m. brachiocephalicus*, for the restricted feeding level group in *m. omohyodeus*, and for boars in *m. omotransversarius*, thus supporting the curvilinear pattern for the whole group.

BUTTERFIELD and BERG (1966a) also found diphasic patterns in *mm. brachiocephalicus, longus colli* and *omotransversarius*, classified as low-average or average-high which is in accordance with the concave pattern in the present study. The *m. splenius*, however, only had a monophasic (although high) pattern; but this muscle was diphasic in the work of LOHSE et al. (1971). Since the muscles of the group in the present study are divided between two groups in the experiments just mentioned, it poses some problems as to the comparability. Nevertheless it might be stated that the concave pattern found is in accordance with the diphasic pattern reported for both groups.

TABLE 4.38. The classification and growth pattern of the muscles of the neck region*.

Muscle	b	s_b	Class	Feeding level group or sex group	Quadratic pattern	Cubic pattern
Mm. recti and *obliqui capitis*	1.02	0.03	A			
M. omotransversarius	0.91	0.03	L	*ad libitum*		
	1.05	0.03	A^+	restricted		
	0.96	0.03	A^-	castrates		
	0.92	0.05	L	sows		
M. splenius					+	
	1.08	0.02	H	restricted		
	1.10	0.02	H	boars		♂ +
	1.02	0.02	A	sows		
M. longissimus capitis et atlantis	1.09	0.02	H			
M. semispinalis capitis	1.06	0.01	A^+			
M. brachiochephalicus	1.02	0.01	A			
M. scalenus dorsalis + *m. scalenus ventralis*	1.02	0.01	A			
M. omohyoideus	1.00	0.04	A			
M. sternocephalicus	1.05	0.06	A^+			
Mm. longus capitis, longus colli etc.	*1.06*	0.01	A^+		+	
Total neck region	*1.04*	0.01	A^+		+	

*The numbers in italics are valid if the high power terms are ignored.

At birth a much higher percentage was found than in later stages (see Fig. 4.22ac), especially *m. splenius* contributed to it. For the muscles having a linear pattern except for *m. sternocephalicus*, the new-born piglets deviated from the regression line with a positive term. But they were well-adapted to the curvilinear pattern of *mm. splenius, longus capitis, longus colli* etc. and the group as a whole, and they also were in line in *m. omotransversarius.*

Feeding level groups and sex groups only had to be formed in *m. omotransversarius* and (considering a linear pattern) in *m. splenius*. The difference in slope between feeding levels for boars in the former and for castrates in the latter muscle resulted in a faster growth at the restricted feeding level. When tested quadraticly and cubicly in case of *m. splenius* also in boars a difference in shape appeared, indicating a faster growth at the restricted feeding level as well. The differences in shape between sexes in this muscle at the *ad libitum* feeding level were those between boars and the other sexes, the boars showing the higher percentages. All other possible sex differences in this muscle were found as differences in constant terms. Although the proportions in the *m. splenius* were significantly higher for boars than for castrates, this difference in proportions was comparatively smaller than the difference in proportions between castrates and sows; the sows having lower percentages. The positive cubic term found in boars resulted in a more diverging curve from that of the other sexes, in spite of a counteracting effect of a negative quadratic term.

Differences in constant terms were further established in most other muscles for differences between feeding levels for one of the sexes or for differences between sexes in various combinations. In the group of total muscles differences in constant terms were those between feeding levels in castrates and between boars and both other sexes at both feeding levels. All differences between feeding levels revealed higher proportions at the restricted level, while all differences between boars and both other sexes showed higher proportions for the boars. The only time that a difference between castrates and sows was found (at the restricted feeding level in *mm. scalenus dorsalis + scalenus ventralis*) the sows had the higher proportion. Influences of nutritional treatment on intrinsic muscles of the neck were also found by ANDERSEN (1975) in cattle (but not for *m. splenius*), and MURRAY and SLEZACEK (1975) in sheep in the way as described in the present study. RICHMOND and BERG (1971b) and CARDEN and GOENAGA (1977), however did not report such influences in pigs.

The increase of the percentages in later stages is dominating, so that an A^+-growth pattern was reached. Though most muscles follow this pattern some deviations occurred. There is the clear difference between feeding levels in *m. omotransversarius*; the *ad libitum* groups and the sows show a L-pattern, while also the castrates and the *ad libitum* fed boars (*b*-value 0.94 ± 0.04) show a tendency towards that pattern. On the other hand *b*-values with an H-pattern were found in *m. splenius* for the restrictedly fed animals and particularly for the boars. A high pattern was also computed for *m. longissimus capitis et atlantis* which is mainly situated between *m. splenius* and *m. semispinalis capitis.*

The height of the *b*-values of the neck muscles was much lower in the results of

TABLE 4.39. The weights of the total of the muscles of the back and loin of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	11.88	13.81	14.96	15.89	15.87	16.03	16.21	14.13
Castrates		13.25	15.29	15.41	16.13	15.72	16.22	14.55
Sows	12.13	14.57	15.22	16.37	16.31	16.24	16.08	14.64
Restricted								
Boars			13.87	14.99	15.91	15.54	15.74	14.58
Castrates			14.63	15.17	15.60	15.23	15.77	14.49
Sows			15.12	15.69	15.96	16.18	15.92	15.57

DAVIES (1974b), but there only the first stages were involved. The values were in reasonable agreement with those of BUTTERFIELD and BERG (1966ab), BERGSTRÖM (1978) and LOHSE et al. (1971). Comparatively low values, however, were found for *m. longissimus capitis et atlantis*, *m. semispinalis capitis* and *m. splenius* listed in the order of each of the references respectively. Some other aberrations occurred in comparison with BERGSTRÖM's results as far as the females were involved.

4.7.2.6. The muscles of the back and loin

The total weights of these muscles expressed as a percentage of total muscle weight are given in Table 4.39. The average variation coefficient was 5.0%, while the constituent muscles rated from 6.3% in *m. longissimus thoracis et lumborum* to 21.9% in *m. longissimus cervicis*. The percentages at the outset (stage I) are about 14%, they increase to more than 16%, at least at the *ad libitum* level, after which they decrease to about 14.5% (cf. Fig. 4.22abc).

The classification and growth pattern for the muscles of the group are dem-

TABLE 4.40. The classification and growth pattern of the muscles of the back and loin*.

Muscle	b	s_b	Class	Quadratic pattern
M. serratus dorsalis cranialis + *m. serratus dorsalis caudalis*	1.03	0.01	A$^+$	
M. iliocostalis	1.06	0.01	A$^+$	
M. longissimus cervicis	1.00	0.02	A	
M. longissimus thoracis et lumborum	*1.02*	0.01	A	–
Mm. multifidi	1.07	0.01	A$^+$	
Total back and loin	*1.04*	0.01	A$^+$	–

*The numbers in italics are valid if the quadratic terms are ignored.

onstrated in Table 4.40. A fully quadratic pattern was established for *m. longissimus thoracis et lumborum*. Since this large muscle determines the results for the group as a whole to a great extent, the total group had a fully convex quadratic pattern as well. Only the new-born boars were in line with the quadratic pattern. The boar piglets were not adapted to the linear pattern in *m. serratus dorsalis cranialis + m. serratus dorsalis caudalis* and *m. iliocostalis*, as both sexes were not in *mm. multifidi.*

Most of the muscles of this group were found to have a diphasic pattern (BUTTERFIELD and BERG, 1966a). Taking into account the new-born stage it agrees with our results. LOHSE et al. (1971) only found a diphasic pattern for *mm. iliocostalis* and *longissimus thoracis et lumborum.*

Considering the *b*-values it is seen that the intrinsic muscles in general follow the pattern of the total of the group. The more deeply situated *m. longissimus cervicis* shows a somewhat lower value; however, the also more deeply situated *mm. multifidi* tend to a faster growth. Because of the (at least) diphasic pattern it is difficult to compare the *b*-values of the present study with those of BUTTERFIELD and BERG (1966a) and LOHSE et al. (1971), as the values are given for the various trajectories only. DAVIES (1974b) found a higher value for the *m. longissimus thoracis et lumborum*, this is for the first stages. As the muscle has a high-average impetus, the value hence for the total trajectory may be lower. In comparison with the data in cattle from BERGSTRÖM'S (1978) experiment it appears that he found comparatively much lower values for *mm. multifidi* and higher values for *m. serratus dorsalis cranialis + m. serratus dorsalis caudalis.*

In the serratus muscles differences in constant terms were found between sexes. Boars had higher proportions than the other sexes. The same was established (at the restricted feeding level) in *m. iliocostalis*, in which in addition sows had higher proportions than castrates. A difference in constant terms between the feeding levels in castrates showed a higher proportion for the *ad libitum* level.

The test results on the second degree polynomial revealed differences in shape between feeding levels in boars and between castrates and the other sexes at the *ad libitum* feeding level. The differences in constant terms were those between sows and the other sexes at both feeding levels. It turned out that sows had the highest percentages in the *m. longissimus thoracis et lumborum* (compare Fig. 4.23ab), whereas boars appeared to have the lowest percentages. With regard to the feeding level the highest percentage was computed for the *ad libitum* level. Fig. 4.22abc may be compared because practically the same differences were found for the total group of muscles. ANDERSEN (1975) reported a similar influence of feeding level on this muscle. CARDEN and GOENAGA (1977) did not find such an influence for the group of muscles surrounding the spinal column that also includes the sublumbar muscles. Thus this agrees with our results, because in both muscle groups the boars were involved, whereas CARDEN and GOENAGA (1977) worked with castrates only.

4.7.2.7. The sublumbar muscles

In Table 4.41 the weights of the sublumbar muscles as a percentage of total

TABLE 4.41. The weights of the total of the sublumbar muscles of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	2.78	2.76	2.77	2.73	2.60	2.47	2.77	2.68
Castrates		2.68	2.74	2.68	2.70	2.91	2.92	2.84
Sows	2.81	2.73	2.69	2.72	2.69	2.86	2.78	2.63
Restricted								
Boars			2.72	2.69	2.93	2.79	2.86	2.71
Castrates			2.64	2.58	2.70	2.80	2.96	2.84
Sows			2.75	2.66	2.75	2.89	2.74	2.93

muscle weight are presented. The average variation coefficient was 6.7%. The percentages of this group of muscles hardly change; they remain at about 2.7–2.9% (see Fig. 4.22abc).

The growth pattern was a linear one from which the new-born animals did not deviate. Because of sex differences in slope between boars and castrates at both feeding levels no common regression coefficient could be calculated. The group of muscles grew faster in castrates. Since no differences in slope between feeding levels were apparent the sex groups could be formed. Boars, castrates and sows had a *b*-value of 1.00 ± 0.01 (A), 1.05 ± 0.01 (A^+) and 1.02 ± 0.01 (A) respectively.

Differences in constant terms were found between feeding levels in boars, the proportions being higher for the restricted feeding level. ANDERSEN (1975) did not find an influence of feeding level in this group, nor did CARDEN and GOENAGA (1977) for the group of muscles surrounding the spinal column. That group also comprises muscles of the back and loin as described earlier. For the same group RICHMOND and BERG (1971b) reported higher proportions for castrates than sows. A tendency to such a difference appeared from this study as far as the sublumbar muscles are involved, but for those of the loin and back the opposite was found.

The height of the *b*-values were in good agreement with those found by BUTTERFIELD and BERG (1966b) and BERGSTRÖM (1978), and were in the range as reported by DAVIES (1974b). The values given by LOHSE et al. (1971) were comparatively higher and the value given by ANDERSEN (1975) for the same combination of sublumbar muscles as in this study (*m. iliacus, m. psoas major, m. psoas minor* and *m. quadratus lumborum*) was comparatively lower.

4.7.2.8. The muscles of the abdominal and thoracic wall

The total of the weights of muscles forming the present group of muscles were likewise expressed as a percentage of total muscle weight and are presented in Table 4.42. The percentages of the group as a whole do not change much (cf. Fig.

TABLE 4.42. The weights of the total of the muscles of the abdominal and thoracic wall of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	12.56	10.92	10.93	10.98	10.32	10.70	10.83	11.09
Castrates		10.71	10.97	10.84	10.47	10.15	10.33	10.98
Sows	12.73	10.74	11.05	11.17	10.64	10.22	10.62	11.13
Restricted								
Boars			10.55	10.67	10.34	10.36	10.11	11.04
Castrates			10.63	10.75	10.14	10.45	9.76	10.31
Sows			10.52	10.42	9.98	10.07	10.62	10.01

4.22abc). They have a tendency to decrease slightly from about 11 to about 10% and after that they increase slightly again to 11%.

The average variation coefficient amounted to 5.1%. The average coefficients of the individual muscles varied from 7.8% in *mm. intercostales* to 14.9% in *m. transversus costarum*. Those of the four abdominal muscles varied from about 9 to 11%.

In Table 4.43 the growth pattern is shown. Beside the total of the group as a whole, the total of the four abdominal muscles was calculated as well. A quadratic pattern was exhibited by boars and castrates in *mm. intercostales*.

A differentiated picture was seen as to the new-born animals. The boar piglets deviated negatively from the regression line in the abdominal muscles, except for *m. rectus abdominis*, and in the total of these muscles. The sow piglets were adapted to the linear pattern of *m. obliquus abdominis externus* and to the group of abdominal muscles as well, but positively deviated in *m. rectus abdominis*. Only the new-born boars were adapted to the curvilinear pattern of the *mm. intercostales*. They positively deviated from the regression line in the other thoracic muscles as well as in the total group of muscles. Except for *m. transversus thoracis*, the sow piglets deviated positively from the regression line for the thoracic muscles as well as for the group as a whole.

Of the muscles of the abdominal wall a diphasic pattern was found for *m. obliquus abdominis externus* by LOHSE et al. (1971) and BUTTERFIELD and BERG (1966a), while the latter also established such a pattern in *m. transversus abdominis*. However, the muscles were classified as having a high-average impetus, whereas in the present study the new-born animals had a negative term. On the other hand LOHSE et al. (1971) listed an average-high pattern for the former muscle. *Mm. intercostales* were found to have a diphasic pattern by LOHSE et al. (1971), while the diaphragm was classified as monophasic. The *mm. intercostales* were too variable to classify according to BUTTERFIELD and BERG (1966a).

From Table 4.43 it can be seen that feeding level groups and sex groups were formed in both transversus muscles of the thoracic wall. Differences in slope between feeding levels existed in boars, that grew faster at the *ad libitum* level. At the *ad libitum* feeding level boars differed in slope from castrates, in that both muscles grew faster in boars than in castrates. A slope difference between boars and sows in *m. transversus costarum* also resulted in a higher growth coefficient for boars.

The *b*-value of the total of the muscles of the abdominal wall was identical to that of the total of the whole group. Cuthbertson and Pomeroy (1964) found that the abdominal group of muscles grew slower than the thoracic group. In contrast to most other muscle groups there was a rather large differentiation among the individual muscles. L and L$^-$-patterns were established in *mm. transversus abdominis* and *transversus thoracis*. Both muscles are more deeply situated. On the other hand *mm. rectus abdominis* and *transversus costarum* deviate from the general pattern with growth coefficients classified as A$^+$ and H, while both muscles actually also belong to the category of less superficial muscles. The diaphragm tends to a lower pattern (A$^-$) and is more deeply situated as well. But in contrast the deep *mm. intercostales* have only an average pattern; they, however, are firmly attached to the relatively fast growing ribs.

The *b*-values found by Davies (1974b) for the muscles of the abdominal wall lay around our value for the *m. rectus abdominis*. The values found by Butterfield and Berg (1966a), Lohse et al. (1971) and Bergström (1978) are still

Table 4.43. The classification and growth pattern of the muscles of the abdominal and thoracic wall*.

Muscle	*b*	s_b	Class	Feeding level group or sex group	Quadratic pattern
M. obliquus abdominis externus	1.02	0.01	A		
M. obliquus abdominis internus	0.97	0.01	A$^-$		
M. transversus abdominis	0.87	0.01	L$^-$		
M. rectus abdominis	1.05	0.01	A$^+$		
Total abdominal wall	0.99	0.01	A		
M. transversus thoracis	0.86	0.02	L$^-$	restricted	
	0.83	0.03	L$^-$	castrates	
	0.91	0.03	L	sows	
M. transversus costarum	1.00	0.02	A	restricted	
	1.04	0.03	A$^+$	castrates	
	1.08	0.03	H	sows	
Diaphragma	0.95	0.02	A$^-$		
Mm. intercostales	*1.01*	0.01	A		♂+,♂̸+
Total abdominal and thoracic wall	0.99	0.01	A		

*The number in italics is valid if the quadratic terms are ignored.

higher. Only the *b*-values reported by ANDERSEN are lower or in the range with those of the present study.

For the remaining muscles of the thoracic wall LOHSE et al. (1971) found lower values, only *m. transversus thoracis* is in line with their results. BERGSTRÖM (1978) reported a higher value for the diaphragm and *m. transversus thoracis*. BUTTERFIELD and BERG (1966a) found a similar value for the last-named muscle as in the present study, but the value for *m. transversus costarum* was lower in their work. They left the *mm. intercostales* unclassified, again muscles showing a curvilinear pattern in the present study.

Many differences in constant terms were established. In all abdominal muscles as well as for the total group of abdominal muscles, and also for the diaphragm, differences between feeding levels were ascertained for all three sexes, except for castrates in *m. transversus abdominis*. There was a tendency in the last-named muscle to a cubic term in the case of castrates. Tested cubicly the feeding level difference would also have been ascertained for castrates in this muscle. Differences between feeding levels were also found for *mm. intercostales* in castrates and sows and for the group as a whole in all three sexes. All these differences between feeding levels resulted in higher proportions at the *ad libitum* level, except for the differences in the diaphragm, where the higher proportions were calculated for the restricted feeding level. For the group as a whole the differences can also be seen in Fig. 4.22abc.

The sex differences were those between castrates and the other sexes at the *ad libitum* feeding level in *m. obliquus abdominis externus*, between boars and the other sexes at the restricted level in *mm. transversus abdominis, rectus abdominis* and *intercostales*, between boars and castrates at the *ad libitum* feeding level in *mm. intercostales* and in the group as a whole, between boars and sows at the restricted feeding level in the group as a whole, and finally between castrates and sows at both feeding levels in *m. transversus costarum*. In most cases the higher proportions were found in boars in comparison with both other sexes, except in *m. transversus abdominis* where boars had the lowest proportions. In cases where castrates and sows differed, the higher proportions were calculated for sows.

A higher proportion of the abdominal muscles on an *ad libitum* feeding level or high energy level was also found by MURRAY and SLEZACEK (1975) in sheep, ANDERSEN (1975) in cattle and CARDEN and GOENAGA (1977) in pigs. RICHMOND and BERG (1971b) did not notice the effect of nutrition, nor did they find sex differences.

4.7.2.9. The muscles of the shoulder girdle region

The total weights of the intrinsic muscles of the group are given in Table 4.44. The percentages, at the outset just below 13%, first slightly decrease to more than 12.5% and then increase to about 14% (cf. Fig. 4.22abc).

The average variation coefficient of the group amounted to only 3.8%, while for the individual muscles it rated from 5.9% in *mm. pectoralis profundus* and *serrati ventrales cervicis* and *thoracis*, to 16.1% in *mm. pectorales superficiales*. The variation voefficient again rises with decreasing weight of muscles.

TABLE 4.44. The weights of the total of the muscles of the shoulder girdle region of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	14.29	12.94	12.75	12.62	13.10	13.82	13.18	14.05
Castrates		12.81	12.81	13.07	12.46	13.31	12.89	13.89
Sows	13.75	12.76	12.58	12.63	12.72	12.83	12.98	13.64
Restricted								
Boars			13.08	12.90	12.86	13.39	13.26	13.95
Castrates			12.97	12.76	12.90	12.95	13.19	13.73
Sows			12.56	12.49	12.82	12.89	13.37	13.46

Table 4.45 gives the growth pattern and classification of the intrinsic muscles and the group. Quadratic terms were calculated for boars and castrates in *m. trapezius*, but in the same muscle a cubic term was calculated for boars as well. So actually boars needed a third degree polynomial for this muscle. This also held true for *m. rhomboideus*, in which at the same time a quadratic pattern for *ad libitum* fed groups was established. Furthermore the *mm. serrati ventrales cervicis* and *thoracis* also demonstrated a quadratic term for castrates.

