

12 Adipose Tissue in Human Evolution

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SUMMARY

The sparse data on the 'natural' distribution and abundance of adipose tissue in primates show that the basic anatomy of human adipose tissue is similar to that of terrestrial monkeys, and so was probably inherited directly from their primate ancestors. Superficial adipose tissue appears to extend over a greater area of the body in humans than in other terrestrial mammals, because of changes in the proportions of the limbs and in the shape of the girdles, the dorso-ventral flattening of the thorax and abdomen and the bipedal posture of the hip, knee and shoulder. The contrasts between humans and other primates have parallels in other mammals, and may be a direct consequence of the increased abundance of adipose tissue, which itself may be of very recent origin.

Experimental and comparative data on the physical properties and natural functions of adipose tissue in mammals are reviewed in this chapter. Superficial adipose tissue does not necessarily contribute significantly to thermal insulation except in specialised aquatic mammals. Anatomical, ecological and biochemical information provides no evidence that the distribution of adipose tissue in modern humans has evolved as an adaptation to thermal insulation, as required by the Aquatic Ape Theory, or as protection from mechanical damage. Other explanations for the exceptional features of human adipose tissue are briefly discussed. The greater fatness and modifications in the distribution of adipose tissue in young women are more likely to be conspicuous indicators of social and sexual status than an adaptation to energy storage for reproduction. The accumulation of mesenteric and omental adipose tissue in men and older women has no parallels in wild mammals and may not be physiologically adaptive.

INTRODUCTION

The anatomical arrangement of adipose tissue plays a central role in several theories of human evolution. For example, most of the secondary sexual structures implicated in Morris's (1967) explanation of some atypical features of human courtship and mating behaviour consist mainly of adipose tissue. The role of superficial adipose tissue as the principal natural insulation of an almost hairless body is an essential principle of the Aquatic Ape Theory or AAT (Hardy, 1960; Cunnane, 1980; Morgan, 1982; Verhaegen, 1985). A major tenet of both theories is that at some stage in the evolutionary history of *Homo* there were major shifts in the anatomical arrangements and the biological functions of adipose tissue. In spite of its importance to these theories, there is surprisingly little scientific information about the comparative anatomy of adipose tissue. Some theorists (Cunnane, 1980; Morgan, 1982; Verhaegen, 1985) have not recognised the relevance of experimental data on the physical

properties of adipose tissue and fur in other aquatic mammals to interpretations of the natural function of these tissues in modern humans and their ancestors. Consequently, anthropologists lack objective criteria by which they can establish which features of human adipose tissue are truly unique, and which have precedents or parallels in other species.

There have been very few critical studies of the natural functions of adipose tissue in humans or other primates. The natural functions of biological structures are easy to suggest but difficult to prove rigorously, particularly for a tissue as variable in abundance as adipose tissue. A frequent source of misunderstanding is confusion of the role played by a tissue or organ in a particular situation, with *adaptation* of that structure to a natural function. For example, the fact that moderately obese young adults survive immersion in cold water for longer than lean individuals does not prove that insulation is *the* function of superficial adipose tissue; the fact that young women suffering from chronic anorexia or engaging in prolonged, strenuous exercise lose body fat and may become infertile does not prove that large quantities of adipose tissue are necessarily or naturally essential for reproduction. Some comparative or historical information is necessary to demonstrate that these properties of adipose tissue have evolved as adaptations to their postulated functions.

The purpose of this chapter is to describe the anatomy of human adipose tissue in relation to that of wild and domesticated mammals and to present a critical review, using comparative, physiological and palaeontological data, of some of the theories that have been proposed to explain the exceptional features of adipose tissue in humans. A fuller understanding of the factors that determine the distribution and abundance of adipose tissue in non-human mammals may help us to assess whether it is necessary or justifiable to postulate a major shift in the anatomical structure or in the natural function of adipose tissue in hominid evolution, as required by the Aquatic Ape Theory.

SOURCES OF INFORMATION ABOUT ADIPOSE TISSUE

Adipose tissue cannot be identified in fossils, so students of evolution must rely heavily upon comparisons between humans and other mammals, and between living races of humans, to identify evolutionary changes in the structure, properties or function of adipose tissue, and reconstruct the circumstances under which such changes might have taken place.

Skinfold thickness and X-ray photography have been used to measure the abundance of adipose tissue. But in certain depots, notably the buttocks (Harrison, 1985), the adipose tissue coheres so strongly to the underlying muscle that it is impossible to measure it accurately with calipers. Until recently, data about the total abundance of adipose tissue

throughout the whole human body could be obtained only from cadavers, most of which were of elderly and ailing subjects (Clarys, Martin and Drinkwater, 1984). Physical techniques of image formation, particularly computed tomography (Keiffer and Heitzman, 1979), now permit accurate, direct measurement of the dimensions of adipose tissue in healthy people. The new technology produces much more data, but such information highlights rather than reduces the problems of interpreting the anatomy of adipose tissue in functional and evolutionary terms.

Disproportionate growth of certain adipose depots is a symptom (and possibly also a cause) of several progressive metabolic disorders (Krotkiewski *et al.*, 1983; Björntorp, 1987) from which modern humans, and probably also mammals in captivity, may suffer for many years before becoming obviously incapacitated. In modern Western populations, particularly those in which such disorders are common, 'average' body dimensions may not correspond to the 'optimal' or 'natural' values. As Tanner and Whitehouse (1975) put it after more than twenty years of measuring superficial adipose tissue in children: 'standards represent what is, not what ought to be'. Any hypothesis involving the social structure, behaviour or ecology of primeval humans is necessarily full of assumptions and inferences from other species, particularly other primates. All non-human descendants of immediate hominid ancestors are extinct, and the ranges of the living species of apes are greatly reduced. Apes readily become obese in captivity, and it is very difficult to study the anatomy of wild specimens. Consequently there is almost no detailed information about the distribution or average abundance of adipose tissue in any species more closely related to humans than cercopithecine monkeys. The habits of the few remaining groups of human hunter-gatherers have been strongly influenced by contact with other cultures, and may not be typical of the primitive condition.