The new-born boars were well-adapted to the curvilinear patterns. The sow piglets deviated with a positive term from the pattern as predicted from the

TABLE 4.45. The classification and growth pattern of the muscles of the shoulder girdle region*.

Muscle	b	s_b	Class	Feeding level group or sex group	Quadratic pattern**	Cubic pattern
M. trapezius	*1.05*	0.01	A^+		♂+; ⚦+	♂+
M. rhomboideus	*1.01*	0.01	A	*ad libitum*	A+	
	1.08	0.02	H	restricted		
						♂+
	1.03	0.02	A^+	castrates		
	1.02	0.02	A^+	sows		
M. latissimus dorsi	1.06	0.01	A^+			
Mm. serrati ventrales cervicis and *thoracis*	*1.03*	0.01	A^+		⚦+	
Mm. pectorales superficiales	0.99	0.01	A			
M. pectoralis profundus	1.01	0.01	A			
Total shoulder girdle region	1.03	0.00	A^+			

*The numbers in italics are valid if the high power terms are ignored.
**A = *ad libitum* feeding level.

regression line in *mm. trapezius* and *latissimus dorsi* as well as in the total group. Furthermore the boar piglets positively deviated in the total group and in the remaining muscles as well, except in *m. pectoralis profundus*.

BUTTERFIELD and BERG (1966a) only found a diphasic pattern in *m. rhomboideus*; LOHSE et al. (1971) on the contrary found diphasic patterns in most of the muscles of the group, though not in *mm. trapezius* and *pectorales superficiales*. The total group is difficult to compare because the just named workers divided the group into a cervical and thoracic part.

Considering the linear pattern, only slope differences between feeding levels were established in *m. rhomboideus*. The *b*-value in boars then was higher at the restricted feeding level. The same difference was found when tested cubicly. In the latter case sex differences in shape between boars and the other sexes at the restricted feeding level were established. The same difference would have been found in constant terms when tested linearly. It resulted in a more concave pattern or higher proportions for boars respectively. The high cubic term in boars means that the difference between the boars and the other sexes will be enlarged particularly in the later stages.

No differences in slope or shape were found in *m. trapezius*. The constant terms differed between boars and the other sexes at both feeding levels, while a difference between feeding levels was calculated in sows. These differences are achieved irrespective of the degree of polynomial tested. There was a higher proportion at the restricted feeding level for the sows. As in *m. rhomboideus* the boars had the highest proportions.

Because of the test on the second degree polynomial where castrates were involved, shape differences in the serratus muscles were computed for castrates between feeding levels and for the sex difference between boars and castrates at the *ad libitum* feeding level. Furthermore for boars a difference in constant terms between feeding levels was found as well. The quadratic term resulted in a more concave pattern for the restrictedly fed castrates. The restricted feeding level showed the higher proportions in boars, while for boars higher proportions than for castrates were computed.

In *m. latissimus dorsi* the feeding levels differed for castrates in the constant terms giving higher proportions at the *ad libitum* feeding level. In this muscle and in the other muscles with a linear pattern as well as in the total group sex differences were found, mainly between boars and castrates at one or both feeding levels. Furthermore differences between castrates and sows were also found, viz. in *m. pectoralis profundus* and in the total group. The differences between castrates and sows resulted in higher proportions for the castrates. The boars had higher proportions in the various muscles than castrates and sows, except in *m. pectoralis profundus* in which castrates had the higher percentages.

ANDERSEN (1975) found effects of nutritional treatment in *mm. latissimus dorsi* and *pectoralis profundus*, so only the former muscle was in accordance with his results. CARDEN and GOENAGA (1977) found an effect for the whole group of muscles; this could not be ascertained in the present study in agreement with the results of RICHMOND and BERG (1971b). They, however, did not find sex differences for this group of muscles either.

The intrinsic muscles of this group followed reasonably well the A^+-pattern of the total of the group. The *mm. pectorales superficiales* tended to grow slower, while *m. rhomboideus* tended to grow faster, at least the restrictly fed groups did. Except for the pectoral and serratus muscles Davies (1974b) found much lower values because of the first part of the trajectory. Especially the *m. rhomboideus* seems to have a higher value in other references than in the present study. The values were in reasonable agreement with those of Bergström (1978), except that he and Andersen (1975) found a higher value for *mm. pectorales superficiales*. On the other hand Lohse et al. (1971) found a lower value for this muscle as well as for the *m. trapezius*.

4.7.2.10. The skin muscles

The cutaneous muscles were also expressed as a percentage of total muscle weight. The results are given in Table 4.46. The percentages steadily increase from about 4 to 4.5–5.5% depending on feeding level and sex (see Fig. 4.22abc). The average variation coefficient amounted to 10.2%.

The muscles were found to have a linear pattern to which the new-born animals were well-adapted. A common *b*-value of 1.13 ± 0.01 (H^+) was calculated. The high value would be in accordance with the superficial position of these muscles.

The height of the value was in agreement with the results of Davies (1974b) and Butterfield and Berg (1966a). The latter also found a monophasic growth pattern, like Lohse et al. (1971). Lohse et al. (1971) and Andersen (1975) found somewhat lower values, whereas Bergström (1978) found higher values, especially for females.

Furthermore sex differences were not reported. In the present study, however, sex differences were found in the constant terms. At the restricted feeding level all sexes mutually differed. Boars had higher proportions for the cutaneous muscle than the other sexes, while castrates exhibited a higher percentage than sows.

Table 4.46. The weights of the skin muscles of the treatment groups for the different dissection stages expressed as a percentage of total side muscle weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	3.10	3.96	4.40	4.64	4.77	5.12	4.86	5.39
Castrates		3.90	4.31	4.18	4.39	4.60	4.61	5.39
Sows	3.08	3.91	4.37	4.41	4.34	4.52	4.41	5.57
Restricted								
Boars			3.86	3.98	4.22	4.62	4.57	5.59
Castrates			3.87	3.98	4.12	4.18	4.26	4.90
Sows			3.82	3.89	3.99	4.14	4.28	4.51

Differences in constant terms between feeding levels were found as well for all three sexes. The higher proportions were calculated for the *ad libitum* level which can also been seen in Fig. 4.22abc. Such differences were not reported earlier.

4.7.2.11. The muscle remnants

The muscles or parts of muscles that turn up in the group of muscle remnants were listed in section 3.7.2.1. (p. 63). The percentages with respect to total muscle weight vary; the average variation coefficient amounted to 49.1%. At mature weight the percentages were higher than in the stages I through VI. It resulted in a common b-value of 1.20 ± 0.06 (H*). The new-born animals deviated from the regression line with a positive term. At birth the *diaphragma pars lumbalis* belongs to this group, but in the normal slaughter procedure it disappears in the loss at slaughter with removal of the viscera.

Including the mature stage the majority of the percentages varied from about 0.3 to about 0.7%, while at birth the percentage rated to about 1%. According to differences in constant terms the boars showed higher percentages than the other sexes.

4.8. GROWTH OF FAT

4.8.1. *General*

Like the other main tissues shape or slope differences were ascertained for the growth of fatty tissue. The increase of side fat weight (y) was related to the increase of total carcass side weight (x). Since differences in constant terms between the *ad libitum* feeding level (A) and the restricted feeding level (R) were found, the regression equations may be written as follows:

			$S.E._D^*$	$S.E._L^*$	$S.E._Q^*$
boars	A	$\ln y = -1.981 + 1.239 \ln x$	0.032	0.021	
	R	$\ln y = -2.106 + 1.239 \ln x$			
castrates	A	$\ln y = -3.017 + 1.894 \ln x - 0.082 \ln^2 x$	0.019	0.098	0.014
	R	$\ln y = -3.135 + 1.894 \ln x - 0.082 \ln^2 x$			
sows	A	$\ln y = -2.156 + 1.326 \ln x$	0.025	0.018	
	R	$\ln y = -2.299 + 1.326 \ln x$			

$^*S.E._D$ = the standard error of the difference between constant terms.
$^*S.E._L$ = the standard error of the slope of the linear term.
$^*S.E._Q$ = the standard error of the shape of the quadratic term.

The sex differences in shape or slope and the growth of fatty tissue in comparison with the other main carcass components were already described in section 4.4.1.

The total side fat weights are given in Table 4.47. These weights served as the independent variates in the regressions for each of the fat depots. The average variation coefficient amounted to 24.0%, which indicates the variable nature of fatty tissue. The coefficient was about twice as high as for bone and muscle tissue.

TABLE 4.47. The weight of total fat in side of the treatment groups for the different dissection stages (in kg).

Feeding level and Sex	Dissection stage							
	0*	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	0.022	1.80	7.26	12.59	16.57	25.63	29.69	49.20
Castrates		1.95	9.38	17.39	23.06	32.46	37.62	62.33
Sows	0.020	2.19	8.11	13.42	20.33	26.01	34.13	64.52
Restricted								
Boars			3.56	7.24	10.61	15.71	22.90	48.17
Castrates			4.32	7.78	14.30	18.93	28.03	66.26
Sows			4.09	6.63	12.21	17.30	25.26	42.76

* Excluding subcutaneous fat.

4.8.2. *Fat weight distribution*

The weights of the fat depots dissected at the different stages expressed as a percentage of total fat weight are presented in Table 4.48. The average variation coefficients for subcutanous, intermuscular and perinephric fat were computed as 4.0, 13.9 and 19.5% respectively.

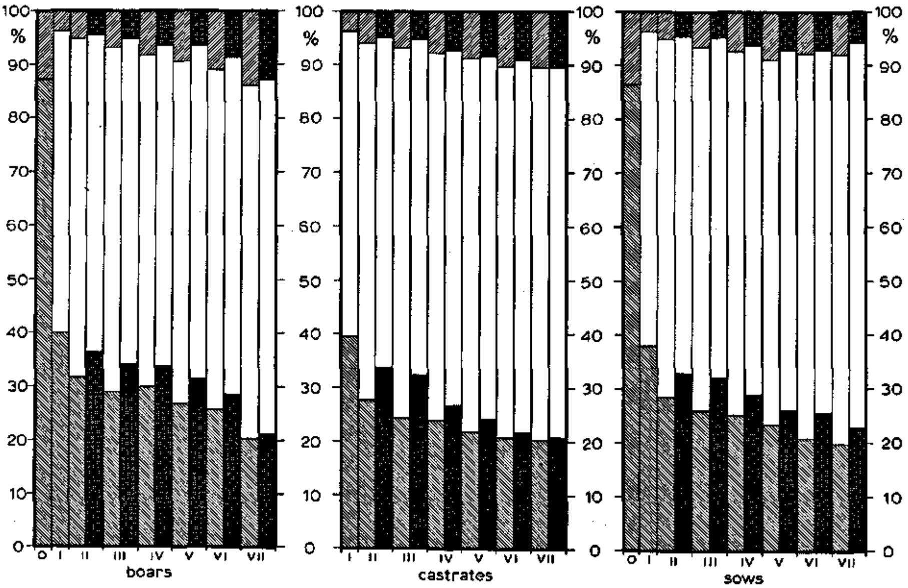

FIG. 4.24. Distribution of fat depots (top: perinephric fat; bottom: intermuscular fat; in between: subcutaneous fat) within total fat at the different dissection stages (roman figures) for boars, castrates and sows on *ad libitum* (dark shaded bars) and on restricted feeding level (light shaded bars).

TABLE 4.48. The weights of the fat depots of the treatment groups for the different dissection stages expressed as a percentage of total side fat weight.

Feeding level and Sex	Dissection stage							
	0*	I	II	III	IV	V	VI	VII
Subcutaneous fat								
Ad libitum								
Boars		56.28	62.02	64.03	61.78	63.74	63.22	65.72
Castrates		56.75	66.22	68.92	68.51	69.54	69.10	69.21
Sows		58.32	66.53	67.48	67.41	67.50	71.41	72.24
Restricted								
Boars			59.21	60.68	59.79	62.01	62.88	65.81
Castrates			61.42	62.44	66.00	67.42	69.30	68.64
Sows			62.67	63.32	64.79	66.63	67.41	71.40
Intermuscular fat								
Ad libitum								
Boars	87.24	39.92	31.69	29.14	29.90	26.87	25.78	20.36
Castrates		39.63	27.71	24.32	23.86	21.69	20.68	20.27
Sows	86.48	37.92	28.52	26.03	25.20	23.39	20.78	19.78
Restricted								
Boars			36.32	34.10	33.78	31.44	28.60	21.36
Castrates			33.73	32.34	26.73	24.20	21.72	20.70
Sows			32.85	31.90	28.97	26.11	25.49	22.89
Perinephric fat								
Ad libitum								
Boars	12.76	3.81	5.29	6.83	8.32	9.39	11.00	13.92
Castrates		3.62	6.07	6.76	7.63	8.77	10.23	10.52
Sows	13.52	3.76	4.95	6.50	7.39	9.11	7.81	7.98
Restricted								
Boars			4.47	5.22	6.43	6.55	8.52	12.83
Castrates			4.85	5.22	7.27	8.39	8.99	10.65
Sows			4.48	4.78	6.24	7.26	7.11	5.71

*Subcutaneous fat was excluded from total fat.

The proportion of subcutaneous fat increases from about 55% to 65–70% depending on sex. Perinephric fat also increases from a percentage just below 4% to more than 10% in the male animals; the females showed a lower percentage at the mature stage. As a consequence the proportion of intermuscular fat has to decrease; it decreases from about 40% to about 20%. An illustration of these patterns is shown in Fig. 4.24. It appears from the figure that feeding level affects the proportion of the fat depots when compared at about the same age.

A remark has to be made with regard to the distribution in the new-born animals. Since a separation between the skin and the subcutaneous fat was difficult to perform, the subcutaneous fat was included in the weights of the skin.

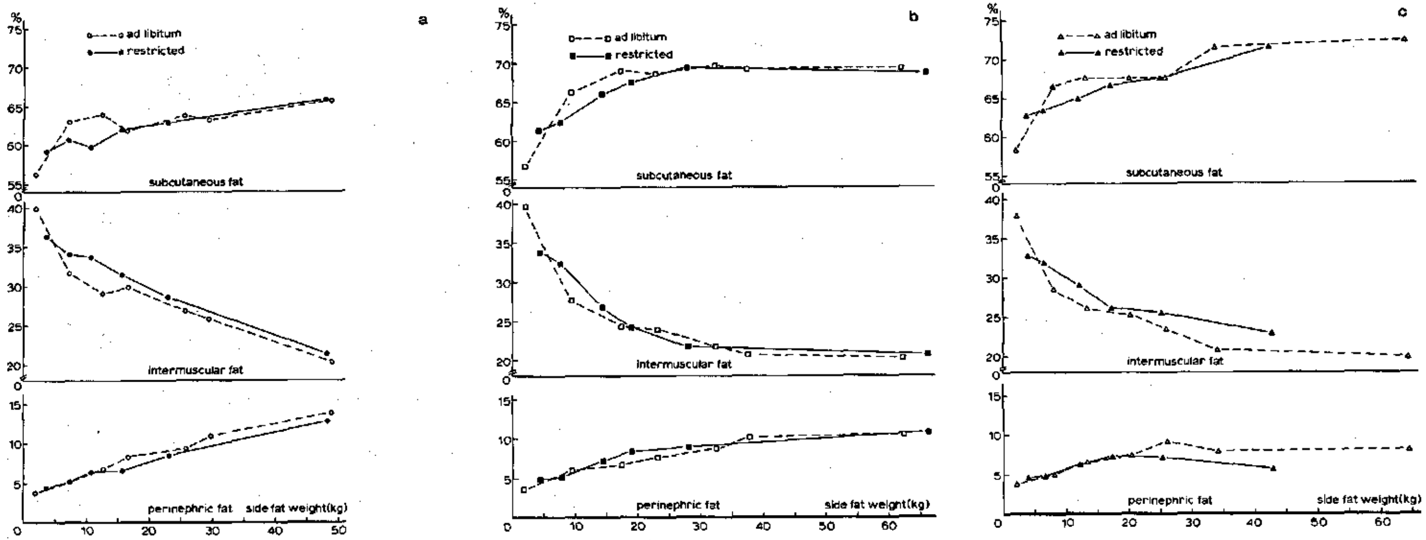

FIG. 4.25abc. Fat weight distribution of fat depots within total fat on *ad libitum* and restricted feeding level in boars (a), castrates (b) and sows (c).

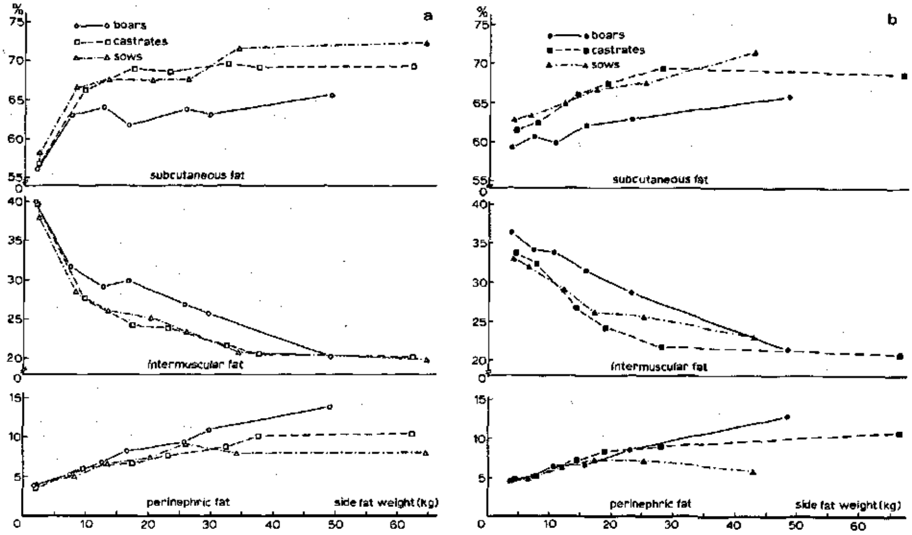

FIG. 4.26ab. Fat weight distribution of fat depots within total fat in boars, castrates and sows on *ad libitum* (a) and restricted feeding level (b).

Two attempts were made to separate both tissues; the results were not uniform. Nevertheless the proportion of subcutaneous fat was estimated at about 75% at birth, which is in reasonable agreement then with that calculated from the data of McMEEKAN (1940a). Consequently the proportions for intermuscular and flare fat decreased to about 22 and about 3% respectively.

The distribution of the fat depots within total fat is visualized in Fig. 4.25abc and Fig. 4.26ab. In the former differences between feeding levels are shown for boars, castrates and sows respectively, while in the latter the sex differences are shown for the *ad libitum* and restricted feeding level respectively. The regression analyses resulted in the classification and growth patterns as is presented in Table 4.49.

Considering the linear pattern it is seen that no differences in slope for subcutaneous and intermuscular fat were found, while the sexes differed for flare fat at both feeding levels. As may be seen from the *b*-values the percentage

TABLE 4.49. The classification and growth pattern of the fat depots*.

Fat depot	b	s_b	Class	Sex group	Quadratic pattern	Cubic pattern
Subcutaneous fat	*1.05*	0.00	A$^+$		⚦−	
Intermuscular fat	*0.81*	0.01	L$^=$		♂−	⚦+
Perinephric fat	*1.40*	0.02	H*	boars	♂+	
	1.33	0.02	H*	castrates		
	1.23	0.03	H*	sows		♀−

* The numbers in italics are valid if the high power terms are ignored.

increase and decrease for the different depots as already described, markedly differed from each other. The flare fat grew faster than the subcutaneous fat. This was already found by McMEEKAN (1940a), HOFMANN and RITTER (1958), and CUTHBERTSON and POMEROY (1964). Changes in the distribution were also reported by SEEBECK (1968b) in sheep. The faster growth of subcutaneous fat over intermuscular fat was mentioned by McMEEKAN (1940b), PÁLSSON and VERGÉS (1952a) (in sheep) and CUTHBERTSON and POMEROY (1964).