In the case of *Homo sapiens* there is an additional source of information: artefacts and drawings of the human body, from many parts of the world and dating from the end of the Pleistocene Ice Age to modern times. Although 35,000 years is a very short time in evolutionary terms, such images tell us something about prehistoric human form, and, perhaps even more important, about how humans viewed themselves. Adipose tissue is conspicuous in only a small minority of the thousands of prehistoric representations of the human form that have been described, so there is no reason to suppose that the obesity on the scale represented in the North-West European Palaeolithic figure shown on Figure 12.1 was typical of the population as a whole. On the other hand, such images are unlikely to be purely imaginary: the artist had probably seen at least a few people with such a body shape. Furthermore, the conspicuous and sometimes exaggerated representations of the adipose masses suggest that

such body conformations had social significance to the population in which they occurred, and may indicate that they were venerated or desired.

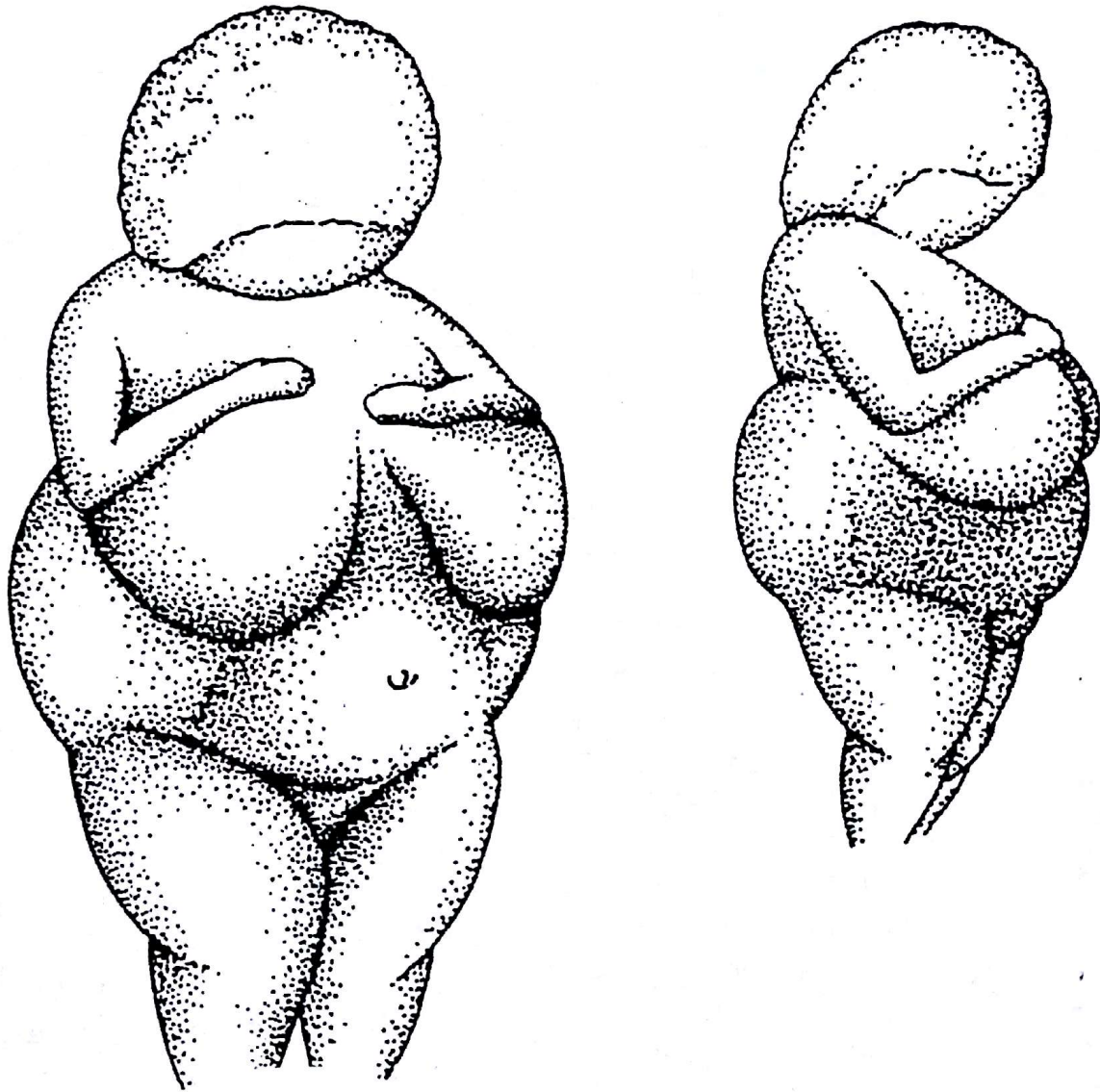


Figure 12.1 Small female figurine of Palaeolithic age from North-West Europe, seen from front and side.

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THE COMPARATIVE ANATOMY OF ADIPOSE TISSUE IN MAMMALS

University-based scientists rarely have the opportunity to examine a wide range of truly wild mammals. Most of their specimens, particularly of large species, come from zoos and other menageries, where exceptionally obese or emaciated animals are more likely to die, and hence to come to the attention of comparative anatomists, than those of normal body composition. Nonetheless, we have examined over two hundred speci-

mens belonging to more than fifty species, and have identified some consistent features of the anatomy of mammalian adipose tissue (Pond and Mattacks, 1985a, 1985b, 1988, 1989; Pond, 1986, 1987c). Mammals and birds differ from the poikilothermic vertebrates in that adipose tissue occurs in a dozen or more discrete depots, associated with several different organs, including viscera and skeletal muscle. Contrary to the impression established by textbooks, in most species of mammals there is no continuous layer of 'subcutaneous' adipose tissue, except in the most obese specimens. The distinct depots can be characterised by site-specific differences in relative adipocyte volume (Pond and Mattacks, 1985a; Pond, 1986), as well as by their anatomical relations to other tissues.