An increase in the percentage of subcutaneous fat with a corresponding decrease of intermuscular fat was reported also by RICHMOND and BERG (1971c). The greatest changes in the percentages were found in the first stages from 23 to 68 kg, which is in perfect agreement with the results of the present study (cf. Fig. 4.25abc in which stage II of the *ad libitum* fed groups also fell at about 68 kg live weight). After that the increase was much smaller. A slight increase from 80 to 100 kg live weight was stated by DUMONT et al. (1973) as well, but they also claimed rather constant percentages from 100 to 140 kg which is only in agreement with the results of the present study as far as castrates are involved (Fig. 4.25b).

From Table 4.49 it appears that for all three fat depots dissected, curvilinear patterns were established. Subcutaneous fat needed a negative quadratic term for castrates. Intermuscular fat needed such a term for boars, whereas in addition a positive cubic term for castrates was ascertained in this depot. In flare fat a positive quadratic term for boars and a negative cubic term for sows were discernible. The neonate boars did not follow the curvilinear patterns in intermuscular and perinephric fat, nor did the neonate sows in the latter fat depot. The sow piglets, however, were in line with the linear pattern of their sex partners in intermuscular fat.

The results of the tests for significant differences between treatment groups will be given according to the growth patterns found. More differences are discernible then, particularly with regard to the shape of the regression. Shape differences between feeding levels were established for boars and sows in intermuscular and perinephric fat respectively. The curves were more convex at the restricted feeding level (Fig. 4.25ac). Shape differences in sexes occurred between boars and castrates in all depots, in flare fat only at the restricted level. At the restricted feeding level castrates differed from sows in all depots, while in flare fat this difference was also found at the *ad libitum* level. In flare fat a further difference between boars and sows was ascertained at both feeding levels. Boars had a more convex pattern than castrates in subcutaneous fat and as a consequence they had a less convex pattern in intermuscular fat. Castrates showed the same picture with respect to sows (Fig. 4.26ab). In flare fat the difference between boars and castrates resulted in a concave pattern for boars and a linear one for castrates (Fig. 4.26b). Furthermore boars and castrates had a less convex pattern than sows in flare fat (Fig. 4.26ab).

Some differences in constant terms remained. The *ad litibum* feeding level resulted in a higher proportion of subcutaneous fat in castrates (Fig. 4.25b) and in a lower proportion of intermuscular fat in sows (Fig. 4.25c). The sex differences resulted in higher proportions of subcutaneous fat in sows with respect to boars at both feeding levels, and as a consequence sows had a lower percentage of intermuscular fat also at both feeding levels (Fig. 4.26ab).

Opposite to the finding in the present study, Seebeck (1968b) reported that, at least in sheep (and all three sexes were involved), practically no sex differences were discernible in fat weight distribution. Richmond and Berg (1971c) did not find significant differences either. But on the other hand Berg and Butterfield (1976c) reported some sex differences in cattle.

Influences of nutritional treatment on fat weight distribution were found by Richmond and Berg (1971c). But their results were contradictory to those of the present study, in that at the higher energy level a higher percentage of intermuscular fat was found. A comparison with the data of Carden and Goenaga (1977) is equivocal, at least for subcutaneous fat, because they included the skin in it, which may influence the distribution. And furthermore linear patterns have to be compared with curvilinear ones. Apart from subcutaneous fat they nevertheless found a faster growth of intermuscular fat at the high energy rations. The results of Fowler and Ross (1974) are more in accordance with those of the present study in that a higher energy diet rendered more subcutaneous fat.

4.8.3. *Backfat thickness*

Along with the increasing amount of subcutaneous fat the depth of backfat also increases. The average backfat thickness, as measured at five locations at the midline (see Fig. 3.2), during the growth period from 25 kg live weight to mature weight, is given in Table 4.50. It increases from less than 1 cm to 4.5–6.5 cm depending on feeding level or sex. Hofmann and Ritter (1958) reported that the increase was highest in the first part of the trajectory they examined (50–210 kg live weight). This is in accordance with the results of the present study, because a convex quadratic pattern was established.

Table 4.50. The average backfat thickness at the midline of the treatment groups for the different dissections stages (in mm).

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars		8.7	19.8	27.4	28.5	36.8	39.2	45.8
Castrates		8.4	25.9	34.4	41.6	48.6	48.3	55.3
Sows		9.1	22.6	31.3	35.8	38.5	48.1	63.9
Restricted								
Boars			12.4	18.8	20.9	27.1	32.1	49.2
Castrates			15.5	20.0	30.3	34.0	41.7	61.1
Sows			13.3	17.9	27.5	30.8	36.7	44.8

Average variation coefficient 17.5%.

TABLE 4.51. The classification and growth pattern of backfat thickness related to total side fat weight.*

Location	b	s_b	Class	Feeding level group or sex group	Quadratic pattern
(1) thickest place shoulder	0.09	0.01	H		
(2) thinnest place back	*0.30*	0.02	H*		–
(3) 10 cm cranial to last rib	*0.27*	0.02	H*		⚦ –, ♀ –
(4) thickest place loin	*0.16*	0.01	H^+	restricted	
	0.16	0.02	H^+	boars	
					♀ –
(5) thinnest place loin	*0.40*	0.02	H*	*ad libitum*	
	0.40	0.02	H*	boars	
	0.43	0.02	H*	sows	♀ –
Average backfat thickness	*0.21*	0.01	H*		–

*The numbers in italics are valid if the quadratic terms are ignored.

The average backfat thickness as well as the thickness at each of the locations were regressed both on total side fat weight and carcass side weight. A fully quadratic pattern was found against each of the independent variates.

In Table 4.51 the classification and growth pattern is given for the regression of backfat thickness at each of the five locations on (the third root of) total side fat weight. A linear pattern was only exhibited by the measurement at the location over the shoulder. At the other locations a fully quadratic pattern or at least a quadratic pattern for sows was established.

Many significant differences were discernible. Differences between feeding levels in shape or slope were ascertained for boars at location (2) and for castrates at location (4) and (5). The patterns were more convex at the *ad libitum* feeding level. The feeding levels further differed in constant terms for boars at all locations except location (1), for castrates at locations (3), (4) and (5), and for sows at locations (2), (4) and (5). Differences between feeding levels in constant terms were found for boars and sows with regard to the average backfat thickness. In all cases the *ad libitum* level led to a greater depth of backfat. WILSON (1968a) has mentioned that the nutritional treatment influenced the fat depth measurements.

Sex differences in shape or slope were established for the difference between boars and sows at the *ad libitum* feeding level at the locations (2), (3), (4) and for average backfat thickness, while boars and castrates only differed in shape at location (2), and castrates and sows (at the restricted feeding level) only at location (5). But for some exceptions all remaining and possible combinations between sexes were significant in constant terms at the various locations and for the average backfat thickness. All these sex differences resulted in a greater depth for castrates and sows than for boars, while in those cases in which castrates and sows differed, a greater depth for castrates was ascertained.

Regressed on total carcass weight instead of total fat weight the differences change slightly, but do not lead to another interpretation.

Considering only a linear pattern it may be seen from Table 4.51 that the *b*-values differ between locations. During growth the fat depth increases most over the loin (at least at the location over the *m. gluteus medius*) and least over the shoulder. However, a clear gradient in anterior-posterior direction is disturbed by the measurements in between, especially by those at the thickest place at the loin. When regressed on total carcass weight, the *b*-values are about 0.17 unit higher. In that case the ranking between the locations did not alter either.

4.9. MEAT QUALITY MEASUREMENTS

A number of meat quality characteristics were measured as described in section 3.5. The results as to these characteristics in general hardly showed any differences, neither between feeding levels nor between sexes. There were no clear trends during growth to be seen in most of the various characteristics measured.

In order to have a reference the measurements were regressed on total carcass side weight as the independent variate. All characteristics exhibited a linear pattern. Only in one of them differences in slope were established, viz. boars and castrates had lower rigor values than sows at the *ad libitum* feeding level, as boars had lower values than castrates at the restricted level. Furthermore castrates and sows differed in constant terms at the restricted feeding level; the latter showed higher rigor values. A difference in constant terms was also found between feeding levels in boars, in that lower values were discernible at the *ad libitum* level.

After somewhat higher initial values the measurements of pH both in *m. semimembranosus* and *m. adductor* stabilized, while in the subjective scores only a slight decrease was seen. Because in sows the pH-values measured in the former muscle were about 0.2 unit consistently higher at the *ad libitum* feeding level, the nutritional treatment was significant in constant terms. The results of the measurements of the rigor value were more irregular. Both intermediate stages seemed to show somewhat lower values.

The pH of *m. semimembranosus*, subjective overall score and transmission value were also regressed on total muscle weight. The only difference with the regressions on carcass weight was that for the pH measurement the difference in constant terms between feeding levels in sows disappeared. The sows fed restrictedly showed higher scores than those fed *ad libitum*.

The transmission value was the only characteristic in which a clear trend could be discovered. Values started at about 30, then remained at a level of 40–60, but at mature weights the values reached 80 in sows, whereas values of over 80 were reached in boars.

5. DISCUSSION

The two main aspects of growth involved in animal production, i.e. the increase in body size per unit time and the morphogenetic process were raised in this study. The latter aspect, the relative growth of tissues and the relative growth of components within each of the main tissues, was the principal aim set.

The groups to be placed on trial at the start of the fattening period (at dissection stage I, at about 25 kg live weight or 10 to 12 weeks of age) were treated in the same way up to that time, i.e. the normal commercial procedure was followed as to castration, weaning and feeding. The nutritional treatment was then introduced. Thus only from that time on it could influence subsequent growth and development.

5.1. LIVE WEIGHT GROWTH

Immediately after imposing the differences in feeding level the animals reacted to it as was illustrated in Fig. 4.1abc. The weighings every fortnight from dissection stage I (and the few weighings before stage I) to maturity gave a satisfactory impression of the weight-age relationship.

The growth rates calculated from stage to stage (Tables 4.2–4.4) showed that the maximum (except for castrates that were one stage earlier) for the *ad libitum* fed animals fell between stage II and III, while for the restrictedly fed groups it was found between stages III and IV. There the inflexion points of the weight-age curves will have to be found. They were estimated from the Text-figures at somewhat below 30% of mature weight for the *ad libitum* fed groups and somewhat over 30% for the restrictedly fed animals. This would imply that as to the inflexion point the VON BERTALANFFY-model would fit best our data in pigs (section 2.2; WALSTRA, to be published). It is also in accordance with the observations of BRODY (1945).

The results as to differences between sexes and between feeding levels in growth rate and feed conversion ratio up to commercial slaughter weight appeared to be in accordance with those obtained in former castration experiments (WALSTRA et al., 1977). After commercial slaughter weight the daily gain of boars surpassed that of castrates at the *ad libitum* feeding level which has to be ascribed to a combined effect of a higher intake and a more favourable lean meat deposition in boars.

5.2. RELATIVE GROWTH

The growth of the various components was described in steps, from (1) carcass weight related to live weight, via (2) main carcass components related to carcass weight to (3) the single components of the tissues related to each of the corresponding tissue weights.

Comparison of the height of the growth coefficients (*b*-values), and also that of the increase in percentages, as found in the various references, with the growth coefficients found in the present study, poses a number of problems, even when the experiments in which joints were dissected are excluded. Firstly, where groups are involved (especially in the case of muscle groups) the constituent components may be different. Another difficulty encountered is that use is made of different independent variates, mainly in describing growth of carcass components. Thirdly, experiments were carried out with very different trajectories over which the values were computed. These differences in circumstances have to be kept in mind when discussing the various characteristics. For the sake of convenience the trajectories (and sexes) studied of the experiments most closely related to the present study are brought together in the following survey:

Reference	*Trajectory*	*Species*	*Sex*
McMeekan (1940abc), Elsley et al. (1964)	birth to 90 kg	pigs	⚦, ♀
Cuthbertson and Pomeroy (1962ab; 1964)	68–118 kg	pigs	⚦
Richmond and Berg (1971abc; 1972)	23–114 kg	pigs	⚦, ♀
Davies (1974ab; 1975)	2– 64 kg	pigs	♀
Cole et al. (1976)	25– 65 kg	pigs	♀
Carden and Goenaga (1977)	30–110 kg	pigs	⚦
Butterfield and Berg (1966ab)	birth to maturity	cattle	⚦
Bergström (1974b; 1977)	1 week to 500/390 kg	cattle	♂/♀
Andersen (1975)	180–540 kg	cattle	♂
Robelin et al. (1974, 1977), Robelin and Geay (1976)	8–19 months	cattle	♂
Robelin (1978)	4–650 kg	cattle	♂, ♀
Lohse et al. (1971)	birth to 1 year/517 days	sheep	♂, ♀/⚦
Prud'hon et al. (1978)	birth to 350 days	sheep	♂, ♀
Cantier et al. (1969), Vezinhet et al. (1972), Cantier et al. (1974), Dulor et al. (1976)	9–182 days	rabbits	♂, ♀

5.2.1. *Carcass growth*

Growth of the carcass related to live weight rendered a *b*-value of 1.10, in accordance with comparable trajectories in sheep. The lower value found by Davies (1974a) may be explained in that in his experiment only the very first stages were involved. The increasing trend in dressing percentage from stage I onwards in the present study (Table 4.7) was preceded by a much higher value at birth. As was described in section 4.3.2 the dressing percentage found was in agreement with that found by others for the intermediate stages. The last stages do not deviate from the findings of HOFMANN and RITTER (1958) either.

5.2.2. *Linear measurements*

FOWLER (1968) and FOWLER and LIVINGSTONE (1972) gave examples (as described in sections 2.4.3.1 and 2.4.3.2) of different results as to the choice of the independent variate. A clear example was also indicated in the present study. Carcass length regressed on muscle + bone weight differed between boars and castrates. The latter were longer. When the length, however, was related to carcass weight the difference not only disappeared but even shifted to the reverse. It is obvious that more fat does not result in greater length measures; boars therefore will be longer than the fatter castrates at a given carcass weight. For the same reason the *ad libitum* fed sows were shorter than the restrictedly fed ones when related to carcass weight, whilst the reverse was found when based on muscle + bone weight. It must be kept in mind in these cases that in order to reach the same muscle + bone weight the fatter animals will be older than the leaner animals.

The fact that at a given carcass weight boars demonstrated a greater thorax depth than castrates is also due to the factor fat. When thorax depth was regressed on carcass length the sex differences disappeared. Likewise the differences between feeding levels were the reverse when related to carcass length instead of carcass weight. Because of the higher amount of fat thorax depth was greater for restrictedly fed groups than for *ad libitum* fed groups for a given carcass weight. Looking at carcass length as the independent variate it may be concluded, based on the A^+ (see p. 69 and p. 70) as well as on the concave patterns found, that the body deepens with respect to length during growth. This is thus in accordance with HAMMOND's (1932a) observations (cf. Fig. 2.1). Changes in form may also be deducted from the finding that at birth leg length related to carcass length was greater than in later stages. The fact that new-born animals need relatively longer limbs may be explained as a functional aspect. When, however, leg length was regressed on carcass weight the result again was the reverse. The neonates then showed a shorter leg due to the relative heavier carcass at birth.

5.2.3. *Growth of the main carcass components*

The results of the present study as to the growth of the main carcass components are in agreement with what is generally found. The percentages of bone and muscle decrease, bone more than muscle, while the percentage of fat increases. Furthermore the percentages offal and skin also decreased. The only striking exception was the percentage of increase of skin in boars. The scarce data in the literature, in pigs (ELSLEY et al., 1964), in bulls (ROBELIN et al., 1974) and in rabbits (CANTIER et al., 1969) (at least examined in a second period), showed *b*-values approaching those in the present study as far as castrates and sows are involved. However, the first mentioned investigators regressed skin on muscle + bone weight and the others regressed it on empty body weight. The latter weight is reasonably comparable with the fasted live weight in the present study. When regressed on fasted live weight a *b*-value of just below 1.00 arises for castrates and sows. Such a value is reported by ROBELIN et al. (1977) for Limousin bulls. In the experiment with rabbits also the entire males were involved. Hence it appears that entire male pigs deviate in this characteristic from their sex partners in the other species. This disparaty may only partly be explained by differences in trajectories, because a number of references as reviewed by WALSTRA et al. (1977) denote significant differences between boars and castrates in castration experiments at the commercial slaughter weight as well.

5.2.3.1. Bone

According to JOHNSON (1974) many differential changes occur during the foetal phase between tissues as well as within tissues e.g. between muscle groups. At birth, however, the tissues would already have their postnatal growth impetus. In his experiment with calves the prenatal growth of bone had a high impetus. The growth coefficient of bone for the first month after birth was, though not significantly, higher than during the second month. This may explain the negative deviating pattern in bone of the new-born animals in the present study. Furthermore, however, it must be kept in mind that the pig carcasses include the head, while its bones were excluded from total bone weight.

The height of the *b*-value found for total bone is intermediate between the values reported by DAVIES (1974a) and COLE et al. (1976). In the light of the trajectories surveyed the higher value found by DAVIES (1974a) is understandable. The *b*-values calculated by ROBELIN et al. (1974), ANDERSEN (1975) and BERG et al. (1978a) in cattle are about similar to those of the present study.

5.2.3.2. Muscle and fat

With regard to the height of the *b*-values of muscle it appeared that those found by COLE et al. (1976) were somewhat higher and those found by DAVIES (1974a) were appreciably higher (0.2 unit for castrates and sows). Particularly here the influence of the trajectory applies. The marked difference with DAVIES' data (calculated for sows) may be explained in that in his work four out of the six dissection stages already fell before stage I of the present study. Since the sows in the present study negatively deviated from the regression line through the later stages, it is thus likely that DAVIES will find higher *b*-values. In later stages fat deposition ever increases and this mainly at the expense of muscle. Therefore the *b*-values for fat in the present study are (0.1–0.2 unit) higher than in the just-named references. Only the *b*-values in boars for muscle and fat approach those found by COLE et al. (1976). The *b*-values reported for muscle in cattle (ANDERSEN, 1975; BERG et al., 1978a) have about the same height as those found in pigs by COLE et al. (1976). The values for fat in cattle on the contrary are higher than in the present study. So there seems to be a relatively faster growth of fat in cattle as compared to pigs. According to ELSLEY et al. (1964) the *b*-values in sheep are also more differentiated than in pigs.

5.2.3.3. Muscle + bone weight as the independent variate

ELSLEY et al. (1964) used muscle + bone weight as the independent variate. The *b*-value calculated by them from MCMEEKAN's (1940c) data for muscle was about the same as ours. The value for bone was lower than in the present study. A difference, however, of 0.02 unit in muscle (which is actually found) means that with a muscle to bone ratio of say five to one the value for bone differ 0.1 unit (0.81 compared with 0.92). Since the *b*-values for bone and muscle in DAVIES' (1974a) experiment did hardly change when the regressions were calculated on muscle + bone weight instead of carcass weight they came in reasonable agreement with those of the present study. The rather stable values in his experiment may be explained by the fact that fat deposition in the early stages remains rather limited. From the data given by COLE et al. (1976) it appears that when regressed on muscle + bone weight, the *b*-values for bone and muscle do increase with respect to those when regressed on carcass weight. Although the value for bone is still lower, that of muscle is similar to ours now. The value for fat, found by COLE et al. (1976), however, did not change in this respect, which is not understandable in the light of the finding in the present study in that over about the same trajectory (stage I to stage II) the muscle to fat ratio decreased from about 2.2 to about 1.4 (cf. Table 4.14). Hence the *b*-value for fat should rise as well.

The long trajectory involved may explain the reasonably good agreement of the *b*-values of each of the main tissues regressed on muscle + bone weight with those reported by BERG and BUTTERFIELD (1966) for steers from 6 to 60 months of age.

5.2.3.4. Influence of feeding level and sex on gross carcass composition

Gross carcass composition appeared to be clearly influenced by nutritional treatment as well as by sex. This is what is normally found and the differences are in the direction with which one is familiar when the performances of the animals are judged at the commercial slaughter weights, e.g. from castration experiments (WALSTRA et al., 1977). During growth this is thus confirmed by the data of the present study and by those reported by RICHMOND and BERG (1971a) and CARDEN and GOENAGA (1977).