Homologous depots can thus be identified in different species, regardless of the body composition of the specimens examined. The principal difference between species is the relative abundance of adipocytes in the various depots; ratios of volumes of adipocytes in identified depots remain remarkably constant over a wide range of species (Pond and Mattacks, 1989). Measurements of the activities of glycolytic enzymes and of lipid turnover *in vivo* confirm the existence of metabolic differences between depots that correlate with the anatomical origin of the adipose depot, not with adipocyte volume *per se* (Mattacks, Sadler and Pond, 1987; Pond and Mattacks, 1987a, 1987b; Pond *et al.*, 1991). Thus, although relative adipocyte volume provides a convenient means of identifying the depots, we do not yet understand its functional significance.

All the usual mammalian depots are present in *Macaca* monkeys, and their cellular dimensions and enzymatic properties are similar to those of other mammals (Pond and Mattacks, 1987b). The typical mammalian pattern of site-specific differences in adipocyte volume was described earlier in baboons, *Papio hamadryas*, by Lewis *et al.* (1983), but they did not recognise the generality of this pattern.

In many mammals, including *Macaca* monkeys, there are additional depots of adipose tissue, some of which may become massive compared to the typical depots and may overlie and obscure them. For example, small quantities of adipose tissue are found medially around the inner surface of the linea alba of the abdominal musculature of carnivores, primates and larger rodents, but not insectivores. In equids, camelids and some other large ungulates, this depot extends over much of the inner ventral wall of the abdomen and can be several centimetres thick in obese specimens. In some carnivores and primates there is also a medial adipose depot on the external surface of the abdominal wall (Figures 12.2 (c), (d)), which in lean *Macaca* monkeys forms a thin, narrow band along the mid-line, but in obese specimens it becomes massive, extending anteriorly to the sternum and laterally to the crest of the ilium.

Unfortunately, there is no detailed information about the anatomy of adipose tissue in any species more closely related to hominids.

The homologies of the adipose depots in wild mammals with those of humans are summarised in Figure 12.2. Both the thickness and the area covered by the adipose tissue vary with body composition; the extent of each depot shown is typical for well-nourished, but not obese, specimens of each species. There are species differences in the proportion of the segments of the limbs and in the shape of the girdles and trunk, as well as in the relative development of the depots. In typical quadrupedal mammals, the thorax and abdomen are flattened laterally, but in humans, the pelvis is exceptionally wide and the trunk is flattened dorso-ventrally. The pelvic girdle is foreshortened and, in the erect posture, the femur is fully extended. Compared to rodents, carnivores and ungulates, the humerus and femur of humans are relatively long, and the carpals, tarsals and digits of the hands and feet are relatively short. In typical mammals (for instance, ungulates and rodents), the normal planes of movement of the scapula and humerus are approximately parallel, but in humans the humerus rotates freely from the shoulder and the femur from the hip.

These changes in posture and skeletal proportions have affected morphology of the adipose tissue as well as that of the musculature. The ventral and side groin depots cover the sartorius, tensor fascia lata and the quadriceps muscles on the anterior surface of the thigh and the ventral and lateral areas of the posterior part of the abdominal wall (Figure 12.2 (d)). In typical mammals, the laterally flattened abdomen extends between relatively short thighs almost to the knee, so these groin depots form a broad band of adipose tissue on the flanks and on the outside of the abdomen. In obese specimens of short-legged species with crouching posture, such as guinea-pigs, the ventral groin depot may be so massive that it appears to extend to the ankles (Figure 12.2 (a)). In humans, the extended hip and relatively long femur result in these depots covering much of the anterior, lateral and medial surfaces of the hip and thigh, forming a 'subcutaneous' layer of adipose tissue from the ventral crest of the ilium to the knee. In middle-aged women these depots may become massive, and their abrupt termination just above the medial and anterior surface of the knee can be clearly seen in obese individuals (Figure 12.1). The outer abdominal wall is covered with the 'paunch', a non-paired adipose depot that originates from the mid-line (Figures 12.1, 12.2 (d)), and which may be thick and extensive in obese monkeys (Pond and Mattacks, 1987b) and in humans, particularly men (Lohman, 1981).

On the anterior, lateral thorax there is a bilaterally symmetrical depot situated medial to the panniculus muscle and lateral to the latissimus dorsi and pectoralis major, and extending along the posterior margin of the triceps brachii to the back of the elbow. It is slight in species such as deer (Figure 12.2 (b)), but extensive in rodents (Figure 12.2 (a)) and