The differences between feeding levels were found as differences in constant terms, while the sex differences mostly (at least when boars were involved) appeared as differences in slope or shape. Since for the carcass components almost all possible differences in constant terms between the sexes were significant, thus the other sex differences were found in the constant terms.

All differences between feeding levels disappeared when muscle or bone weight was regressed on muscle + bone weight, thus confirming the results of ELSLEY et al. (1964) who re-analyzed the data of MCMEEKAN (1940c). All but one difference between sexes disappeared as a difference in slope or shape; the differences between boars and sows remained as differences in constant terms. Furthermore the difference between castrates and sows in bone and the difference between boars and sows in muscle changed into the reverse. Sows had more bone than castrates at a given carcass weight, due to the higher amount of fat in castrates, but castrates had more bone at a given muscle + bone weight. And boars had more muscle than sows at a given carcass weight, due to the higher amount of fat in sows, but sows had more muscle than boars at a given muscle + bone weight, because boars had still more bone than sows.

5.2.4. *Muscle to bone ratio*

The different growth coefficients found for bone as compared to muscle already denoted that the muscle to bone ratio has to alter during growth. The ratio increased, particularly during the first stages (Fig. 4.9abc and Fig. 4.10ab). The high growth impetus of bone found in calves in the prenatal phase (JOHNSON, 1974; ROBELIN, 1978) brings a relatively well-developed skeleton at birth. It explains the negative deviation from the regression line of the muscle to bone ratio of the neonates.

The ratio was not influenced by feeding level which is in accordance with the literature. Sex, however, did influence the ratio in that the ratio was in favour of boars as compared to castrates, but the opposite holds when compared with sows. A difference between castrates and sows was not found by RICHMOND and BERG (1971a). However, a difference in favour of the sows as in the present study (cf. Table 4.13 *ad libitum* feeding level) was also found by PEDERSEN (1973).

5.2.5. *Muscle to fat ratio*

The muscle to fat ratio rendered the expected differences: those between boars and the other sexes (in slope) in favour of the boars, while (in constant terms) sows had a more favourable ratio than castrates. Furthermore all *ad libitum* fed groups showed a less favourable ratio. Because of the different *b*-values of muscle and fat the ratio itself decreased during growth.

5.2.6. *Growth of offal components*

As for total bone and muscle, the percentage of offal in all three sexes was lower at the *ad libitum* feeding level. It must be kept in mind that head and feet consist mainly of bone and muscle. The higher percentage of offal in boars as compared to the other sexes may be partly due to the factor fat, but when regressed on muscle + bone weight the sex differences remain, at least with respect to sows, which may indicate a functional aspect of the heavier head in male animals as a secondary sex characteristic. Castrates in this respect behave more like boars.

Splitting of the carcass may affect the weight of the head of the carcass half to be dissected. This was checked by the regression of the ratio of the heads of both carcass halves on the sum of these halves. A linear pattern was found including the new-born animals and feeding level nor sex did influence the ratio. However, it appeared that in one out of the six treatment groups a significant deviation from zero for the *b*-value was found, i.e. the ratio was not independent of carcass weight in the restrictedly fed sows. Because of the counteracting effect of the *ln a*-value, however, it does not mean that the left head relative to the right head would become ever smaller with increasing carcass weight. Nevertheless it may have influenced the sex differences (as to the head and the component offal) and the difference between feeding levels in sows to some extent.

The relatively heavier head at birth is also given a functional meaning. The head as a protective container of the brain (FOWLER, 1968) would be well-developed because it must give space to the brain as the coordinator of the various body functions.

When the sum of the heads and the sum of the feet were regressed on the sum of both carcass halves, the calculated *b*-values were in the range with those found in cattle by ROBELIN et al. (1974, 1977) and ROBELIN (1978) respectively.

Within the component offal the head is growing faster than the feet, which may be due to the higher bone content of the feet. Boars had a lighter head than the other sexes, just as the castrates at the *ad libitum* feeding had a lighter head than at the restricted feeding. In feet evidently the opposite was and has to be found. The sex effect may be due to a somewhat less deposition of fat in the head region of boars, so that they reach the same total weight of offal components later than the other sexes. Since the percentage head decreases from stage to stage the head in boars therefore within offal may be lighter than in the fatter castrates and sows.

The kidneys with respect to total offal also showed differences between boars and the other sexes; compared with castrates they had a heavier kidney but compared with sows they had a lighter one. Boars also differed from the other sexes (with heavier weights of the kidneys) when the sum of both kidneys was regressed on live weight. Since the carcass as a whole ever increased with respect to live weight, the total of the organs hence must decrease. The kidneys follow this general pattern. The *b*-value (0.71) calculated was in reasonable agreement with the literature.

In contrast with the kidneys, the testes (related also to live weight) followed a fully distinct pattern. Because of the sharp rise after birth up to puberty and the stabilizing trend in later stages the quadratic terms had a high coefficient. Since in the later stages similar percentages for the feeding levels were found (Table 4.16), while a significant difference between feeding levels was established, it could only lead to a faster prepubertal growth of the testes discernible at the restricted feeding level. Owing to the strong bending curve the neonate boars positively deviated from it, so that a clear S-shaped curve resulted for the growth of the testes. When testes growth was considered linear with live weight growth only a common, but high (1.46), *b*-value was established. High values were also reported in the literature.

The ratio of the left and right testis regressed on live weight demonstrated that there was no change in the ratio during growth, because the *b*-value of the ratio did not differ significantly from zero. Given this result and the finding that the *ln a*-value did not differ from zero either, thus resulted in the left and right testis having the same weight. Such similarities point at symmetric growth in both carcass halves. It could also be tested for the left and right kidney and for the feet of the left and right carcass halves. No significant differences were found as to *b*-

values or intercepts deviating from zero for these components as well. In all cases the neonates were in line with these findings.

5.2.7. *Bone weight distribution*

The bone weight distribution changed during growth, at least when individual bones are considered. The bone groups hardly change: the vertebrae had an A-pattern, while the total of the thoracic and pelvic limb bones was in general just below average. A faster growth than average (A^+-pattern) was achieved by scapula, *os coxae*, ribs and sternum. The last-named bone, however, is subject to high variation due to splitting of the carcass. The patella tended to an A^+-pattern. The long bones of both fore and hind limb had an A^--pattern or a tendency towards it, whereas the growth of the *os femoris* tended to a L-pattern. It is in contrast to the findings of MCMEEKAN (1940abc) that the bones of the fore limb tend to grow faster than those of the hind limb. However, such tendencies were also apparent in results of CUTHBERTSON and POMEROY (1962b) and RICHMOND and BERG (1972), and in those of PÁLSSON and VERGÉS (1952ab) in sheep as well. On the other hand DAVIES' (1975) data follow the pattern described by MCMEEKAN.

The feet had a growth coefficient lower (L^--pattern) than the more proximal bones in both limbs, in spite of other tissues surrounding the bones of the feet having higher *b*-values than bone. A growth gradient down the limbs, however, is disturbed by the ranking of the long bones (consistently by the corresponding bones) in both limbs, although the differences are small. Also the growth coefficient of the patella did not fit in. The deviating pattern in the patella was also found by others. With regard to the humerus it appears from the literature that at least in pigs, except the data of MCMEEKAN (1940abc), its deviating pattern seems to be regular as it was also found by CUTHBERTSON and POMEROY (1962b) and DAVIES (1975) (at least in Large White), while the results of RICHMOND and BERG (1972) show a similar tendency. Moreover the same is reported in rabbits (DULOR et al., 1976) but not in ruminants. The situation in the *os femoris* was about similar in that again CUTHBERTSON and POMEROY (1962b), and also JONES et al. (1978) found this bone deviating in cattle, while similar tendencies may be found in the results of RICHMOND and BERG (1972) as well.

An anterior-posterior growth gradient was disturbed by the thoracic vertebrae, because they showed a faster growth than the lumbar vertebrae. Support for this result was found by CUTHBERTSON and POMEROY (1962b). But on the other hand 'the second phase of active growth' (growth in a later phase would be faster than in an earlier phase) in the cervical vertebrae suggested by them, and also found by others, could not be confirmed.

The vertebrae and the sternum were subject to more variation than the limb bones. Here splitting of the carcass may at least partly be responsible, and in the case of the sternum it surely was. Splitting of the carcass did not result in systematic deviations, which is based on the regression of the ratio of the left and the right cold carcass weight on the sum of both halves. The *b*-values and the intercepts fluctuated round zero and hence did not deviate from the A-pattern, although two out of six treatment groups just reached significancy. In general both halves were of similar weight. Nevertheless along the splitting line variation still may occur. Therefore the vertebrae and sternum were excluded from total bone weight. The average variation coefficient, however, of the new total bone weight appeared to be only slightly less than of the total bone weight which included the vertebrae. The changes in the *b*-values were unimportant, while alterations in the number of differences between feeding levels or between sexes rather extended. Moreover the average variation coefficient of the total vertebrae is only slightly higher than that of the other groups. The higher variation, therefore, may be sought within the group of the vertebrae, possibly in the length of the individual vertebrae rather than in splitting of the carcass. Consequently some belief has to be given to the variable picture for the vertebrae in Fig. 4.14–4.18. Furthermore BERGSTRÖM (to be published) found such peaks at corresponding positions in cattle as well.

Comparison of the height of the *b*-values in pigs is only possible with those of DAVIES (1975) as far as the limb bones are involved. DAVIES (1975) found somewhat higher values in the *os femoris* and patella. As may be seen from Figs. 4.14 and 4.16 the neonates negatively deviate from the linear pattern (the boar piglets followed the curvilinear pattern) in the *os femoris*; this was also established for the patella as appeared from the regression analysis. The curves first increase up to stage I and then decrease, which may explain the difference with DAVIES' results, again due to the different trajectory.

With regard to the vertebrae the values found in the present study were intermediate between those found in cattle and those found in sheep. For the ribs the value was comparatively low. The growth coefficients for the limb bones found in ruminants were more differentiated, e.g. a higher value for the scapula and *os coxae* and lower values for the long bones.

5.2.8. *Influence of feeding level and sex on bone weight distribution*

Bone weight distribution was found to be influenced by feeding level and sex. The *ad libitum* feeding level enhanced the growth in the humerus, patella and total of the pelvic limb bones, whereas in the scapula and in the total vertebrae a faster growth was ascertained at the restricted level. Differences in constant terms resulted in a higher percentage for the ribs and the radius + ulna at the *ad libitum* level, whereas the *os femoris* had a higher percentage at the restricted level. The differences between feeding levels were generally established for one of the sexes. CARDEN and GOENAGA (1977) found differences (in the same direction) in slope for the scapula and in adjusted means for the *os femoris*, so in accordance with the results of the present study. The only difference ascertained by RICHMOND and BERG (1972) was also in the scapula, but in the opposite direction. In sheep FOWLER (1968, based on data of PÁLSSON and VERGÉS, 1952ab) calculated differences in ribs, humerus and radius + ulna, all having lower percentages at the restricted level, again in accordance with the present study. The finding in ribs may be explained as a functional aspect as outlined by FOWLER (1968) in that more space is needed for the thoracic organs and those anteriorly situated in the abdominal cavity at an *ad libitum* feeding level. The explanation as given by the Cambridge School of workers, in that later maturing parts are affected more under restricted food supply (dependent on the time at which it is introduced), cannot be confirmed. The difference in ribs and scapula is opposite to what has been suggested, whilst in the *os coxae* no differences were established at all.

Differences in slope between sexes were found in all long bones. In the thoracic limb the differences mainly concerned those between boars and sows at the *ad libitum* feeding level (with a faster growth in boars), while in the pelvic limb mainly differences between castrates and the other sexes at the restricted level were involved (with a faster growth in castrates). In the total of the thoracic limb bones boars also showed a faster growth than castrates. The differences in constant terms mainly concerned those between boars and sows at the restricted feeding level and between castrates and sows at the *ad libitum* level, not only in all long bones but also in ribs and scapula. The sows exhibited lower percentages than the other sexes in all long bones and in the total of the limb bones, but in the ribs and scapula they had higher percentages. Thus the lower percentage of total bone in sows is reflected in most individual bones. RICHMOND and BERG (1972) only found a significant difference in the scapula in the same direction as in the present study. On the other hand the heavier *os coxae* in sows as compared to boars as found by FOWLER and LIVINGSTONE (1972) could not be confirmed. Also in sheep hardly differences between sexes were found (SEEBECK, 1968b; PRUD'HON et al., 1978).

The treatment effects found in the present study were stronger (i.e. differences were discernible in more bones) than was previously reported, particularly true for the influence of sex on the bone weight distribution.

5.2.9. *Linear measurements of bones*

The increase in bone length, as was seen from Fig. 4.19, relatively diminished in the last stages when related to bone weight, but relatively increased when related to carcass length supported by the concave patterns resulting from the regressions. The former case means that mature length of bone is reached earlier than mature bone weight. Moreover the length of long bones of the restrictedly fed groups parallelled that of the *ad libitum* fed ones during the last stages.

The lagging behind of the length of the bones in relation to bone weight, where the proceeding mineralization plays a role too, led to an increase of the weight to length ratio. The ratio (Fig. 4.20) was lowest in the scapula, because this bone lengthened relatively more than the other bones measured. It was somewhat lower in the *os femoris*, because this bone had a comparatively lower bone weight. Thickness of the bones may interfere as well. In fact the radius appeared to be relatively thin. The weight to length ratio, however, kept pace with the others, because the smaller width was offset by a greater length. This of course resulted in a length to thickness ratio standing out for this bone. The development of length and thickness in the other long bones (humerus and *os femoris*) occurred in a more regular way, similar to what was found by WENHAM et al. (1973). The older statements that thickening of bones would take place in later stages (McMEEKAN, 1940abc; CUTHBERTSON and POMEROY, 1962b; and PÁLSSON and VERGÉS, 1952ab in sheep as well) therefore could not be confirmed. The tendency towards a decreasing ratio between length and thickness in the humerus (Table 4.27) in the later stages, results from a relatively diminishing length growth.

When related to carcass length the length of the limb bones, except the scapula, relatively lagged behind. Thus the form of the body changes; the animal grows relatively more in length than in height. It hence deepens, which is in accordance with the relatively greater thorax depth and the relatively greater leg length at birth as was described earlier. The latter effect was confirmed by a relatively shorter *os femoris* for the new-born boars. Furthermore it appeared that the neonates had a relatively lower weight to length ratio in the long bones. In general they did not deviate from later stages for bone length and length to thickness ratio. A satisfactory explanation for the relative increase in the last stages in bone length relative to carcass length cannot be given, one reason might be that the animal is protected from getting too long for mechanical reasons, to withstand the downward forces of the trunk.

Length growth of the scapula relative to carcass length clearly deviated from growth of other bones. As it is situated alongside the ribs, it is more connected with the growth of the ribs and the deepening of the thorax than with the pattern of the long bones. The radius, however, also exhibited a somewhat higher *b*-value. Although it has grown together with the ulna, the latter showed a somewhat lower value. There is no likely explanation. Such results on the other hand may also be deducted from the experiment of WENHAM et al. (1973). In addition they found that the tibia (to a lesser extent) behaved like the radius.

Thickness of the measured bones was hardly influenced by feeding level and sex, in contrast with their effect on length growth. The general picture was that bones were longer at the restricted feeding level for the same total bone weight as well as for the same carcass length. It was reflected in the length to thickness ratio only for the *os femoris*. The results found for the weight to length ratios of the bones revealed that the *ad libitum* feeding level led to higher ratios at a given total bone weight.

With regard to the influence of sex it appeared that the long bones were longer in boars than in the other sexes at the same carcass length. Boars also showed a higher bone weight to length ratio. In the cases reported boars had the highest length to thickness ratio as well. Only a few differences between castrates and sows were found. The castrates mostly showed the higher ratios. Compared at the same total bone weight, however, castrates had longer bones than the other sexes, mainly occurring at the restricted feeding level as was found for the weights of the individual bones.

The third root of weight was introduced in the dependent variables as soon as a length measurement was related to a weight measurement, in order to obtain a possible scattering of the pattern of the *b*-values around zero. It appeared from the *b*-values of the regression of the weight to length ratio on total bone weight that only those established for three of the treatment groups in the humerus did not significantly differ from zero. Instead of the 1/3 power a somewhat higher value may be actually calculated. For it is possible, given the results of the regression, to calculate the power needed in order to obtain independence of total bone weight, thus when the *b*-value equals zero. Considering a linear pattern, the power needed for the four bones examined varied from 0.33 to 0.42. So the 1/3 power of weight as suggested in the model was less justified than had been expected.

5.2.10. *Muscle weight distribution*

Like bone weight distribution, muscle weight distribution also alters during growth. The growth patterns of the individual muscles were comprehensively elucidated in the various sections of the preceding chapter. The standard muscle groups, however, have not been compared in their mutual relationship. Moreover since the majority of the individual muscles followed the growth pattern of the group to which they belonged reasonably well, the muscle weight distribution will mainly be discussed on the basis of the standard muscle groups.

5.2.10.1. Growth patterns of muscle groups

The growth patterns for the whole trajectory, as illustrated in Fig. 4.22ac and Fig. 4.23a, differ for the various muscle groups, but exhibit about the same course for feeding levels and sexes. It was seen that the greatest changes mainly occurred between birth and the first dissection stage (at about 26 kg live weight). This had been contended also by CUTHBERTSON and POMEROY (1964) and RICHMOND and BERG (1971b), while in cattle the main changes were reported for the early stages as well (BERG and BUTTERFIELD, 1975, 1976ac; BERGSTRÖM, 1978; BERG et al., 1978b). However, it does not mean that the new-born animals then also will deviate from the growth pattern as predicted from the regression line. For the existence of a curvilinear pattern in the group of muscles of the neck region and in that of the back and loin, allowed the neonates to be well-adapted to the overall pattern. Nevertheless the curve in the latter group bended too much for the new-born sows, so that they positively deviated from it. Further curvilinear patterns were established in the group of muscles of the proximal thoracic limb for the restrictedly fed groups and castrates, and in the group of muscles of the proximal pelvic limb for castrates only. All other groups showed a linear pattern from which the neonates deviated, negatively in the proximal and distal pelvic limb group of muscles and positively in the group of muscles of the shoulder girdle region and that of the thorax and abdomen, while the boar piglets also positively deviated from the pattern of the group of muscles of the proximal thoracic limb.

It may be obvious from the preceding paragraph that in determining whether the relative growth of a given variable proceeds according to a mono or diphasic (or multiphasic) pattern, the new-born stage is of importance. Taking into account the new-born stage, actually only the group of muscles of the distal thoracic limb and the sublumbar and skin muscles have a linear pattern. It is in accordance with the pattern found by BUTTERFIELD and BERG (1966ab) and

LOHSE et al. (1971) (in the case of the sublumbar muscles estimated from the patterns of the constituent individual muscles), except that in the former reference the distal thoracic muscles were given a low-average impetus. Further a linear pattern was reported in both references for the group of muscles of the distal pelvic limb. BERGSTRÖM (1978) also found a linear pattern for the four groups of muscles mentioned (as deducted from the significancy tests on the *b*-values), except for females in the distal thoracic limb muscles. Furthermore LOHSE et al. (1971) found a linear pattern for the group of muscles of the proximal pelvic limb and the abdominal group of muscles. The latter (sub)group had a linear pattern in the present study for sows only. For some muscle groups it is more difficult to judge, because the grouping of muscles is dissimilar. But looking at the individual muscles it may be concluded that in general in all other cases diphasic patterns were established. Deviating from the other references ROBELIN et al. (1977) found a curvilinear pattern for the sublumbar muscles.

In pigs CARDEN and GOENAGA (1977) only used a linear regression model and DAVIES (1974b) concluded that solely linear growth patterns were found. Moreover RICHMOND and BERG (1971b) found significant differences in the percentages during growth for the group of muscles of neck and thorax only, while CUTHBERTSON and POMEROY (1964) reported that changes in the percentages increase between the first and second period were of minor importance. So in pigs, except for the present study, hardly any non-linear patterns were found for muscle groups. It must be added, however, that RICHMOND and BERG (1971b) undoubtedly would have found non-linear patterns had they tested their first dissection stage group (23 kg live weight) against the higher weight groups. Again the trajectory over which the results have been calculated determines the answer. In case of DAVIES (1974b) work in particular the trajectory deviates from the others; already four dissection stages were involved before 20 kg live weight was reached, while the other two stages lay before 65 kg which is about dissection stage II in the present study. In many cases the combination of the new-born stage and the later stages of growth lead to a multiphasic or curvilinear pattern. Up to 65 kg the bending of the curve (without the long tail) is apparently too weak (though it is surprising in the case of the group of muscles of the proximal pelvic limb) to attain significancy, and perhaps the number of three animals per dissection stage plays a role as well.

5.2.10.2. Growth patterns of individual muscles

A linear growth pattern was not only established for the various muscle groups, but DAVIES (1947b) did find it for the individual muscles as well, for the same reasons. Whether mono or multiphasic patterns for individual muscles in farm animals did occur, was tested for different *b*-values during growth only in cattle by BUTTERFIELD and BERG (1966a), BERGSTRÖM (1978) and partly by ROBELIN et al. (1974, 1977), and in sheep by LOHSE et al. (1971). As to the growth patterns of the individual muscles striking similarities as well as contradictory results were found. When ROBELIN et al. (1974, 1977) are left out of consideration, all references mentioned a diphasic pattern in accordance with the present study for *m. longissimus thoracis et lumborum*, *m. iliocostalis* and *m. obliquus abdominis externus*. In two of the references a diphasic pattern in accordance with ours was found for *m. biceps femoris*, *m. gluteus medius*, *m. semitendinosus*, *m. semimembranosus*, *m. adductor*, *m. deltoideus*, *m. subscapularis*, *m. teres minor*, *m. splenius*, *m. brachiocephalicus*, *mm. longus capitis*, *longus colli* etc., *m. serratus dorsalis cranialis* + *m. serratus dorsalis caudalis*, *mm. intercostales*, *m. rhomboideus*, *m. latissimus dorsi* and *mm. serrati ventrales cervicis* and *thoracis*. Diphasic patterns were also found in *m. quadriceps femoris*, at least in parts of it, because in the literature the muscle is subdivided into the four heads. Furthermore in a number of other muscles only one of the references was in agreement with the results of the present study, or in other references diphasic patterns were established, whereas a linear pattern in the present study was found.

According to BUTTERFIELD and BERG (1966a) a number of muscles were too variable to classify. Since they did not go further as a diphasic pattern, it might be that muscles having a clear curvilinear pattern with probably a triphasic pattern were not discovered, e.g. *m. infraspinatus* and *mm. intercostales*.

The average variation coefficients for the individual muscles within the muscle groups generally varied from 6 to 16%. Furthermore they were higher as the weight of the muscles decreased, except in the group of muscles of the neck region. There errors in splitting of the carcass interfered, leading occasionally to high variation coefficients. On the other hand the findings reported by BERGSTRÖM (1978) that in identical twin pairs the between-pair variation in weight of muscles was much larger than the within-pair variation, also for smaller muscles, point at the reliability of the dissection work. This may mean that the smaller muscles also biologically have a greater variability than the larger ones.

5.2.10.3. Height of growth coefficients of muscle groups

With regard to the height of the *b*-values of the muscle groups those found by BUTTERFIELD and BERG (1966b), LOHSE et al. (1971) and BERGSTRÖM (1978) were generally in reasonable agreement with results of the present study. However, marked differences were found as well. The most striking deviation was the lower *b*-value (more than 0.1 unit) in pigs for the abdominal muscles in comparison with those in ruminants. It may be explained as a functional aspect in that the ruminants possess a relatively higher amount of alimentary tract and gut fill. CUTHBERTSON and POMEROY (1964) reported a decreasing growth of the limb muscles and an increasing growth of the other groups, so in accordance with the *b*-values found in the present study, except for the abdominal and thoracic group of muscles. Apart from other isolated differences (e.g. LOHSE et al. (1971) found a higher *b*-value for the muscles of the proximal pelvic limb, and a lower value for the skin muscles, while BERGSTRÖM (1978) found a higher value for the latter group), the group of muscles of the distal thoracic limb was found to have a higher *b*-value (about 0.08 unit) in pigs than in ruminants. No explanation can be given directed to a functional aspect. Based on the statements of BERG and BUTTERFIELD (1976c) that cattle are more agile than pigs it rather should have been the reverse.

It is obvious that the *b*-values calculated by DAVIES (1974b) will deviate more due to the trajectory. From Figs. 4.22a and 4.22c it may be predicted that DAVIES (1974b) found a lower value in case of a decrease from the new-born stage to stage I and an increase in the opposite case. For the subgroup of abdominal muscles DAVIES found higher values for the muscles which deviated negatively from the regression line. The difference was small for the group of muscles of the distal thoracic limb, understandable because this group was found to have a linear pattern. The values given by DAVIES (1974b) were in the range or about equal for the sublumbar and skin muscles, which were both groups with a linear pattern.

5.2.10.4. Height of growth coefficients of individual muscles

The same as in the preceding paragraph may also be stated for the individual muscles. With respect to the comparison with the *b*-values calculated in the ruminants some remarks may be made. In general they are in good agreement when the values of the constituent muscles are not far from the average of the groups that were about in line with the group averages of the present study. The largest deviations were found in the muscles of the abdominal wall and to a lesser extent also in those of the thoracic wall. In all muscle groups some muscles are to be found that have *b*-values which are not in accordance with *b*-values in one or more references. On the other hand in some cases muscles can be indicated that deviate from an expected pattern, but their *b*-values are nevertheless affirmed in one of the references. The calculated values are most similar to BERGSTRÖM'S (1978) work. It may partly be a consequence of the same dissection technique as POMEROY (1978) pointed at the similar results reached by the workers of the Cambridge School. But there are also deviations from BERGSTRÖM'S results, while there is agreement in his work with others. Furthermore it can be stated that in ruminants there is a greater differentiation in the *b*-values within the various muscle groups than in pigs.

In most muscle groups some muscles deviate from the pattern of the group as a whole. The greatest deviations were established in the group of muscles of the abdomen and thorax. Within muscle groups, muscles may be more deeply or more superficially situated, while others have an intermediate position. Although the classification may sometimes be somewhat arbitrary, in many cases the more deeply situated muscles (and hence more closely situated to the skeleton) revealed a lower growth pattern, whereas the more superficially situated ones exhibited the higher *b*-values. Physical reasons may play a role in this respect. And muscles in an intermediate position most resemble the average pattern of the group. But a number of exceptions were mentioned as well, e.g. the *mm. biceps femoris, gluteus medius, triceps brachii, omotransversarius* and *pectorales superficiales* had comparatively too low *b*-values, while *mm. obturatorius externus, multifidi, rectus abdominis, transversus costarum* and *intercostales* demonstrated comparatively too high values. It is tempting to ascribe the dissonant pattern in *mm. transversus costarum* and *intercostales* to the comparatively higher growth pattern of the ribs and the dissonant pattern in *m. obturatorius* *externus* to the higher pattern of the *os coxae*. On the other hand BERG and BUTTERFIELD (1976c) reject a causal relationship between weight increase of a particular bone and that of the muscles surrounding it, which is based a.o. on examples of BUTTERFIELD and BERG (1966a) and BRÄNNÄNG (1971). Furthermore the close relationship between a higher increase of the scapula and the *m. subscapularis* as found by CUTHBERTSON and POMEROY (1964) could not be confirmed in the present study either. Associated with the high growth impetus of bone, *mm. supraspinatus* and *infraspinatus* ought to grow in the same way. The latter muscle did not, while the former in fact had an A^+-pattern, but at the same time it is a muscle tending to a more superficial position.

Growth patterns of muscles as related to a more deep or superficial position need not necessarily be related to smaller or larger muscles respectively, cf. the A^--pattern of *mm. semimembranosus*, *quadriceps femoris* and *triceps brachii*. A disto-proximal or ventro-dorsal growth gradient may interfere in the alleged relationship as well.

5.2.10.5. Growth gradients

Considering the *b*-values of the muscle groups a disto-proximal growth gradient was established in both limbs, proceeding via the sublumbar muscles to the dorsal region on the one hand, and via the muscles of the shoulder girdle region to the dorsal and neck region on the other. The picture was completed by a gradient over the trunk from ventral to dorsal. The centripetal pattern is found in cattle (BUTTERFIELD and BERG, 1966b; BERGSTRÖM, 1978; BERG et al., 1978b), in sheep (LOHSE et al., 1971) as well as in pigs (MCMEEKAN, 1940abc; DAVIES, 1947b). However, in cattle rather a dorso-ventral pattern was ascertained, but LOHSE et al. (1971) in sheep found the gradient as in our results. MCMEEKAN (1940abc) and DAVIES (1974b) did find an anterior-posterior gradient in contrast to our results. It may again be due to the trajectory over the early stages. When later stages are involved, such a gradient is not found in cattle as well as in sheep or rather is the reverse (BERG et al., 1978b). It is ascribed to a masculinization process; BERGSTRÖM (1978) in fact found an anterior-posterior gradient in the females. This process was also confirmed in the present study. Although not all differences were significant, the majority of the muscles of the neck region and those anteriorly situated within the shoulder girdle region showed higher *b*-values in boars than in the other sexes. Pronounced examples occurred in *mm. splenius* and *rhomboideus*. Except for the quadratic pattern for all treatment groups in the former muscle and for the *ad libitum* groups in the latter, boars exhibited a positive cubic term in addition. It means that in the case of *m. splenius*, although a negative quadratic term counteracted the positive cubic term, in later stages the difference between the boars and the other sexes relatively increases, i.e. the difference between boars and sows at 15 kg side muscle weight was about 7%, and at 45 kg side muscle weight it amounted to about 14%; between boars and castrates the differences were about 2 and 10% respectively. Thus there was an attempt for masculinization in castrates too, but they do not diverge from sows at heavier weights. Such effects were also described by BERG and BUTTERFIELD (1976c).

Another feature of the splenius muscle has to be highlighted. This muscle in particular contributes to the higher proportion of the group of muscles of the neck region at birth. The *m. splenius* hence has a relatively high proportion at birth as well as upon maturing, made possible by the fully concave quadratic pattern to which in addition the cubic term in boars contributes as was described above. Together with *mm. longus capitis, longus colli etc.* it determines the quadratic pattern of the group as a whole. Its higher proportion is functionally necessary, for the relatively heavier head at birth has to be borne.

In order to understand the pattern that both muscle groups of the pelvic limb showed a rise (Fig. 4.22ac) after birth up to stage I, whilst those of the thoracic limb tended to a downward pattern, the study of prenatal growth may help. According to JOHNSON (1974) the muscle groups of the limbs (in calves) had a faster growth than other groups prenatally; thus being a preparatory growth to their function after birth. The postnatal level, however, was already reached in the thoracic limb at birth, but not yet in the pelvic limb.

Since muscles are acting mostly over more than one bone, it was difficult to relate increase of bones to increase of muscles. The general pattern of the growth gradients of the muscle groups over the animals' body is roughly resembled by that of the bones or bone groups. An example is also found in that the group of muscles of the neck region and the anteriorly situated muscles of the shoulder girdle region being heavier in boars, may be associated with the relatively higher proportion of long bones of the thoracic limb in boars. The growth of cervical vertebrae, however, and also of lumbar vertebrae was comparatively low with respect to muscle groups in that region. Yet harmony of growth has to be maintained, and that seems possible within rather wide limits with regard to the weight of the muscles, cf. the deviating muscle distribution of the animal discussed on p. 90. Fat deposition may vary to a great extent in this respect.

5.2.11. *Influence of feeding level and sex on muscle weight distribution*

Differences in slope or shape of the regression in the muscle groups were only established for the group of muscles of back and loin and for that of the sublumbar muscles. Differences in constant terms in all other groups were found, except in the group of muscles of the proximal thoracic limb. In this group thus no significant differences were ascertained neither for the influence of feeding level nor for the influence of sex, both in the present study and in the literature. Since the group was found to have an average growth pattern as well, it is hence the most stable muscle group of the carcass.

With regard to the individual muscles differences between feeding levels as well as between sexes were computed. In a minority of the muscles differences in slope or shape were established. Most differences appeared in the constant terms. In 12 muscles, which is about 20% of the total amount of individual muscles dissected, no differences at all were discernible. Most of them were situated in the proximal pelvic limb. In the groups as a whole in which no differences were found, differences did appear in individual muscles, but then they rendered opposite results. But for some exceptions the differences between feeding levels and sexes followed those of the group to which they belonged.

5.2.11.1. Influence of feeding level on muscle weight distribution

In most muscle groups differences between feeding levels were found, occurring for one of the sexes only, for two or for all three sexes. Apart from this fact or whether the differences were found in slope or in constant terms, the picture is that at the *ad libitum* feeding level the groups of muscles of the trunk (abdomen, thorax, back and loin), including the skin muscles show a higher proportion, whereas those of the neck region and the limbs, including the sublumbar muscles have a lower proportion.

The higher proportion of the muscles of the abdominal and thoracic wall was to be expected based on the experiments of HEAP and LODGE (1967). FOWLER (1968), LOHSE et al. (1971) and FOWLER and LIVINGSTONE (1972) pointed at the functional aspect. It is explained as the functional demand induced by the *ad libitum* feeding when more space is needed for the abdominal contents. The effect was also found by MURRAY and SLEZACEK (1975) in sheep and CARDEN and GOENAGA (1977) in pigs, but not by RICHMOND and BERG (1971b) though a tendency to the effect was apparent.

Although JOHNSON et al. (1973) in cattle as well as DAVIES and PRYOR (1977) in pigs found that intramuscular fat did not influence muscle weight distribution with increasing amounts of total fat, comparison at the same muscle weight, however, means that *ad libitum* fed animals e.g. contain relatively more fat and have a relatively lighter head. The latter may have led to the lower proportion of the group of muscles of the neck region. The *ad libitum* fed animals are comparatively more mature which, as a consequence of the growth patterns, renders a lower proportion in the limbs, especially in the proximal part of the pelvic limb. This was also found by MURRAY and SLEZACEK (1975), but not by CARDEN and GOENAGA (1977) and RICHMOND and BERG (1971b). Although in the two last-mentioned references no differences in the group of muscles surrounding spinal column (largely comparable with the group of muscles of the back and loin + the sublumbar muscles in the present study) were found, this needs not to disagree with our findings, because they were established for boars only.

In the literature only ANDERSEN (1975) in cattle listed differences between feeding levels for individual muscles. In the cases where differences were found in the present study they were mostly found by ANDERSEN (1975) as well, but in a rather large number of other muscles the results were contradictory.

5.2.11.2. Influence of sex on muscle weight distribution

Except for both groups of muscles of the thoracic limb, all groups showed differences between sexes. These differences were mainly found between boars and the other sexes, and much less between castrates and sows. The latter result means that in comparison with RICHMOND and BERG (1971b) agreement may be found when sex differences did appear, because boars were involved in the present study. On the other hand there was disagreement too; in three cases where differences between castrates and sows were found in the present study they were not found by RICHMOND and BERG (1971b), while in two cases where they did find differences, the differences were absent or tended to the opposite direction.

Because of the masculinization process boars showed a higher proportion in the group of muscles of the neck region, which was still present in the group of muscles of the shoulder girdle region (with respect to sows) and in that of the thorax including the skin muscles. In the subgroup of abdominal muscles no sex differences were found. As a consequence boars had a lower proportion of the more expensive groups of muscles (proximal pelvic limb, sublumbar muscles and back and loin). Castrates followed the boars in those cases where a difference between castrates and sows was found.

5.2.12. *Fat weight distribution*

Fat weight distribution changed during growth. The faster growth of flare fat over subcutaneous fat (MCMEEKAN, 1940a; HOFMANN and RITTER, 1958; CUTHBERTSON and POMEROY, 1964) and that of the latter fat depot over intermuscular fat (MCMEEKAN, 1940b; PÁLSSON and VERGÉS, 1952a; CUTHBERTSON and POMEROY, 1964) was in accordance with the literature. When other fat depots are included (total internal fat, intramuscular fat), the patterns will differ, e.g. intermuscluar fat increases along with subcutaneous fat (JOHNSON et al., 1972).

The changes in the intermediate stages were in reasonable agreement with results of DUMONT et al. (1973), while RICHMOND and BERG (1971c) reported the greatest changes in the first stages, which is also in accordance with the present study (cf. Fig. 4.25abc). During the first stages in all three sexes the *ad libitum* groups differed the most from the restrictedly fed groups. It is understandable, because after inducing the nutritional treatment the greatest differences in live weight growth appeared, so that the later developing subcutaneous fat with respect to intermuscular fat had the most benefit of it. As a consequence the opposite is seen in the intermuscular fat, since perinephric fat is not yet affected.

5.2.13. *Influence of feeding level on fat weight distribution*

For the whole trajectory the influence of feeding level on fat weight distribution was rather limited. A higher proportion for the *ad libitum* feeding level was only found for castrates in subcutaneous fat and for sows in flare fat, while in boars and sows a relatively lower amount of intermuscular fat was established at the *ad libitum* level. The first mentioned difference could be expected based on results of castration experiments (WALSTRA et al., 1977). Boars have relatively heavier fore and hind quarters. The heavier central part in castrates, more pronounced when fed *ad libitum*, contains much of the subcutaneous fat. RICHMOND and BERG (1971c) and CARDEN and GOENAGA (1977) found the reverse effect for intermuscular fat, whereas, however, FOWLER and ROSS (1974) as in the present study found more subcutaneous fat at a higher energy diet.

5.2.14. *Influence of sex on fat weight distribution*

Since significant quadratic and cubic terms for the different sexes were established many differences in shape between sexes did occur. As could be expected from the castration experiments mentioned above, boars contained relatively less subcutaneous fat. Because of the negative quadratic term castrates had a lower proportion of this fat at later stages than sows. As a consequence boars had relatively more intermuscular fat. But because of the negative quadratic term in boars and the positive cubic term in castrates these sexes ultimately approached each other at a later stage (cf. Fig. 4.26ab). Boars showed a relatively higher amount of flare fat than the other sexes; it grew according to a concave pattern in boars. On the other hand the sows had less flare fat than the other sexes at later stages in that they diverge from the the others by virtue of a cubic negative term. Sex differences in any of these fat depots were not found by RICHMOND and BERG (1971c). Their results, however, may be nevertheless in accordance with ours, because due to the different shapes the curves for castrates and sows cross each other in the stages they were examining.
In sheep SEEBECK (1968b) did not find sex differences either, but he included entire males in his experiments. On the other hand small but significant differences between sexes were reported by BERG and BUTTERFIELD (1976c) in cattle.

The ratio of the flare fat of the left and right carcass half regressed on the sum of both carcass halves revealed that the *b*-value of the ratio differed significantly from zero. It hence means that the ratio is not constant and changes with increasing carcass weight. The flare fat of the right half grew faster. Especially in earlier stages the weight in the right half would be higher. A plausible explanation cannot be given.

5.2.15. *Backfat thickness*

According to the convex pattern found, backfat thickness increased most in earlier stages in accordance with findings of HOFMANN and RITTER (1958). The depth measurements were influenced by feeding level which is also found by WILSON (1968a). *Ad libitum* feeding rendered greater depths of backfat for average backfat as well as at the different locations, except at the shoulder. Sex differences were established at all five locations as well as for average backfat. The boars had lower fat depths than the other sexes, while in a number of cases also sows showed smaller depths than castrates.

Apart from the quadratic terms, the various locations were differentially influenced during growth. Between the lowest *b*-value over the shoulder and the highest *b*-value over *m. gluteus medius* no clear growth gradient was found. Of the locations measured, backfat depth over the shoulder most closely increased along with total fat weight. In cattle KEMPSTER et al. (1976) rather found a gradient in opposite direction.