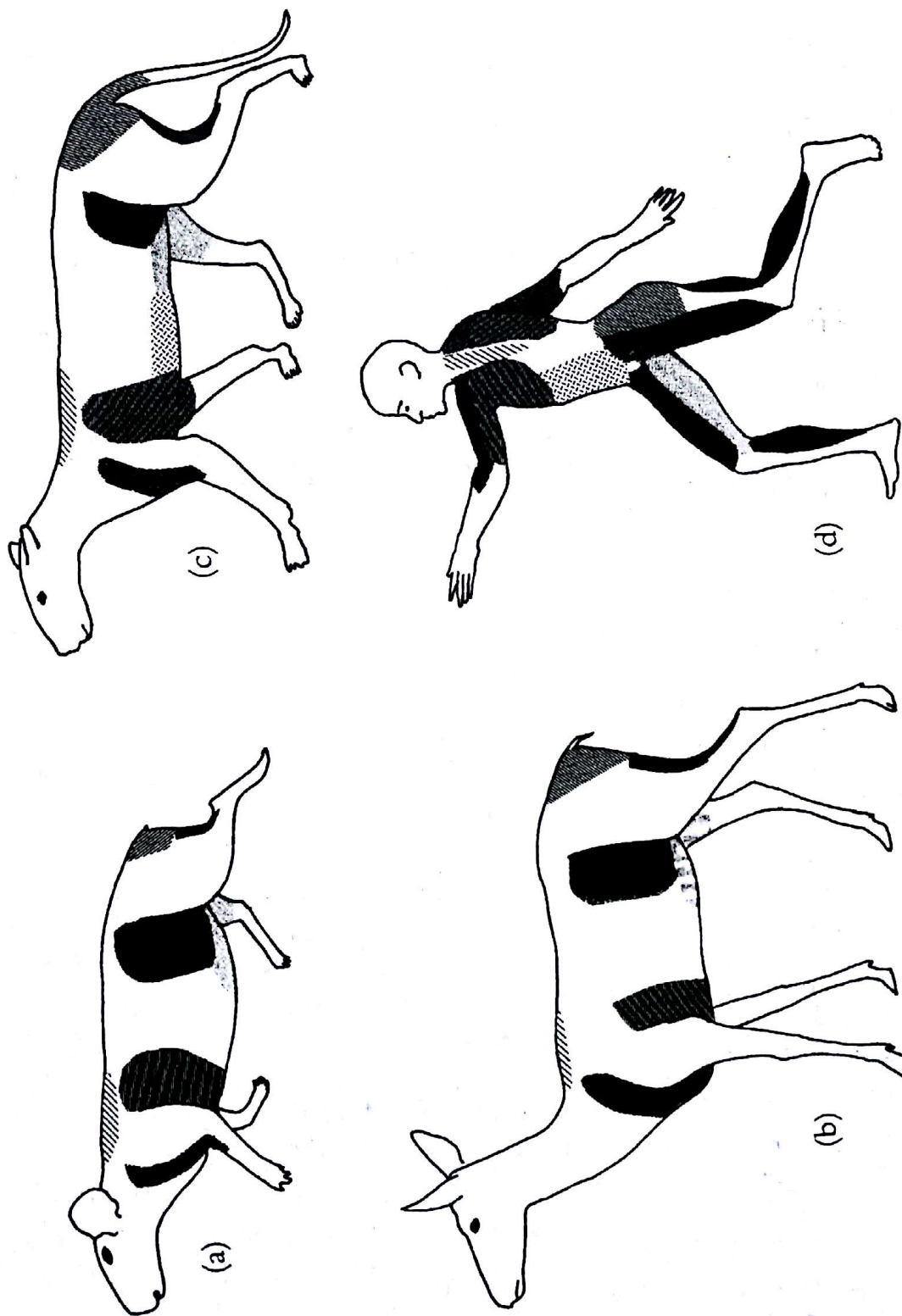


Figure 12.2 The principal superficial adipose in (a) guinea-pig, (b) deer, (c) tiger, (d) male human. The specimens are drawn in postures that show as much as possible. Homologous deposits have the same style of shading. Shading indicates the relative area, not the relative volume, of the deposits.

carnivores (Figure 12.2 (c)). This depot has the same anatomical relations in primates, including humans, but, because of the reduction of the panniculus muscle, the relatively long humerus, the extension and rotation of the shoulder and the dorso-ventral flattening of the thorax, it extends over the ventral, lateral and dorsal surfaces of the chest and over the posterior and medial sides of the upper arm, where it overlies the triceps muscle (Figure 12.2 (d)). On the dorsal side of the thorax it forms the 'subscapular' sites, and on the ventral side it is associated with the mammary glands. Thus a depot that in quadrupedal mammals forms a condensed mass on the lateral thorax, appears to form an extensive 'subcutaneous' layer of adipose tissue over the chest and upper arm in humans. In men, both parts of this depot are approximately similar in thickness, but in women the pectoral portion is enlarged and forms the adipose tissue components of the breasts.

The adipose tissue over the human triceps muscle and that over the 'subscapular' site are among the easiest to examine with skinfold calipers. They are often recorded as though they were independent measures of fatness (e.g., Garn, Sullivan and Hawthorne, 1987). However, it is clear from the comparative anatomy that they are in fact parts of the same depot; no wonder measurements of their thickness correlate so much more highly with each other than with other depots (Garn *et al.*; Bouchard, 1987). The pair of depots that form the buttocks in humans is homologous with the (normally small) depots around the crest of the ischia and the proximal part of the tail in other mammals. Even in obese women, in whom the buttock depots may be massive, adipose tissue is almost absent on the mid-line over the sacrum and tapers sharply just below the dorsal crest of the ilium.

In most cursorial mammals, the knee is flexed and the three flexor muscles insert along the tibia, thereby covering the gastrocnemius muscle along most of its length. The popliteal depot is bounded laterally by the biceps femoris, medially by the semitendinosus and semimembranosus and ventrally by the gastrocnemius muscles, and envelopes the sciatic nerve, the femoral artery, the saphenous vein and popliteal lymph node. Therefore, in guinea-pigs and deer (Figures 12.2 (a), (b)) almost the whole of the popliteal depot is enclosed within the groove so formed, and only a small area of its posterior edge near the saphenous vein is in contact with the skin. The flexor muscles of the knee are inserted more proximally in climbing mammals such as felids, thereby exposing more of the gastrocnemius muscle and the popliteal adipose depot (Figure 12.2 (c)). But in humans, the flexor muscles are inserted just below the knee, which, in the fully erect posture, is extended completely. Consequently, most of the gastrocnemius muscle is not covered by the biceps femoris and semitendinosus muscles. The anatomical relations of the popliteal depot are the same as in other mammals, but the change in the site of

insertion of the knee flexor muscles on to the tibia means that it extends from the back of the thigh to the ankle. The proximal part fills the groove at the back of the knee, where it can be clearly seen as a distinct mass even when overlain by other adipose tissue extending from depots on the medial and lateral sides of the thigh (Keiffer and Heitzman, 1979). In quadrupedal mammals, very little of the gastrocnemius muscle is in contact with the skin, but in humans the whole muscle is covered with skin, making the distal part of the popliteal depot appear to be 'subcutaneous'. In view of its origin as an intermuscular depot, it is not surprising that the dimensions of this adipose mass correlate very weakly with those of other superficial depots, and may shrink while adipose tissue elsewhere on the same person is expanding (Borkan and Norris, 1977).

In all mammals studied, including juvenile baboons (Lewis *et al.*, 1983), the central and posterior regions consist of relatively large adipocytes which have several atypical properties, including an exceptionally high capacity for glucose uptake (Mattacks, Sadler and Pond, 1987; Pond and Mattacks, 1987a) and a higher rate of fatty acid/triacylglycerol cycling than any of the eight other intra-abdominal and superficial depots studied (Mattacks and Pond, 1988). Both these properties increase with exercise and may be interpreted as enabling the popliteal depot to act as a local source of lipid for the adjacent locomotory muscles. In spite of the change in its anatomical relations, the adipose tissue on the calf retains the structural and biochemical features of a typical intermuscular depot (Evans, Mattacks and Pond, unpublished data, 1991).

Thus, although the basic features of the anatomy of human adipose tissue can be identified in other primates, changes in the proportions and posture of the limbs and trunk combine to create the *illusion* that there is 'subcutaneous' adipose tissue over a greater proportion of the body of humans than is the case in most other mammals. In moderately obese people (who form the great majority of those studied in modern Western populations), adjacent depots may overlap each other, making them difficult to identify at dissection and almost impossible to distinguish by palpation or medical imaging technology in living subjects. For example, components of the 'subcutaneous' adipose tissue that originate from the 'paunch' on the outer wall of the abdomen are clearly medial in origin, while those on the anterior thorax, back and hip are clearly bilaterally symmetrical. In lean persons, superficial adipose tissue is minimal on the dorsal mid-line over the spine, and on the ventral mid-line over the sternum and between the breasts. However, in moderately obese people the depots overlies each other, forming an almost continuous layer of 'subcutaneous' adipose tissue. Pearl and Johnson (1983) studied the fascias separating the layers of superficial adipose tissue that may have originated from adjoining depots. They reported that the fascia is maximal on the

thorax and abdomen (where the bilateral depots overlap the medial paunch) and least developed on the medial thigh (covered by groin depot only) and on the lower leg (covered by popliteal depot only), as expected from the foregoing interpretation of the anatomy of human adipose tissue.

THE EFFECTS OF ADIPOSE TISSUE ABUNDANCE ON ITS DISTRIBUTION

The impression of massive subcutaneous adipose tissue in humans is further promoted by the fact that most humans, particularly women, are much fatter than most wild mammals. The proportion of the total adipose tissue in superficial and intra-abdominal depots varies considerably between individuals of similar body composition, but 'subcutaneous' adipose tissue is particularly characteristic of children and young women (Enzi *et al.*, 1986). There is some evidence that in other naturally obese mammals the proportion of adipose tissue in superficial depots may be greater in females. In captivity, the dwarf hamster, *Phodopus sungorus*, spontaneously becomes up to 38 per cent adipose tissue (Pond, Sadler and Mattacks, 1987), without showing any significant disturbances of behaviour or fertility. This proportion of adipose tissue is similar to that of 'normal' humans. In *Phodopus* the superficial adipose depots may become so massive that they cover the limbs to which they are attached, but, although they may seem to form a continuous layer of tissue, the individual depots can easily be distinguished and separated by dissection. The proportion of adipose tissue in superficial depots is greater in females, and the difference increases with increasing fatness. One possible explanation for these effects is that massive intra-abdominal adipose depots are incompatible with the production of relatively large litters.

In some, but by no means all, other wild mammals that become obese naturally – for example, the European badger (Figure 12.3) – the proportion of adipose tissue in superficial depots also increases with increasing fatness. In other words, in such species an apparent shift in the *distribution* of adipose tissue arises as a direct consequence of an increase in its *abundance*. This effect may partially explain the relatively large quantities of adipose tissue in women and children, most of whom have proportionately more adipose tissue than men of similar age, diet and habits (Bailey and Katch, 1981). Obesity is comparatively rare in adolescent boys and young men, but such individuals resemble women (and contrast with obese older men) in having thick, extensive superficial adipose tissue on the thighs, hips, upper arms and abdomen. Comparison of skinfold thickness of traditional and recently urbanised Canadian Eskimos also gave Schaefer (1977) the impression that in young adults of

both sexes 'normal' adipose tissue is mainly internal, but 'additional' fat is deposited in superficial depots.

However, some features of adipose tissue in women, notably its presence in the greatly enlarged and rounded breasts and buttocks, cannot be explained simply as the consequence of its greater abundance. These features are not prominent until puberty and there are no corresponding sex differences in other primates (Pond and Mattacks, 1987b). In typical mammals most of the adipocytes (in small, fast-growing rodents, possibly all) form during suckling, and enlarge when-