5.2.16. *Meat quality measurements*

With regard to the various meat quality characteristics it appeared that hardly any difference for feeding level or sex was discernible. During growth the values did not alter much either. Only the transmission value in mature boars and sows was enlarged. Higher transmission values (> 70) are generally associated with PSE-meat. Thus the results of the transmission value are not in accordance with those of the subjective evaluation and pH-measurement. The higher transmission value found at the mature stage in boars and sows suggests a lower solubility of the muscle proteins, but no likely explanation can be given. It was achieved apparently independent of the denaturating processes normally considered to be responsible for the occurrence of PSE-meat.

5.2.17. *Use of the allometric equation*

It was already clear from the literature studied that the allometric equation as such would not be applicable when longer trajectories were involved. Preliminary calculations on the present material confirmed this. Therefore high power terms were added to the allometric equation. It appeared that many times a high power term was needed. Cubic terms were found only for a certain sex group; quadratic terms on the contrary were established for sex groups as well as for feeding level groups and sometimes as a combination of them. Fully quadratic patterns were ascertained as well.

High power terms appeared to be needed in description of growth of carcass components, growth of offal components and organs, growth of some bones and for several ratios concerning bone measurements, growth of certain muscles and muscle groups, and in growth of fat depots and for backfat thickness. When in addition the new-born stages are taken into account a higher power term would have been needed many times more.

Of the muscles listed by BUTTERFIELD and BERG (1966a) in cattle and by LOHSE et al. (1971) in sheep about 60% had a monophasic pattern. In the present study of the dissected muscles approximately 30% had a fully linear pattern, i.e. including the new-born stage. Another 20% was linear for only one of the sexes, because alternately only one of them at birth deviated from the regression line. When the new-born stage is left out of consideration approximately 20% of the muscles in one way or another needed a high power term.

Since diphasic or multiphasic patterns give unnatural intersections, high power polynomials were preferred in the present study. Their use on the other hand also bears some problem in interpretation, e.g. comparing a linear pattern with a curvilinear one and comparing two curvilinear patterns with different coefficients. One still has to calculate whether higher or lower percentages for different values of the independent variate will appear. In many cases the existence of a higher power term rendered a curvilinear pattern which was considered as a smooth improvement of the straight line of the allometric relationship.

5.2.18. *Importance of changes in distributions*

One of the objectives in animal production is the optimalization of the increase of the amount of meat in the carcass. Having described growth patterns of parts relative to given entities in the way mentioned above, a further question is whether factors exist that influence these patterns and muscle weight distribution in particular. An immediate improvement would be the use of boars for meat production. Feeding level also easily influences gross carcass composition. McMeekan (1940abc) stated that tissues (relative to age or body weight) grew differentially after nutritional treatment and that within any of the major tissues growth gradients existed. Parts with the highest growth intensity were retarded most by feed restriction. Wallace (1948) contended that calculations had to be done on the basis of equal tissue weight, and Elsley et al. (1964) after re-analysis of McMeekan's data in this way, in fact ascertained that differential changes were small or absent. Such results appear in the literature more often then. But more and more evidence is coming up indicating that also on a within-tissue basis the distribution may be influenced by feeding level and sex. Especially in the present study sex differences were found, but these were mainly accounted for by the boars.

Most of the time the shifts in muscle or bone weight distribution are said to be of no practical importance. Based on the regressions found one may calculate the changes in muscle weight distribution. The most valuable part, i.c. the total of muscles of the proximal pelvic limb, had a percentage that was 0.39 and 0.63 higher at the restricted feeding level than at the *ad libitum* feeding level for castrates and sows respectively. When the small changes of the sublumbar muscles are introduced also, it ultimately (in average) results in about 150 g more of the high-priced muscles at the commercial slaughter weight. At the same time the weight of the *os femoris* decreases a little. One loses, however, about 30 g of the *m. longissimus thoracis et lumborum*. A similar calculation can be made when boars instead of castrates would be fattened. The greatest difference amounted to 1.3%. Apart from feeding level, it would result in about 330 and 250 g more in castrates and sows respectively. One may gain another 100 and 150 g respectively when the last-named muscle is taken into consideration.

It is a matter of choice whether such differences are of importance. In any case the unfavourable sex difference for boars is by no way in proportion to what may be gained from increase in total amount of meat by fattening boars. The influence of feeding level seems to be of minor importance. Although the effect of selection on more valuable parts is doubted, nobody actually tried it. The doubts are based on the findings that after many years of selection for meatier animals the distribution had not changed (Berg and Butterfield, 1976a) and on the relationship between form and function, strongly defended by Bryden (1969). On the other hand sex differences and also breed differences point at genetic variation.

6. SUMMARY

An experiment was carried out to study growth from birth to maturity in Dutch Landrace pigs based on complete anatomical dissection. The assessment of a detailed description of the compositional changes during growth was the primary objective of this study. In order to examine whether growth patterns would be influenced by feeding level and sex, six treatment groups were formed, being the combinations of the three sexes (entire males, castrated males and females) and two feeding levels (*ad libitum vs* a restricted level).

The literature was comprehensively reviewed with regard to relative growth of the main components and their constituent parts. Since the principles by which the changes in the body occur and the laws to which the processes of growth obey originate from a general and basic concept, the studies carried out in other farm animals were discussed as well.

The experiment was set up as a cross-sectional design in which 7 dissection stages were involved. From dissection stage I (at an age of 10–12 weeks and about 25 kg live weight) onwards animals were slaughtered at 6 week intervals up to dissection stage V, followed by an interval of 14 weeks up to dissection stage VI, while the last dissection (stage VII) was carried out at or near maturity. Littermates were allotted to the treatment groups and they were assigned at random beforehand to the different dissection stages to avoid if possible that they should be slaughtered at the same stage. Later on dissection stage 0, involving new-born animals of different weights and of both sexes, was added for completion of a total view over the whole trajectory. The experiment was carried out in 4 replicates that partly ran alongside each other. In principle each dissection stage comprised 8 animals per treatment group. A number of animals had to be withdrawn from the experiment because of leg weakness or various other reasons. Ultimately 283 animals were dissected.

The difference in feeding level was introduced at the actual start of the experiment at dissection stage I. The restricted feeding level imposed was directly related to the *ad libitum* level, in that restrictedly fed groups in addition to the maintenance requirement received half of the feed for production of the *ad libitum* fed groups of the same weight and sex. The *ad libitum* fed animals had free access to feed during the whole 24 hours period. Beyond 225 kg live weight the restricted level was no longer associated to the *ad libitum* level and was fixed at 3.1 kg per day up till mature weight.

The carcass halves were dissected in different ways. The right half was dissected according to the institute's (I.V.O.) standard method into commercial joints. The left half was used for complete anatomical dissection, except for the head and feet, into individual bones and muscles and into three fat depots (subcutaneous, intermuscular and flare fat). In addition some linear measurements were taken, such as carcass length, leg length, thoracic depth, length and thickness of bones, backfat depth at the midline, while also some meat quality characteristics were measured.

The relative growth of parts, y, to given entities, x, was described by means of the allometric equation $y = ax^b$ in its logarithmic form, where b is the growth coefficient describing growth of y proportionate to x. Since primary attempts in ordering the material had revealed that high power terms would be needed, such terms (up to and including a fourth degree term) were added to the equation. This high power polynomial was ultimately used for regressions through dissection stages I to VII. An indicator variable was incorporated in the model for dissection stage 0. The power terms were orthogonalized on all preceding terms. The b-values presented in various tables then correspond to the b of the linear model, even when a high power term was needed.

A first classification of the growth patterns was achieved according to the high power term needed in each of the six treatment groups. It determined whether sex groups (the combination of the treatment groups of the same sex) or feeding level groups (the combination of the treatment groups with the three different sexes of the same feeding level) could be formed, but with the restriction that the proportion of the residual variance (after taking into account the linear term) for each of the treatment groups at issue had to be 10% at least. When all 6 or 5 treatment groups exhibited a quadratic term, the pattern was considered quadratic irrespective of the proportion of the residual variance. A similar procedure was followed within the linear pattern based on significant differences in slope between treatment groups. The b-values were further classified into classes of 0.05 unit proceeding from an average class (A) between 0.975 and 1.025 to both sides, an upper end with the classes A^+, H, H^+ and H* and a lower end having A^-, L, L^- and $L^=$ growth patterns. Bone, muscle and fat weight distribution were studied within each of the respective tissues.

Although it will discriminate against a number of significant differences, it is impractical to refer to all discernible results. Therefore of the results obtained only the more general trends and conclusions will be mentioned. This is done point by point and generally following the various headings of the preceding chapter depicted by an extra interruption in the text. In cases where a linear growth pattern is mentioned it means linear according to the logarithmic form of the allometric equation through stages I–VII.

1. Pigs grew well up to dissection stage V which is at about 125 to 165 kg live weight depending on feeding level. The maximum live weight growth for boars and sows was about 825 en 750 g/day respectively between stages II and III, and for castrates about 845 g/day between stages I and II. At the restricted feeding level the maximum growth rate shifted to a further stage and was about 80, 110 and 210 g/day lower than at the *ad libitum* feeding level for the sexes respectively. The feed conversion ratios in general increased with the increase in live weight and were the most favourable at the restricted level as well as in boars, while castrates exhibited the highest ratios.

The weighings every fortnight allowed the drawing of weight-age relationships for a diminishing number of animals. From the Text-figures the inflexion point was estimated at about 30% of mature weight. The growth curves seemed to flatten at about 320 kg in boars and castrates, and also *ad libitum* fed sows approached this weight, while the restrictedly fed females reached about 260 kg live weight. Remaining single animals of all three sexes reached higher final weights.

2. The carcass grew linearly and at a faster rate than live weight. After birth the dressing percentage decreased at first, but it increased with 10% through stages I–VII. The dressing percentage in general was higher in the fatter animals.
3. The linear A^--pattern and the negative cubic term in the males indicate that carcass length relatively diminished with increasing carcass weight. Boars were longer than castrates when related to carcass weight, but at a given muscle + bone weight the reverse was found. *Ad libitum* fed sows based on carcass weight had a smaller carcass length than restrictedly fed ones, but when based on muscle + bone weight they were longer. This is another example in addition to others mentioned in the literature that the choice of the independent variate may determine the direction of the effect, especially when such a variable factor as fat is involved. This influence of fat was illustrated also in the thorax depth. The higher amount of fat caused that for a given carcass weight restrictedly fed groups had a greater depth than *ad libitum* fed ones, but when related to carcass length the reverse was found.
4. Thorax depth showed an A^+ or a concave pattern with respect to carcass length. Since furthermore leg length related to carcass length at birth was relatively greater than in later stages, it is clear that during growth animals change in form, they relatively deepen. This was confirmed in that the increase in length of the long bones of the limbs lagged behind to that of carcass length.

5. The composition of the carcass markedly changed during growth. Without reference to quadratic patterns found, common *b*-values for each of the sexes were established. Castrates and sows resembled each other. In the order of faster growth the values were about 0.70, 0.75, 0.85, 0.90 and 1.35 for the components offal, bone, muscle, skin and fat respectively. Muscle thus grew faster than bone, but both tissues grew slower than the carcass to which they were related. In boars the same order was found, but at a clearly different level: about 0.75, 0.80, 0.90, 1.10 and 1.25 respectively. Only fat increased at a faster rate than the carcass, except the striking higher growth of skin in boars in which this characteristic deviates from growth in males of other species.

Carcass composition also differed with regard to feeding level. The unfavourable influence on the amount of fat after *ad libitum* feeding disappeared when muscle or bone weight was regressed on muscle + bone weight. For a given muscle + bone weight castrates had more bone than sows. Boars had less muscle than sows due to a higher bone weight, but more muscle when related to carcass weight.

6. The muscle to bone ratio increased during growth, especially in the early stages because of the relatively well-developed skeleton at birth. The ratio is not influenced by feeding level. Sows had the most favourable ratio, followed by boars.

7. The muscle to fat ratio decreased during growth, for castrates and sows to below unity. Castrates had the most unfavourable ratio, followed by sows. *Ad libitum* feeding unfavourably influenced the ratio.

8. Boars had a heavier head than the other sexes. It may be a secondary sex characteristic as the difference remained after regression on muscle + bone weight. The head at birth had a relatively high percentage, about 18 % of carcass weight, which swiftly decreased and stabilized at about 4 to 5%. Within total offal the head grew faster than the feet, while boars had a relatively lighter head than the other sexes. This may be due to a somewhat less deposition of fat in the head region of boars.

9. The kidneys followed the decreasing pattern of the total of organs and viscera when related to live weight. Within total offal boars differed from the other sexes. Growth of testes was distinctly different from that of kidneys. Initially they grew fast in relation to live weight, because they were relatively undeveloped at birth, and reached mature proportions already in the intermediate stages after the prepubertal growth.

10. The ratios of the left and right testis, kidney and feet revealed that after regression on live weight, the b-value as well as the $\ln a$-value did not deviate from zero, meaning that the ratio not only remained constant but also that the weights were equal, indicating symmetric growth.

11. Bone weight distribution alters during growth. Bone groups hardly changed, but within the groups some bones had an A^+-pattern: scapula, *os coxae*, ribs and sternum, while the long bones tended to an A^--pattern. Although the feet and the proximal bones of the limbs had distinct b-values growth gradients down the limb were disturbed by the ranking of the long bones, though the differences were small. A somewhat higher growth pattern in the thoracic vertebrae disturbed a growth gradient along the axial skeleton. The growth coefficients of the bones of the thoracic limb tended to be higher than those of the corresponding bones of the pelvic limb.

12. Feeding level and sex influenced bone weight distribution. After *ad libitum* feeding a higher proportion was found in humerus, radius + ulna, total of pelvic limb bones and ribs, but a lower proportion in scapula and *os femoris*. The higher proportion in ribs is given a functional meaning. The lower percentage of total bone in the carcass in sows was reflected in the long bones as well as in the total of the bones of both limbs. Sows had a greater proportion of ribs and scapula. The proportion of long bones in the thoracic limb was higher in boars than in castrates, while the opposite was found in those of the pelvic limb.

13. A variable picture was found in the vertebrae. As this might influence the distribution and patterns of other bones a new total bone weight excluding the

vertebrae and sternum was tried as the independent variate. Almost nothing changed in the situation and no further insight was gained. The higher variation was ascribed to length of the vertebrae rather than to errors in splitting of the carcass, because in general no systematic differences between weights of the carcass halves were established based on the result of regression of the ratio of both halves on the sum of them.

14. The relative diminishing increase in bone length in later stages led to the conclusion that bone length is earlier maturing than bone weight. Because of a proceeding mineralization also, the weight to length ratio increased. Since the scapula alongside the ribs had lengthened more than other bones, the ratio was lowest in this bone. *Ad libitum* feeding resulted in higher ratios at a given total bone weight. The radius was relatively thin, but its length kept pace with the others, hence resulting in a length to thickness ratio standing out. Increase in length and thickness of other long bones occured in a regular way. It means that an alleged decreasing length to thickness ratio could not be confirmed.

15. Bone thickness was hardly influenced by feeding level or sex. At a given total bone weight as well as at a given carcass length, however, the bones were longer at the restricted feeding level. Boars had the longest bones when compared at the same carcass length, while at the same total bone weight castrates had the longest bones.

16. In the weight to length ratios the third root of weight was incorporated in the variable. Only in a few cases the 1/3 power of weight was exactly justified. In most cases a weight proportionate to a power of somewhat below 0.4 would have led to independence of total bone weight.

17. Muscle weight distribution also changed during growth. About the same course in muscle groups was exhibited for feeding levels and sexes. The main changes occur during the early stages, already before dissection stage I. In many cases, therefore, the neonates appeared not to be adapted to the regression lines through the later stages, but they were in line with the fully quadratic positive and negative pattern for the group of muscles of the neck region and that of back and loin respectively. The group of muscles of the proximal thoracic limb showed a positive quadratic term for the restrictedly fed groups and castrates, while castrates also had a negative quadratic term in the group of muscles of the proximal pelvic limb.

18. A mono or diphasic pattern is largely dependent on the new-born stage. When the neonates were taken into consideration together with the patterns already mentioned, a fully linear pattern could only be established for the group of muscles of the distal thoracic limb and for the sublumbar and skin muscles.

19. In most muscle groups some muscles deviate from the pattern of the group; they were found in the group of abdominal and thoracic muscles in particular. But for a number of exceptions it appeared that more deeply situated muscles in many cases exhibited a lower growth pattern, whereas the more superficially situated ones revealed a higher growth pattern. Muscles in an

intermediate position showed an average pattern. Disto-proximal and ventro-dorsal growth gradients may interfere in this respect.

20. It is difficult to relate growth of individual bones to that of the muscles surrounding them, because often muscles act over more than one bone. Only a rough relationship existed for regions of the body according to the growth gradients. In accordance with a somewhat higher pattern of the bones of the thoracic limb with respect to that of the pelvic limb, the muscles in the regions did. But the higher growth pattern of the group of neck muscles was not found for the cervical vertebrae.

21. A disto-proximal growth gradient was established in both limbs, proceeding via the sublumbar muscles to the dorsal region, and via the shoulder girdle region to the neck and to the dorsal region too. Furthermore a gradient over the trunk from ventral to dorsal completed the picture. An anterior-posterior gradient was not found.

22. Upon maturing a masculinization process occurred in that the group of muscles of the neck region relatively increased together with some anteriorly situated muscles of the shoulder girdle region. Pronounced examples were found in *m. splenius* and *m. rhomboideus*, both bearing a positive cubic term in boars. Castrates were intermediate in this respect. The higher proportion of long bones in the thoracic limb in boars is in accordance with this masculinization process.

23. At birth the relatively heavy head has to be borne which is made possible by a higher proportion of the group of neck muscles to which *m. splenius* contributed in particular.

24. The most stable group of muscles is that of the proximal thoracic limb. Apart from the average growth pattern it is not influenced by feeding level nor by sex. Feeding level influenced the distribution in other groups in that *ad libitum* feeding resulted in a higher proportion of the groups of muscles of the trunk (abdomen, thorax, back and loin, skin muscles), whereas a lower proportion was found in those of the neck region and the limbs including the sublumbar muscles. A functional meaning was given to the higher proportion of the abdominal and thoracic muscle group, while the relatively lighter head might have contributed to the lower proportion of muscles of the neck region.

25. In most muscle groups a sex influence was discernible, mainly due to a difference between boars and the other sexes. The boars had a higher proportion in the muscles of the neck, proceeding to the group of muscles of the shoulder girdle region and in that of the thorax, including the skin muscles. The boars had a lower proportion in the groups of expensive muscles.

26. But for some exceptions the influence of feeding level and sex on the individual muscles largely followed that of the standard muscle group.

27. Fat weight distribution changed during growth as well. Subcutaneous fat and flare fat increased, whereas intermuscular fat decreased. Flare fat had the highest growth pattern.

28. Feeding level hardly influenced the fat weight distribution. *Ad libitum*

feeding resulted in more subcutaneous fat in castrates, and less intermuscular fat in boars and sows.

29. Clear influences of sex on fat weight distribution were established. Boars contained less subcutaneous fat. This is also valid for castrates at later stages with respect to sows. Boars had more intermuscular fat than castrates, but because of the opposite high power terms they meet again at later stages. Boars also produced more flare fat than the other sexes.

30. Backfat thickness as related to total side fat weight showed a concave pattern and increased most in earlier stages. *Ad libitum* feeding rendered a thicker fat layer. The backfat depth was smaller in boars than in the other sexes, while also sows had a smaller fat depth than castrates in a number of cases.

31. An anterior to posterior growth gradient in backfat depth could not be ascertained, because it would be disturbed in the intermediate locations. Fat depth over the shoulder followed most closely that of total fat weight.

32. There were hardly any changes discernible in the meat quality characteristics measured, while for feeding level and sex no influence was found.

33. In many cases growth patterns of part to whole relationships had to be described by means of high power terms. Unless one does accept unnatural intersections, the allometric equation is not applicable for longer trajectories. Curvilinear patterns avoid intersections or multiphasic patterns.

About 30% of the individual muscles revealed a linear pattern for the whole trajectory from birth to maturity. Apart from the new-born stage about 20% of the muscles needed a high power term in one way or another.

34. The most striking difference between pigs and ruminants as to the height of the *b*-values of muscles, is in the muscles of the abdominal wall that were higher in the latter species, which was ascribed to relatively greater contents of the abdominal cavity. No satisfactory explanation could be given for the higher proportion of the group of distal thoracic muscles being higher in pigs.

The growth coefficients of the individual muscles and individual bones are more differentiated in ruminants than in pigs.

Striking similarities as well as contradictory results were found in comparing results of the present study with those found in the literature and in comparing results of several references mutually. Most of the results found were in accordance with the literature; also seemingly deviating results may found yet to be supported by one of the references.

Most of the differences in height of the *b*-values can be ascribed to the examination of different trajectories. The influences of sex on within-tissue distribution were more often found in the present study than in the literature. They, however, were largely explained by including boars in the present study. Apart from the commercial importance, more and more evidence has been collected in recent years, including the present study, that feeding level also does influence the muscle weight distribution.

35. The influence of feeding level on muscle weight distribution seems commercially of subsidiary importance. The influence of sex does have commercial importance in that 400–450 g of high-priced muscles may be earned at commercial slaughter weight in castrates and sows in comparison with boars. This, however, counteracts the more favourable effect of total lean meat deposition in boars, but it is not in proportion to what may be gained from increase in the total amount of meat produced by fattening of boars.

7. SAMENVATTING

Er werd een proef uitgevoerd ter bestudering van de groei bij Nederlands Landvarken vanaf de geboorte tot volwassen stadium, waarbij de karkassen volledig anatomisch werden uitgesneden. Het voornaamste doel van deze studie was het geven van een gedetailleerde beschrijving van de veranderingen in lichaamssamenstelling gedurende de groei. Teneinde na te gaan of de groeipatronen zouden worden beïnvloed door voederniveau en sexe werden zes behandelingsgroepen gevormd, bestaande uit de combinaties van de drie sexen (beren, borgen en zeugen) en twee voederniveaus (*ad libitum vs* beperkt niveau).

Een uitgebreid overzicht werd gegeven van de literatuur met betrekking tot de relatieve groei van de hoofdcomponenten en van de onderdelen daarvan. Aangezien aan de principes via welke de veranderingen in het lichaam plaatsvinden en de wetmatigheden waaraan de groeiprocessen gehoorzamen een algemeen geldend en fundamenteel concept ten grondslag ligt, werd ook de literatuur met betrekking tot andere landbouwhuisdieren besproken.

De proef werd opgezet als een transversale proef met 7 opeenvolgende slachtmomenten. Vanaf slachtmoment I (op een leeftijd van 10–12 weken en ongeveer op een levend gezicht van 25 kg) werden dieren geslacht met tussenpozen van 6 weken tot aan slachtmoment V, waarna een interval van 14 weken volgde tot slachtmoment VI, terwijl de laatste uitsnijdingen werden uitgevoerd (slachtmoment VII) wanneer het volwassen stadium geacht mocht worden bereikt te zijn. Toomgenoten werden verdeeld over de behandelingsgroepen, terwijl zij van te voren at random werden toegewezen aan de verschillende slachtmomenten om zoveel mogelijk te vermijden dat toomgenoten zouden worden geslacht op gelijke momenten. Om een overzicht over het gehele traject te krijgen werd op een later tijdstip slachtmoment 0 toegevoegd, dat pasgeboren dieren van verschillend gewicht en van beide sexen omvatte. De proef werd uitgevoerd in 4 herhalingen die gedeeltelijk parallel liepen. In opzet bestond elk slachtmoment uit 8 dieren per behandelingsgroep. Een aantal dieren moest uit de proef worden genomen vanwege ernstige vormen van beengebreken of om verschillende andere redenen. Uiteindelijk werden 283 dieren uitgesneden.

Het verschil in voederniveau werd aangelegd bij de eigenlijke start van de proef op slachtmoment I. Het beperkte voederniveau werd rechtstreeks gerelateerd aan het *ad libitum* niveau, doordat de beperkt gevoerde groepen boven hun onderhoudsbehoefte de helft van het produktievoer van de *ad libitum* gevoerde groepen van hetzelfde gewicht en dezelfde sexe kregen verstrekt. De *ad libitum* gevoerde groepen hadden gedurende het gehele etmaal toegang tot het voer. Boven 225 kg levend gewicht was het beperkte niveau niet langer meer gerelateerd aan het *ad libitum* niveau en werd het constant gehouden op 3,1 kg per dag tot aan volwassen gewicht.

De beide karkashelften werden op verschillende wijze uitgesneden. De rechterhelft werd uitgesneden volgens de IVO-standaardmethode in commerciële deelstukken. De linkerhelft werd gebruikt voor de volledige anatomische dissectie (behalve de kop en de ondervoeten), waarbij individuele botten en spieren en drie vetdepots (subcutaan, intermusculair en reuzel) werden uitgesneden. Bovendien werden enkele lineaire maten genomen, zoals karkaslengte, stomplengte, borstdiepte, lengte en dikte van botten, spekdikte op de mediaan, terwijl ook enkele vleeskwaliteitskenmerken werden gemeten.

De relatieve groei van delen, y, ten opzichte van eenheden, x, werd beschreven met behulp van de allometrische formule $y = ax^b$ in zijn logarithmische vorm, waarbij b de groeicoëfficiënt is die de groei van y beschrijft proportioneel ten opzichte van x. Aangezien uit eerdere pogingen om het materiaal te ordenen gebleken was dat hogeregraadstermen nodig zouden zijn, werden dergelijke termen (tot en met vierdegraads) toegevoegd aan de vergelijking. Deze hogeregraadspolynoom werd uiteindelijk gebruikt voor de regressies voor de slachtmomenten I tot en met VII. Voor slachtmoment 0 werd een indicator-variabele in het model opgenomen. De hogeregraadstermen werden georthogonaliseerd op alle voorafgaande termen. De b-waarden welke in de tabellen staan vermeld corresponderen met de b van het lineaire model, ook indien een hogeregraadsterm nodig was.

Een eerste indeling van de groeipatronen werd verkregen op grond van de benodigde hogeregraadsterm voor elk van de 6 behandelingsgroepen. Deze bepaalde of sexegroepen (de combinatie van de behandelingsgroepen van dezelfde sexe) en/of voederniveaugroepen (de combinatie van de behandelingsgroepen met de drie verschillende sexen van hetzelfde voederniveau) konden worden gevormd, echter met de restrictie dat het aandeel van de restvariantie (nadat rekening werd gehouden met de lineaire term) voor elk van de betrokken behandelingsgroepen tenminste 10% moest bedragen. Wanneer 6 of 5 behandelingsgroepen een kwadratische term vertoonden werd het patroon zonder meer beschouwd als kwadratisch. Eenzelfde procedure werd gevolgd binnen het lineaire patroon, gebaseerd op significante verschillen in helling tussen behandelingsgroepen. De b-waarden werden verder ingedeeld in klassen. Daarbij werd uitgegaan van een gemiddelde klasse (A) gelegen tussen 0,975 en 1,025, die zowel naar boven als naar beneden gevolgd werd door klassen (A^+, H, H^+ en H^* respectievelijk A^-, L, L^- en $L^=$) met klassebreedtes van 0,05 eenheden. De bot-, spier- en vetverdeling werd bestudeerd binnen elk van de betrokken weefsels.

Omdat het onpractisch is alle verkregen resultaten weer te geven zullen alleen de meer algemene trends en conclusies worden vermeld, hoewel daarmee een aantal significante verschillen onrecht wordt aangedaan. De resultaten worden puntsgewijs weergegeven, waarbij grotendeels de indeling van hoofdstuk 5 is gevolgd, telkens aangegeven door onderbrekingen in de tekst. In de gevallen waarin wordt verwezen naar een lineair groeipatroon betekent lineair dat lineariteit is gevonden op basis van de logarithmische vorm van de allometrische formule waarbij de stadia I–VII betrokken zijn.

1. De varkens groeiden goed tot aan slachtmoment V, hetgeen afhankelijk van het voederniveau bij ongeveer 125 tot 165 kg levend gewicht ligt. De maximum levend gewichtstoename voor beren en zeugen bedroeg ongeveer 825 respectievelijk 780 g/dag liggend tussen de slachtmomenten II en III, en voor borgen bedroeg deze ongeveer 845 g/dag tussen de slachtmomenten I en II. Op het beperkte voederniveau verschoof de maximum groeisnelheid naar een volgend stadium en lag voor de sexen respectievelijk ongeveer 80, 110 en 210 g/dag lager dan op het *ad libitum* voederniveau. De voederconversie steeg in het algemeen met toenemend levend gewicht en was het gunstigst op het beperkte voederniveau zowel als bij de beren, terwijl de borgen de hoogste voederconversie lieten zien.

Op basis van de veertiendaagse wegingen was het mogelijk een groeicurve te construeren, zij het voor een verminderend aantal dieren. Het uit de figuren geschatte inflectiepunt lag op ongeveer 30% van het volwassen gewicht. De groeicurves leken af te vlakken bij ongeveer 320 kg bij beren en borgen, maar ook *ad libitum* gevoerde zeugen benaderden dit gewicht, terwijl de beperkt gevoerde zeugen ongeveer een gewicht van 260 kg bereikten. Enkele dieren bereikten aan het eind bij alle drie sexen hogere eindgewichten.

2. Het karkas groeide lineair en sneller ten opzichte van het levend gewicht. Na de geboorte daalde eerst het aanhoudingspercentage, maar vanaf slachtmoment I tot VII nam het met 10% toe. Het aanhoudingspercentage was in het algemeen hoger bij de vettere dieren.

3. Het lineaire A^--patroon en de negatieve kubische term bij de mannelijke dieren duiden er op dat de karkaslengte relatief afnam bij toenemend karkasgewicht. Beren waren langer dan borgen op basis van het karkasgewicht. Vergeleken op basis van het spier + beengewicht werd het tegengestelde gevonden. *Ad libitum* gevoerde zeugen hadden een kleinere karkaslengte dan de beperkt gevoerde op een bepaald karkasgewicht, maar ten opzichte van een bepaald spier + beengewicht waren zij langer. Dit is opnieuw een voorbeeld buiten andere in de literatuur genoemde voorbeelden dat de keuze van de onafhankelijke variabele de richting van het effect kan bepalen, vooral wanneer een zo variabele factor als vet daarbij is betrokken. Deze invloed van het vet werd ook geïllustreerd aan de hand van de borstkasdiepte. Ten gevolge van de grotere hoeveelheid vet hadden de *ad libitum* gevoerde groepen een geringere borstkasdiepte dan de beperkt gevoerde op karkasgewichtsbasis. Het omgekeerde werd gevonden op basis van de karkaslengte.

4. De borstkasdiepte vertoonde een A^+- of een concaaf patroon ten opzichte van karkaslengte. Aangezien verder de stomplengte in relatie tot karkaslengte bij de geboorte relatief groter was dan in latere stadia, is het duidelijk dat tijdens de groei dieren veranderen van vorm; zij worden relatief dieper. Dit werd bevestigd doordat de toename in lengte van de pijpbeenderen van de ledematen relatief achterbleef bij die van de karkaslengte.

5. Tijdens de groei vond een opvallende verandering plaats in de karkassa-

menstelling. Zonder te letten op de gevonden kwadratische patronen, werden gemeenschappelijke *b*-waarden vastgesteld voor elk van de sexen. Borgen en zeugen geleken op elkaar. Opklimmend naar snellere groei waren de waarden ongeveer 0,70, 0,75, 0,85, 0,90 en 1,35 respectievelijk voor de componenten afval, bot, spieren, huid en vet. Spieren groeiden dus sneller dan bot, maar beiden groeiden langzamer in relatie tot het karkas. Bij beren werd dezelfde volgorde gevonden, maar de waarden lagen duidelijk op een ander niveau, respectievelijk: 0,75, 0,80, 0,90, 1,10 en 1,25. Behalve de opmerkelijk hogere groei-intensiteit van de huid bij beren, afwijkend van die bij mannelijke dieren van andere diersoorten, bleek alleen vet in zijn algemeenheid sneller te groeien dan het karkas.

De karkassamenstelling verschilde ook met betrekking tot voederniveau. De ongunstige invloed op de hoeveelheid vet bij *ad libitum* voeding verdween wanneer voor het gewicht van spieren en bot de regressie werd uitgevoerd op spier + beengewicht. Voor een bepaald spier + beengewicht hadden borgen meer bot dan zeugen. Ten gevolge van een hoger beengewicht hadden beren minder spieren dan zeugen. Op basis van het karkasgewicht hadden beren echter meer spieren dan zeugen.

6. De spier-beenverhouding steeg tijdens de groei, vooral in de eerste stadia vanwege een relatief goed ontwikkeld skelet bij de geboorte. De verhouding wordt niet beïnvloed door voederniveau. Zeugen hadden de gunstigste verhouding, gevolgd door de beren.

7. De spier-vetverhouding daalde tijdens de groei, voor borgen en zeugen tot beneden 1,0. De borgen hadden de ongunstigste verhouding, gevolgd door de zeugen. *Ad libitum* voeding beïnvloedde de verhouding in ongunstige zin.

8. Beren hadden een zwaardere kop dan de andere sexen. Dit kan een secundair geslachtskenmerk zijn daar het verschil bleef bestaan na regressie op spier + beengewicht. De kop had bij de geboorte een relatief hoog percentage, ongeveer 18% van het karkasgewicht. Het percentage daalde daarna snel tot een niveau van 4 à 5%. Binnen totaal afval groeide de kop sneller dan de ondervoeten, terwijl beren een relatief lichtere kop hadden dan de andere sexen, mogelijk ten gevolge van een enigszins geringere vetafzetting in de kop bij beren.

9. De nieren volgden het dalende patroon van het totaal van organen en ingewanden in relatie tot levend gewicht. Binnen totaal afval verschilden de beren van de andere sexen. Het groeipatroon van de testes was duidelijk verschillend van dat van de nieren. Aanvankelijk groeiden zij snel in relatie tot levend gewicht, omdat zij relatief onderontwikkeld waren bij de geboorte, maar bereikten hun uiteindelijke niveau reeds in de tussenliggende stadia direct volgend op de prepubertale groei.

10. Na regressie van de verhoudingen van de linker en rechter testes, nieren en ondervoeten uit de linker- en rechterhelft op levend gewicht, bleek dat zowel de *b*-waarde als de *ln a*-waarde niet afweek van nul, hetgeen betekent dat niet alleen de verhouding constant bleef maar dat ook de gewichten gelijk waren, wat op symmetrische groei wijst.

11. De botgewichtsverdeling verandert tijdens de groei. Botgroepen echter veranderden nauwelijks, maar binnen de groepen hadden sommige botten een A^+-patroon: schouderblad, bekken, ribben en borstbeen, terwijl de pijpbeenderen tendeerden naar een A^--patroon. Hoewel de ondervoeten en de proximale botten van de ledematen duidelijk verschilden in *b*-waarden werden groeigradiënten over de ledematen verstoord door de volgorde bij de pijpbeenderen, hoewel de verschillen daar slechts klein waren. Een enigszins hogere groeiintensiteit bij de borstwervels wezen niet op een groeigradiënt langs het axiaal skelet. De groeicoëfficiënten van de botten van de voorste ledematen tendeerden naar een hogere waarde dan die van de corresponderende botten van de achterste ledematen.

12. Voederniveau en sexe beïnvloedden de botgewichtsverdeling. Bij *ad libitum* voeding werd een hoger aandeel gevonden voor *humerus*, *radius* + *ulna*, totaal van de botten van de achterste ledematen en ribben, maar een lager aandeel voor schouderblad en *os femoris*. Aan het groter aandeel voor de ribben wordt een functionele betekenis gegeven. Het lagere percentage voor totaal bot in het karkas bij de zeugen werd weerspiegeld in zowel de pijpbeenderen als in het totaal van de botten van beide ledematen. Zeugen hadden een hoger percentage ribben en schouderblad. Het aandeel van de pijpbeenderen in de voorste ledematen was bij beren hoger dan bij borgen, terwijl het omgekeerde werd gevonden voor die van de achterste ledematen.

13. De wervels vertoonden een variabel beeld. Omdat dit de verdeling en de patronen voor andere botten zou kunnen beïnvloeden werd als onafhankelijke variabele een nieuw totaal botgewicht geïntroduceerd, waarbij de wervels en het borstbeen in mindering werden gebracht op het oorspronkelijke botgewicht. In de situatie kwam nauwelijks verandering en het leverde geen nieuwe inzichten op. De grotere variatie werd eerder toegeschreven aan de lengte van de wervels dan aan fouten bij splijten van het karkas, omdat in het algemeen geen systematische verschillen tussen de gewichten van de beide karkashelften werden vastgesteld, gebaseerd op de resultaten van de regressie van de verhouding van beide helften op de som ervan.

14. De relatieve vermindering in de toename van de botlengte in latere stadia leidde tot de conclusie dat botlengte eerder het volwassen stadium bereikt dan botgewicht. Mede vanwege een voortschrijdende mineralisatie steeg de gewichtlengteverhouding. Aangezien het schouderblad gelegen langs de ribben meer in lengte toenam dan andere botten, lag genoemde verhouding het laagst bij dit bot. *Ad libitum* voeding resulteerde in hogere verhoudingen op een bepaald totaal botgewicht. De *radius* bleek relatief dun te zijn, maar de lengte ervan bleef niet achter bij die van andere botten, zodat voor dit bot een afwijkende lengte-dikteverhouding het gevolg was. Andere pijpbeenderen namen regelmatig toe in lengte en dikte. Dit betekent dat een soms in de literatuur beweerde dalende lengte-dikteverhouding niet kon worden bevestigd.

15. Botdikte werd nauwelijks beïnvloed door voederniveau of sexe. Voor een bepaald totaal botgewicht en ook voor een gegeven karkaslengte zijn de botten

echter langer op het beperkte voederniveau. Beren hadden de langste botten wanneer vergeleken werd op eenzelfde karkaslengte, terwijl bij eenzelfde totaal botgewicht de borgen de langste botten hadden.

16. Bij de gewicht-lengteverhouding werd de derdemachtswortel van het gewicht in de variabele ingevoerd. Slechts in een enkel geval bleek de 1/3 macht van het gewicht exact juist te zijn. In de meeste gevallen zou een gewicht proportioneel tot een macht van even beneden 0,4 tot onafhankelijkheid van het totale botgewicht hebben geleid.

17. Ook de spiergewichtsverdeling veranderde tijdens de groei. De spiergroepen vertoonden ongeveer eenzelfde patroon voor de voederniveaus en de sexen. De belangrijkste veranderingen komen voor gedurende de eerste stadia, reeds voor slachtmoment I. In vele gevallen weken daarom de pasgeboren dieren af van de regressielijn door de latere stadia, maar zij waren wel aangepast aan het volledig kwadratisch positieve en negatieve patroon respectievelijk voor de groep van halsspieren en die van rug en lende. De groep van de proximale schouderspieren vertoonde een positieve kwadratische term voor de beperkt gevoerde groepen en voor borgen. Verder werd voor de borgen een negatieve kwadratische term gevonden voor de groep van proximale spieren van de heup en dij.

18. Een mono- of difasisch patroon is vooral afhankelijk van het pasgeboren stadium. Wanneer de pasgeboren dieren in de beschouwing werden betrokken samen met de reeds genoemde patronen, kon een volledig lineair patroon alleen worden vastgesteld voor de groep van distale schouderspieren en voor de sublumbale en de huidspieren.

19. In de meeste spiergroepen volgen niet alle spieren het patroon van de groep; met name in de groep van spieren van borstkas en buikwand. Op een aantal uitzonderingen na bleek dat de meer dieper gelegen spieren een lagere groei-intensiteit vertoonden, terwijl de meer oppervlakkig gelegen spieren een hogere intensiteit lieten zien. Intermediair gelegen spieren hadden veelal een A-patroon. Disto-proximale en ventro-dorsale groeigradiënten kunnen in dit opzicht verstorend werken.

20. Het blijkt moeilijk te zijn de groei van individuele botten in verband te brengen met die van hen omringende spieren, omdat de spieren vaak over meerdere botten werken. Alleen grovere verbanden bestonden voor lichaamsregionen via de groeigradiënten. Een enigszins hoger patroon van de botten van de voorste ledematen ten opzichte van dat van de achterste ledematen was in overeenstemming met overeenkomstige patronen van de spieren in deze regionen. Maar het hogere patroon voor de groep van de halsspieren werd niet gevonden bij de halswervels.