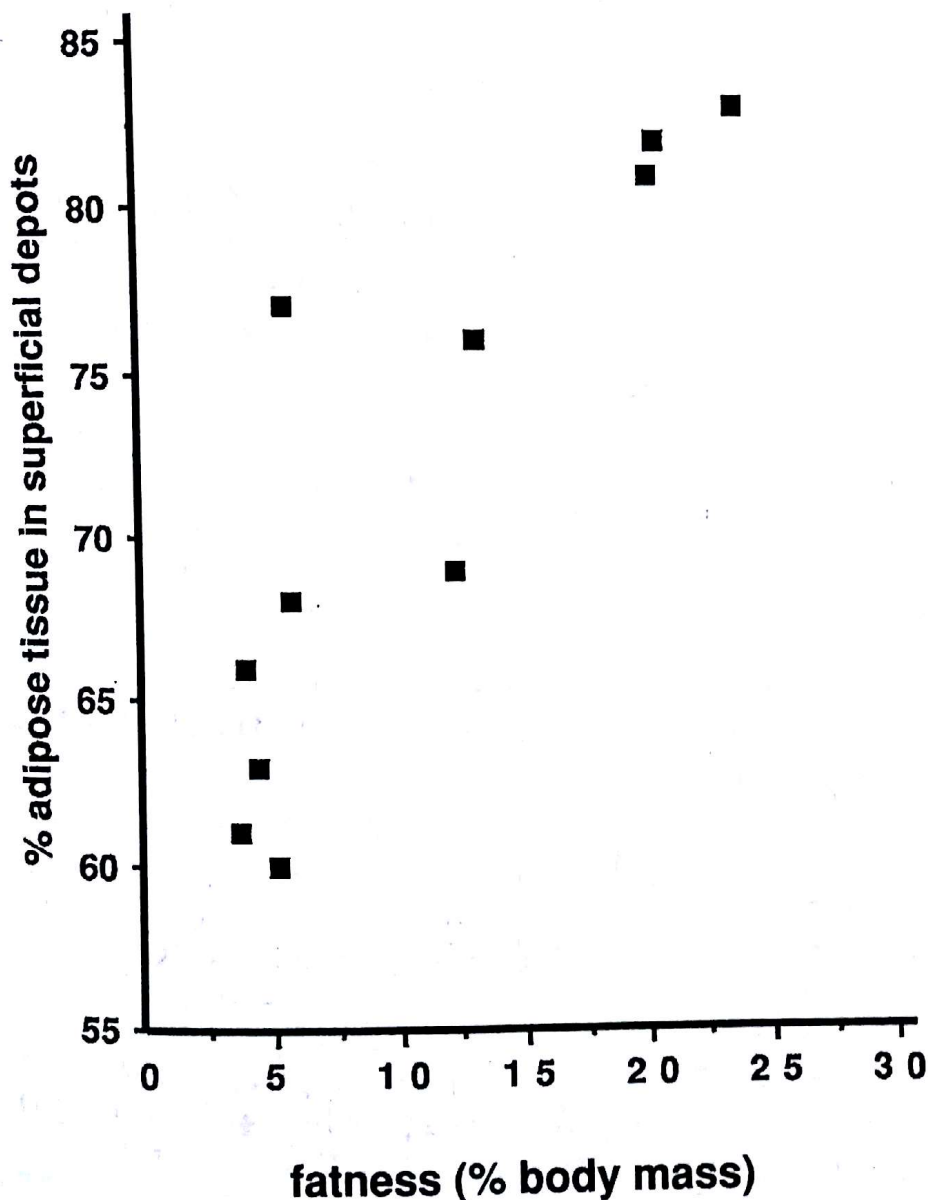


Figure 12.3 Mass of adipose tissue in superficial depots as a percentage of the total dissectible adipose tissue in 11 adult male badgers *Meles meles* (total body mass 8.8–13.6 kg), collected at random from southern England.

ever nutritional status promotes it (Kirtland and Gurr, 1979). Pregnancy may lead to adipose tissue expansion, but there are few detectable changes at sexual maturity. However, in humans puberty is accompanied by changes in the relative growth of adipose tissue in both sexes, which in girls are particularly extensive and conspicuous (Marshall and Tanner, 1986). Thus both in the timing of its expansion and in its distribution, the adipose tissue of women deviates further from other primates than does that of men (Pond and Mattacks, 1987b).

Only cetaceans, pinnipeds and a few species of carnivores and rodents normally have as much fat as 'typical' humans, although other wild species may become obese following long periods of confinement, and domesticated strains of mammals and birds are often obese (Pond, 1978; Pond and Mattacks, 1985b; Pond, 1987c). In such 'exceptionally' obese specimens, the normal superficial depots increase in both thickness and area to form an almost continuous layer of adipose tissue under the skin, including such unlikely sites as in the tail and ears. The effect is particularly prevalent among the Carnivora, possibly because the abdominal cavity is relatively small in these mammals, with the liver and the guts each amounting to only about 2 per cent of the body mass in large species such as lions (Pond and Ramsay, 1991). However, the fact that 'subcutaneous' adipose tissue is found in a few specimens under abnormal conditions does not mean that it is functional or natural in these wild mammals, or in humans.

This analysis shows that the basic elements of the anatomy of human adipose tissue can be identified in non-human primates and that the anatomical steps leading to the distribution of adipose tissue in modern humans can be elucidated from the comparison with other mammals. The exceptional features of the anatomy of human adipose tissue are a direct consequence of the changes in body proportions and in its total abundance. The modern condition can be explained without postulating a major evolutionary shift in the distribution of adipose tissue, as required by the Aquatic Ape Theory. Three major features peculiar to humans are:

- (1) The average fatness of humans is much greater than that of monkeys.
- (2) Superficial adipose tissue is much more conspicuous in humans, partly as a result of its greater abundance, but also because of hair reduction.
- (3) There are substantial sex differences in both abundance and distribution of adipose tissue that appear in early childhood but increase markedly at puberty.

THE FUNCTIONS OF ADIPOSE TISSUE IN HUMANS AND OTHER MAMMALS

The principal, and best understood, function of metabolically active adipose tissue is as a long-term energy store.* In this role its mass varies greatly, sometimes over a short time. In a swimming, running or flying animal, a load with variable mass would cause minimum disruption to balance and posture if it were located at the centre of gravity. The lipid stores of many fishes, amphibians and reptiles are concentrated into a few localised depots, often situated inside the abdomen (Pond, 1978). But mammals and birds differ from the poikilothermic vertebrates in that adipose tissue occurs in a dozen or more discrete depots, associated with several different organs, including viscera, skeletal muscle and the skin. The most widely disseminated explanation for this situation is that adipose tissue acts as insulation and/or as support for other organs. In other words, adipose tissue is believed to have acquired additional functions that require it to be widely distributed over the body surface and around 'delicate' organs. Both of these roles are to some extent incompatible with its original role as an energy store. Insulative capacity is proportional to thickness, so to function effectively and continuously as an insulator the superficial adipose tissue should expand and shrink homogeneously, and be thickest over the most exposed or most vulnerable organs.

The notions that the superficial adipose tissue is adapted to insulate the body against heat loss and/or to protect underlying tissues from mechanical damage are two of the most firmly established of all theories in biology. The insulation theory is widely quoted in both the learned and the elementary biological literature, almost invariably without supporting anatomical or experimental evidence, and it is a major tenet of the Aquatic Ape Theory. Some recent examples include: 'Over most of the body it [the human hypodermis] forms a layer of adipose tissue which provides thermal insulation and mechanical protection' (Wood and Bladon, 1985); 'The primary function of fat deposits in other [non-human] animals is insulation from the cold' (Brown and Konner, 1987). Cunnane (1980) and Verhaegen (1985) also assumed that the principal function of superficial adipose tissue in all homeotherms is insulation. In spite of its widespread acceptance, very few data support the insulation theory, even in the case of some aquatic mammals.

Still air and stagnant water are effective thermal insulators, and the formation of a stagnant layer of air or water around the body is the principal mechanism of heat retention in many aquatic mammals and birds. However, the specific conductivity of adipose tissue is only a little

* Structural adipose tissue such as the paw pads of carnivores and the depots around and behind the eye is metabolically inert.

less than half that of stagnant water (Frisch, Øritsland and Krog, 1974), and numerous observations on mammals native to cold climates suggest that its contribution to insulation may be minimal. More than twenty-five years ago, Irving *et al.* (1962) measured the skin and core temperatures of Alaskan fur seals, *Callorhinus ursinus*, during experimental immersion in cold sea water. Even after prolonged immersion, the skin of the adult seals was only 5°C less than the deep body temperature. The thick, water-repellent fur trapped a layer of air that effectively insulated the surface of the skin from the ice-cold water. Polar bear fur is wetttable, but the woolly underfur and stiffer guard hairs maintain a stagnant layer of water next to the skin that insulates the body like a diver's wetsuit and that provides effective insulation for several hours of immersion in cold water (Øritsland, 1970; Frisch, *et al.*, 1974). The availability of seals, the principal food of polar bears, is seasonal and irregular, and they accumulate large quantities of adipose tissue, much of it in superficial depots (Øritsland, 1970; Pond *et al.*, 1991). However, allometric comparison of the distribution of adipose tissue in polar bears with that of other Carnivora shows that the proportion of adipose tissue in superficial depots and its partitioning between the anterior and posterior areas of the body, are no different from that which would be expected in a temperate-zone carnivore of similar size and body composition (Pond and Ramsay, 1991). These data do not support the hypothesis that the large quantities of adipose tissue in superficial depots are *adapted* to function as thermal insulation. The biochemical properties of the subcutaneous adipose tissue also suggest that they contribute little to passive insulation in the arctic species (Pond *et al.*, 1991).

Although in hairless cetaceans such as fin whales, 96 per cent of the total adipose tissue is superficial (Pond and Mattacks, 1988a), the blubber over the most exposed areas of the back and shoulders is similar in thickness to that on the outer abdominal wall, and all the superficial depots are depleted at about the same rate (Lockyer, McConnell and Waters, 1985). In semi-aquatic mammals such as coypu (*Myocastor coypu*) and otters (*Lutra lutra*), the distribution of adipose tissue is not significantly different from that of their terrestrial relatives, nor is that of thick-furred or tropical species obviously different from that of temperate and thin-furred forms (Pond and Mattacks, 1985b; Pond, 1987a, 1987b; Pond and Ramsay, 1991). Even the hairless hippopotamus is very lean (Hillaby, 1962), although other non-ruminant artiodactyls, the terrestrial pigs and peccaries, have substantial quantities of subcutaneous fat. Pinnipeds are the only aquatic mammals for which there is evidence of an adaptive change in the partitioning of adipose tissue between internal depots (where it contributes nothing to insulation) and superficial sites (where it could combine the functions of energy store and insulator); almost all of the substantial quantities of adipose tissue in seals is superficial (Irving *et al.*, 1962; Pond and Mattacks, 1985b).

Many small hibernating mammals accumulate large quantities of adipose tissue before hibernation, much of which is in superficial depots, but its anatomical location may not indicate that its major function is insulation (Webb and Schnabel, 1983) and there are other equally plausible explanations for its distribution. Thus thick layers of 'subcutaneous' adipose tissue form on the back and thorax of hedgehogs (*Erinaceus europaeus*) but there is none on the abdominal wall, suggesting that the arrangement may have more to do with facilitating the defence posture of 'rolling into a ball' than with insulation. The edible dormouse *Glis glis* develops dissectible adipose tissue amounting to more than 30 per cent by weight before hibernation, but less than 70 per cent of it is in superficial depots, and the 'subcutaneous' fat is not uniform in thickness (Pond, unpublished observations). As in badgers (Figure 12.3), selective accumulation of adipose tissue in the superficial depots may be the simplest way of accommodating a large but transient increase in body mass with the minimum disruption to movement.

The biochemical data are also inconsistent with the notion that adipose tissue in superficial depots is adapted to act as an insulator in terrestrial or semi-aquatic mammals. The dwarf hamster, *Phodopus sungorus* (see page 202) is small (adult body mass 25–60g) and remains active throughout the year in the severe climate of Mongolia and Siberia. We measured the rates of lipid synthesis *in vivo* in the major adipose depots of this species at rest and after an hour of moderate exercise (Mattacks and Pond, 1988). The rates of lipid turnover in the various 'superficial' adipose depots are far from constant, and it would not bring about adaptive changes in the thickness of insulation in response to long-term or short-term changes in exercise regime. Intra-abdominal and groin depots show minimal structural and metabolic (Mattacks and Pond, 1988) response to exercise, but lipid from adipose tissue in interscapular and shoulder depots is readily mobilised during exercise. These depots on the back, neck and shoulder are situated between major organs and areas of skin most exposed to the elements, and hence would be much more important as insulators than the groin depots that spread over and hence 'insulate' the principal locomotory muscles of the hind limb. In fact, it is the intra-abdominal depots that have the metabolic properties that would be expected of adipose tissue of which the principal function is insulation. If the homologous depots in humans have similar properties then the insulating function of adipose tissue is clearly not as well integrated as it could be with its role as an energy source during prolonged exercise or starvation.