21. Een disto-proximale groeigradiënt kwam voor in beide ledematen, welke verder loopt via de sublumbale spieren naar de rug en lende, en via de groep van de schoudergordelspieren naar de hals en ook naar de rug. Het beeld wordt gecompleteerd door een gradiënt over de romp van ventraal naar dorsaal. Een gradiënt van craniaal naar caudaal werd niet gevonden.

22. Bij de nadering van het volwassen stadium trad een masculinisatieproces op, doordat de groep van de halsspieren relatief toenam tesamen met een aantal meer craniaal gelegen spieren van de schoudergordel. Uitgesproken voorbeelden waren *m. splenius* en *m. rhomboideus*, welke beide een positieve cubische term bij beren vertoonden. Borgen gedroegen zich intermediair in dit opzicht. Het hogere aandeel voor de pijpbeenderen in de voorste ledematen bij de beren is in overeenstemming met het masculinisatieproces.

23. De relatief zware kop bij de geboorte kan worden gedragen, doordat de groep van halsspieren een groter aandeel heeft in dat stadium, waartoe vooral de *m. splenius* een bijdrage levert.

24. De meest stabiele spiergroep is die van de proximale schouder. Afgezien van het gemiddelde groeipatroon wordt zij niet beïnvloed door voederniveau noch door sexe. Voederniveau had een invloed op de verdeling bij de andere groepen, doordat op *ad libitum* voederniveau de groepen spieren van de romp (buik, borst, rug en lende, huidspieren) een hoger percentage vertegenwoordigden, terwijl een lager aandeel werd gevonden bij de groepen van de hals en die van de ledematen inclusief de sublumbale spieren. Een functionele betekenis wordt gehecht aan het hogere percentage van de groep van spieren van borstkas en buikwand, terwijl het relatief lichtere hoofd kan hebben bijgedragen tot het lagere percentage van de groep van halsspieren.

25. Bij de meeste spiergroepen was een sexe-invloed aantoonbaar; dit betrof voornamelijk het verschil tussen beren en de andere sexen. De beren hadden een hoger aandeel bij de groep van halsspieren wat zich voortzette naar de groep van schoudergordelspieren en naar die van de borstkas, inclusief de huidspieren. De beren hadden daardoor een lager percentage in de groepen met dure spieren (proximale spieren van de heup en dij, sublumbale spieren en spieren van de rug en lende).

26. De invloed van voederniveau en sexe op de individuele spieren volgde op enkele uitzonderingen na die op de standaardspiergroep.

27. De gewichtsverdeling van de vetweefsels veranderde eveneens tijdens de groei. Subcutaan vet en reuzel namen toe, terwijl intermusculair vet daalde ten opzichte van het totale vetgewicht. Reuzel vertoonde het hoogste groeipatroon.

28. Voederniveau beïnvloedde nauwelijks de vetverdeling. *Ad libitum* voeding resulteerde in meer subcutaan vet bij borgen, en minder intermusculair vet bij beren en zeugen.

29. Er werden duidelijke sexe-invloeden op de vetverdeling vastgesteld. Beren bevatten minder subcutaan vet. Bij de latere stadia gold dit ook voor borgen ten opzichte van zeugen. Beren hadden meer intermusculair vet dan borgen, maar vanwege de tegengestelde hogeregraadstermen ontmoetten de regressielijnen elkaar weer in de laatste stadia. Eveneens hadden beren meer reuzel dan de andere sexen.

30. Spekdikte in relatie tot totaal vetgewicht vertoonde een concaaf patroon en zij nam het sterkst toe in de eerste stadia. *Ad libitum* voeding leverde een

dikkere speklaag op. Beren hadden dunner spek dan de andere sexen, terwijl in een aantal gevallen ook bij zeugen de spekdikte kleiner was dan bij borgen.

31. Op grond van de *b*-waarden op de tussenliggende meetplaatsen kon geen gradiënt voor spekdikte lopend van craniaal naar caudaal worden vastgesteld. De spekdikte boven de schouder sloot het best aan bij de toename van het totale vetgewicht.

32. Er waren nauwelijks veranderingen aantoonbaar in de gemeten vleeskwaliteitskenmerken in relatie tot de groei. Geen invloed werd gevonden voor voederniveau en sexe.

33. In vele gevallen moesten de groeipatronen van onderdelen ten opzichte van de eenheden worden beschreven door middel van hogeregraadstermen. Tenzij men onnatuurlijke breekpunten in de curves accepteert, is de allometrische formule niet bruikbaar voor langere trajecten. Een kromlijnig verband vermijdt breekpunten of multifasische patronen.

Bij ongeveer 30% van de individuele spieren werd een lineair patroon gevonden voor het gehele traject van geboorte tot volwassen stadium. Afgezien van het pasgeboren stadium was er bij 20% van de spieren op de een of andere wijze een hogeregraadsterm nodig.

34. Het meest opvallende verschil tussen varkens en herkauwers met betrekking tot de hoogte van de *b*-waarden van spieren, lag bij de spieren van de buikwand die hoger waren bij de laatstgenoemde diersoort. Het verschil werd toegeschreven aan een relatief grotere vulling van de buikholte. Er kon geen bevredigende verklaring worden gegeven voor het hogere percentage van de groep van distale schouderspieren bij varkens.

De groeicoëfficiënten van de individuele spieren en botten zijn meer gedifferentieerd bij herkauwers dan bij varkens.

Zowel opvallende overeenkomsten als tegenstrijdigheden werden gevonden bij vergelijking van de resultaten van de onderhavige studie met die welke gevonden waren in de literatuur en bij vergelijking van de literatuurgegevens onderling. De meeste van de gevonden resultaten waren in overeenstemming met die in de literatuur; ook schijnbaar afwijkende resultaten kunnen worden gevonden die toch worden ondersteund door een literatuurgegeven.

De meeste van de verschillen in de hoogte van de *b*-waarden kunnen worden toegeschreven aan het bestuderen van verschillende trajecten. De sexe-invloeden op de verdeling van de componenten binnen weefsels werden in deze studie vaker gevonden dan in de literatuur. Zij kwamen echter grotendeels voort uit het feit dat in de onderhavige proef beren waren opgenomen. Afgezien van het commercieel belang, leveren recentere studies (de huidige inbegrepen) steeds meer aanwijzingen, dat ook voederniveau de spierverdeling beïnvloedt.

35. De invloed van voederniveau op de spierverdeling lijkt commercieel van ondergeschikt belang. Dit in tegenstelling tot de invloed van de sexe daarop. Op

het commerciële slachtgewicht zouden borgen en zeugen 400–450 g meer van de duurdere spiergroepen hebben. Dit werkt echter in tegen het gunstiger effect van de totale aanzet van mager vlees bij beren, maar het staat niet in verhouding tot datgene wat kan worden opgebracht door de toename van de totale hoeveelheid vlees die zou worden geproduceerd bij het mesten van beren.

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Appendix 1. Feed intake between dissection stages and cumulative feed intake of boars, castrates and sows on *ad libitum* and restricted feeding level (in kg/day).*

Dissection stage	*Ad libitum*						Restricted					
	Feed intake between stages			Cumulative feed intake			Feed intake between stages			Cumulative feed intake		
	♂	⚦	♀	♂	⚦	♀	♂	⚦	♀	♂	⚦	♀
I												
	2.90	3.07	3.14				1.31	1.33	1.34			
II				2.90	3.07	3.14				1.31	1.33	1.34
	3.86	4.21	3.83				2.06	2.08	2.06			
III				3.31	3.58	3.49				1.64	1.66	1.66
	3.87	3.90	4.15				2.61	2.66	2.61			
IV				3.47	3.67	3.73				1.97	2.02	2.00
	3.93	3.61	4.15				2.83	2.83	2.82			
V				3.63	3.67	3.87				2.19	2.22	2.22
	4.09	3.18	3.65				2.79	2.69	2.82			
VI				3.85	3.60	3.79				2.40	2.38	2.40
	4.93	4.17	4.14				2.99	3.03	2.94			
VII				4.53	3.95	3.99				2.83	2.86	2.72

*The feed intake for the different treatment groups was calculated as the mean intake over the four replicates (supplied with different energy contents in the diets) and for the diminishing number of animals listed in Tables 4.2–4.4.

APPENDIX 2. Weight and age with their standard deviations at the different stages used in constructing the curves for live weight growth. The decreasing numbers of animals correspond to those in Text-Fig. 4.1abc.

Age stage or dissection stage and feeding level*		Boars					Castrates					Sows				
		n	weight kg	s.d.	age days	s.d.	n	weight kg	s.d.	age days	s.d.	n	weight kg	s.d.	age days	s.d.
At birth	A	52	1.6	0.3			50	1.6	0.3			51	1.5	0.4		
	R	50	1.5	0.3			52	1.5	0.3			51	1.6	0.3		
At about 4 weeks	A	38	6.7	1.3	27.9	1.3	37	6.9	1.6	27.8	1.3	37	7.1	1.4	27.7	1.3
	R	36	6.7	1.5	28.0	1.4	40	7.0	1.7	28.0	1.3	38	6.9	1.4	27.7	1.3
At weaning	A	52	13.4	3.9	45.5	6.5	50	13.9	4.3	45.6	6.5	51	14.3	4.0	45.6	6.5
	R	50	13.5	3.8	45.6	6.6	52	13.9	4.2	45.0	6.3	51	14.1	4.1	45.6	6.4
I	A	52	26.1	3.8	78.7	7.5	50	25.7	5.0	79.1	7.2	49	26.8	3.4	79.6	7.7
	R	50	24.9	3.1	80.0	7.9	51	25.4	3.5	79.1	8.2	51	25.4	3.3	79.8	7.5
II	A	49	65.6	9.7	128.5	7.6	45	66.6	8.1	128.3	7.1	46	64.7	10.6	129.1	7.8
	R	47	45.1	5.8	128.9	7.0	49	45.2	6.8	129.7	7.5	47	46.1	5.9	129.0	7.4
III	A	40	98.5	14.0	167.7	8.4	38	99.7	10.9	167.0	7.6	35	94.4	12.5	166.3	6.9
	R	39	71.7	12.4	167.9	8.0	41	70.5	11.2	169.0	8.6	40	71.7	9.1	168.2	7.5
IV	A	26	132.9	16.8	214.2	9.8	31	129.0	14.7	212.2	10.2	29	125.5	15.9	211.8	9.3
	R	31	105.4	15.9	213.8	9.8	33	98.4	14.7	213.5	9.9	31	100.9	11.9	212.5	8.5
V	A	18	162.6	19.4	259.5	9.3	23	156.7	16.9	257.4	9.2	21	151.9	15.1	256.4	8.9
	R	24	140.2	13.8	258.9	7.1	24	125.7	12.9	258.3	8.0	23	129.4	10.1	258.3	6.5
VI	A	10	207.6	20.3	351.1	10.3	11	185.7	17.9	348.5	10.9	15	185.9	14.1	347.6	6.1
	R	15	186.8	12.1	348.5	5.8	16	169.5	17.8	349.0	7.9	12	165.9	14.7	349.1	8.2
Up to maturity	A											8	206.0	8.5	390.3	5.5
	R	8	268.3	24.7	657.9	6.2	8	198.8	23.4	418.0	10.1	8	195.4	20.8	435.1	8.8
	A						7	202.9	20.9	402.0	10.5	7	217.7	12.8	417.7	5.7
	R	7	288.0	25.8	814.4	9.1	7	282.6	24.2	782.7	10.6	7	213.4	25.9	505.6	10.0
	A						6	221.7	19.7	444.7	10.9	6	272.0	18.2	657.5	4.8
	R	6	294.7	26.9	898.5	9.9	6	330.3	14.8	1176.7	10.7	6	246.5	18.9	658.3	10.4
	A	5	300.0	36.5	690.6	9.6	5	272.2	14.5	707.2	5.6	5	279.6	11.4	671.2	5.3
	R						5	324.4	6.6	1259.6	8.4					
	A						4	275.0	12.3	719.0	3.2	4	284.0	10.9	714.8	4.6
	R	4	325.6	36.6	1278.0	11.5	4	321.5	6.2	1304.0	7.5	4	294.5	15.3	704.0	11.1
	A	3	322.3	35.1	788.3	13.5	3	276.7	22.3	775.3	3.8	3	310.3	17.5	1110.0	8.2
	R						3	320.3	9.5	1315.0	5.6	3	262.3	4.0	886.0	13.5
	A	2	318.0	50.9	816.5	19.1	2	339.0	5.7	1257.0	4.2	2	315.5	21.9	1148.5	7.8
	R	2	300.5	23.3	1427.5	3.5	2	325.5	12.0	1343.5	7.8	2	264.0	2.8	907.0	8.5
	A	1	342		873		1	333		1386		1	342		1392	
	R	1	343		1439		1	326		1408		1	256		1179	

*A = *ad libitum* R = restricted

APPENDIX 3. The leg length of the treatment groups for the different dissection stages (in cm).

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Ad libitum								
Boars	9.6	24.5	32.4	35.9	39.6	44.7	46.6	54.6
Castrates		24.8	31.3	34.9	38.5	41.6	46.4	50.9
Sows	9.6	25.1	32.4	35.6	38.2	41.6	43.6	50.8
Restricted								
Boars			29.3	34.4	38.8	41.8	47.8	52.1
Castrates			29.3	33.6	37.9	40.3	44.9	54.8
Sows			29.9	34.2	37.7	41.0	43.8	52.9

Average variation coefficient 4.9%.

APPENDIX 4. The inner thorax depth of the treatment groups for the different dissection stages, as measured from the 5th thoracic vertebra to the sternum (1) horizontally and (2) to the juncture of the 5th rib (in cm).

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Thorax depth 1*								
Ad libitum								
Boars	5.6	13.0	16.1	18.4	21.3	22.3	24.1	30.6
Castrates		12.6	16.8	17.6	19.4	21.3	24.7	28.9
Sows	5.4	12.5	16.6	18.8	19.6	21.3	23.4	27.9
Restricted								
Boars			15.1	17.8	19.7	22.1	23.5	29.1
Castrates			14.3	17.0	19.4	19.7	22.4	29.3
Sows			14.8	17.6	19.8	20.6	22.8	28.3
Thorax depth 2**								
Ad libitum								
Boars		14.1	17.6	19.4	23.4	23.6	25.9	32.9
Castrates		13.6	17.6	18.1	20.4	23.3	26.3	31.3
Sows		13.5	17.5	19.7	20.4	22.9	24.9	29.9
Restricted								
Boars			16.4	18.9	21.5	24.1	24.9	30.6
Castrates			15.3	18.8	20.9	21.6	24.3	31.3
Sows			16.3	18.8	20.8	22.4	24.0	30.9

*Average variation coefficient 6.9%.
**Average variation coefficient 7.4%.

APPENDIX 5. The weight of the feet and the kidney of the treatment groups for the different dissection stages expressed as a percentage of carcass side weight.

Feeding level and Sex	Dissection stage							
	0	I	II	III	IV	V	VI	VII
Feet*								
Ad libitum								
Boars	5.89	4.16	3.23	2.76	2.71	2.34	2.36	1.87
Castrates		4.21	2.88	2.31	2.14	2.06	2.09	1.89
Sows	5.89	3.81	2.99	2.55	2.31	2.10	1.88	1.55
Restricted								
Boars			3.91	3.36	3.01	2.90	2.66	1.95
Castrates			3.57	3.13	2.60	2.45	2.18	1.79
Sows			3.65	3.13	2.66	2.43	2.22	1.92
Kidney**								
Ad libitum								
Boars	0.95	0.64	0.50	0.40	0.37	0.34	0.29	0.27
Castrates		0.64	0.48	0.37	0.29	0.27	0.23	0.19
Sows	1.00	0.58	0.53	0.39	0.34	0.29	0.23	0.22
Restricted								
Boars			0.53	0.43	0.37	0.35	0.29	0.26
Castrates			0.46	0.36	0.30	0.27	0.25	0.20
Sows			0.45	0.35	0.34	0.28	0.28	0.24

*Average variation coefficient 10.3%.
**Average variation coefficient 12.8%.

APPENDIX 6. The weight of the individual muscles expressed as a percentage of total muscle weight, based on the results of the regressions of the weights of the various muscles on total side muscle weight ($=x$)*.

Muscle	%
1. m. longissimus thoracis et lumborum	11.04
2. m. biceps femoris	6.16
3. m. quadriceps femoris	5.50
4. m. semimembranosus	4.93
5. m. pectoralis profundus	4.34
6. m. triceps brachii	4.34
7. mm. cutanei trunci and colli	4.32
8. m. gluteus medius	3.83
9. mm. serrati ventrales cervicis and thoracis	3.81
10. mm. multifidi	3.49
11. mm. intercostales	3.24
12. mm. iliopsoas and psoas minor + m. quadratus lumborum	2.74
13. m. obliquus externus abdominis	2.33
14. m. latissimus dorsi	2.17

15.	m. semitendinosus	2.13
16.	m. supraspinatus	2.00
17.	mm. flexores and extensores (thoracic limb)	1.97
18.	m. infraspinatus	1.79
19.	mm. flexores and extensores (pelvic limb)	1.70
20.	m. semispinalis capitis	1.70
21.	m. gastrocnemius	1.68
22.	m. rectus abdominis	1.57
23.	m. adductor	1.48
24.	m. tranversus abdominis	1.42
25.	m. splenius	1.11
26.	m. obliquus internus abdominis	1.10
27.	m. gracilis	1.07
28.	m. brachiocephalicus	1.04
29.	m. trapezius	1.00
30.	m. gluteus superficialis	0.99
31.	mm. longus capitis, longus colli, etc.	0.90
32.	m. tensor fasciae latae	0.87
33.	m. rhomboideus	0.84
34.	mm. pectorales superficiales	0.77
35.	m. obturatorius externus	0.72
36.	m. subscapularis	0.72
37.	m. iliocostalis	0.63
38.	mm. recti and obliqui capitis	0.63
39.	m. teres major	0.56
40.	m. gluteus accessorius	0.55
41.	diaphragma partes costales and sternales	0.55
42.	m. sternocephalicus	0.51
43.	m. brachialis	0.47
44.	m. gluteus profundus	0.43
45.	m. serratus dorsalis cranialis + m. serratus dorsalis caudalis	0.41
46.	m. biceps brachii	0.40
47.	m. pectineus	0.38
48.	m. deltoideus	0.36
49.	m. soleus	0.36
50.	m. scalenus dorsalis + m. scalenus ventralis	0.34
51.	m. tensor fasciae antebrachii	0.31
52.	m. flexor digitorum superficialis	0.30
53.	m. longissimus capitis et atlantis	0.18
54.	m. teres minor	0.18
55.	m. longissimus cervicis	0.18
56.	m. transversus thoracis	0.15
57.	mm. gemelli + m. quadratus femoris	0.14
58.	m. omotransversarius	0.12
59.	m. coracobrachialis	0.10
60.	m. sartorius	0.09
61.	m. transversus costarum	0.07
62.	m. omohyoideus	0.03
	muscle remnants	0.38
	Total	99.62

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*$x = 16$ kg and corresponds to the overall regression (for the polynomial needed) over the treatment groups at the time of commercial slaughter weight.

CURRICULUM VITAE

P. Walstra werd geboren op 26 april 1937 te Tjerkgaast (gem. Doniawerstal). Na het behalen van het einddiploma der Rijks H.L.S. te Groningen in 1956 werd de militaire dienstplicht vervuld. In 1958 begon hij zijn studie aan de Landbouwhogeschool te Wageningen in de richting veeteelt. Na het kandidaatsexamen in 1963 werd het ingenieursexamen afgelegd in 1967 in het hoofdvak veevoeding. Daarnaast werden de fysiologie der landbouwhuisdieren, de gezondheids- en ziekteleer der landbouwhuisdieren en de landbouwarchitectuur als bijvakken gekozen.

Sinds maart 1967 is hij als wetenschappelijk medewerker verbonden aan het Instituut voor Veeteeltkundig Onderzoek 'Schoonoord' te Zeist.