As already explained, there are few major differences in the distribution of adipose tissue between humans and furred primates. The relative thicknesses of the superficial depots are not consistent with the role of insulation in air or in water: the back, head and neck are much more

exposed to the elements during both walking upright and swimming than the ventral trunk or the inner surface of the thigh, but superficial adipose tissue is thickest over the ventral abdominal wall (paunch) and, in women, on the thorax (breast adipose tissue) and on the proximal segments of the limbs (Figure 12.2 (d)). As in most terrestrial mammals, adipose tissue along the dorsal mid-line anterior to the pelvis is minimal, amounting to a thin, fibrous layer in all but the most obese people (Clarys, Martin and Drinkwater, 1984). There is no evidence that the 'subcutaneous' adipose tissue is selectively spared in starvation: Ashwell *et al.* (1986) found that in obese women on a severely restricted diet the superficial and intra-abdominal depots are depleted at about the same rate. Johnston, Cohen and Beller (1985) concluded that the greatest differences between the arctic and temperate-zone races were in the proportions of the skeleton and musculature, not in the distribution or abundance of adipose tissue. In a carefully planned study, Schaefer (1977) demonstrated that Eskimos pursuing a traditional lifestyle and diet have less subcutaneous adipose tissue than Canadians of European descent. Laboratory studies of young men also showed that heat loss in cold water depends more upon body proportions and muscle development than upon skinfold thickness (Toner, Sanka, Foley and Pandolf, 1986). Humans are fatter at birth than almost all other mammalian neonates (Adolph and Heggeness, 1971) and, because infants are much more sedentary than adults, adipose tissue might be expected to be more important as an insulator. Even so, the ability of neonates to maintain a constant body temperature correlates more closely with their lean body mass than with the thickness of their superficial tissue (Johnston, *et al.*, 1985).

Most of the paintings and figurines from the end of the last glaciation, when the climate was colder than it is now, show humans as 'stick men'. In the minority of artefacts in which body contour is represented, the medial abdominal 'paunch', the breasts, buttocks and the lateral and medial thigh depots are shown as distinct bulges, but the shoulders, arms and lower leg are shown as lean (Figure 12.1). There is no indication of a smooth, continuous layer suitable for insulation or streamlining.

Another explanation for the distribution of adipose tissue is its role in the protection of vital organs (Pond, 1978; Wood and Bladon, 1985). In many harem-forming mammals such as red deer and elephant seals, the males become fatter before the breeding season, and eat little and lose weight during the rut. In certain species some of the additional adipose tissue accumulates on conspicuous sites, making the animal appear more massive. In a few such species, notably elephant seals, such prominent superficial adipose depots also sustain many of the injuries inflicted by rival males (Halliday, 1980). However, such ideas cannot explain known sex- and age-related differences in the distribution of human adipose

tissue. Although anthropologists argue about the role of hunting and intra-specific conflict, it is generally accepted that only adult males were involved in most forms of physical combat (Daly and Wilson, 1983). But in almost all living races, superficial 'protective' adipose tissue is thicker and more extensive in women than in men, and in children and the elderly than in young adults. Adipose tissue is not distributed in a way that would protect delicate and vulnerable parts of the body: it is minimal over exposed vital organs such as the head and neck. Those who have bruised the coccyx or sacrum would probably confirm that some protective padding over these areas of the spine would prevent prolonged discomfort, but, as in typical caudate mammals, adipose tissue over the 'tail' is minimal even when it is massive on the adjacent buttocks and thighs. Neither site-specific differences in the collagen content of adipose tissue nor the allometric scaling of collagen content to body mass is consistent with the idea that adipose tissue is adapted to the protection of vital organs (Pond and Mattacks, 1989).

SEX DIFFERENCES IN THE ANATOMY OF HUMAN ADIPOSE TISSUE

Sex differences in the distribution of adipose tissue are among the most familiar and distinctive features of our species, and one of the most difficult to reconcile with the Aquatic Ape Theory. Verhaegen (1985) postulated that male aquatic apes fished while the females gathered plant food. However, such a scenario predicts that males would be more exposed to cold and should therefore have more superficial adipose tissue than females, but the opposite is the case in all living human races.

Many of the supposed contrasts between humans and other mammals in the *distribution* of adipose tissue, and many, but not all, of the sex differences, are a simple and direct consequence of sex or species differences in its *abundance*. Therefore, we have to answer the questions: Why are humans so fat, and when in their evolutionary history did they become so fat? Why are women and children so much fatter than men? Are these properties adaptive? If so, what causal or historical relationship does increased fatness have to other specifically human features, such as reduction of hair, bipedalism, low fecundity, delayed maturity and elaborate social behaviour? What is the significance of sex and individual differences in the shape of certain superficial depots?

Sex differences in the abundance of adipose tissue

In many animals, nutrient stores increase prior to reproduction and are depleted while the energy demands of courtship, pregnancy and incubation or feeding of the young are high. In many mammals there are endocrine mechanisms that prevent conception, or promote spontaneous

Is it? more/baby fat?
in skin-water

abortion, if maternal energy stores are insufficient. Some authors, notably Frisch and McArthur (1974) and Frisch (1988), have been impressed by the observation that among American women raised on rich, Western diets, menstruation and ovulation are inhibited when the mass of adipose tissue falls below 15 per cent of the body mass, and have insisted that the phenomenon is adaptive. The hypothesis that a high proportion of adipose tissue is essential to fertility seems attractive enough when only information from modern, Westernised humans is considered, but when viewed in the context of comparative data on fecundity and energetics of reproduction in wild mammals, some serious difficulties emerge.

Adipose tissue of some wild mammals, including that of most non-human primates, is normally present in such small quantities that its contribution to the total energetic cost of reproduction must be small. Furthermore, the extra nutritional requirements for pregnancy and lactation of primates, particularly the large species, are very low compared to other mammals, mainly because primates grow exceptionally slowly both *in utero* and after birth. The energetic cost of human reproduction is very low; among women in The Gambia, West Africa, who are engaged in farming and similar traditional occupations, the energetic cost of reproduction is so low that it is difficult to measure (Prentice and Prentice, 1988), and the correlation between milk production and skinfold thickness is surprisingly weak, even among lean women eating a barely adequate diet (Prentice, Prentice and Whitehead, 1981). As in most other mammals, appetite, intestinal area and digestive efficiency increase in women during late pregnancy and in lactation (Pond, 1977), suggesting that much of the additional requirements of breast-feeding are normally met by increased intake and utilisation of dietary nutrients. There is no evidence that humans, or indeed any other primate, are adapted to suckle their offspring for long periods without feeding, as do polar bears (Ramsay and Stirling, 1988). The lipid content of the milk of most higher primates, including humans, is much lower than that of most other mammals (Ben Shaul, 1962). So, although adipose tissue is present in many women in quantities sufficient to support a baby through the whole of pregnancy and much of the lactation period, there is little direct evidence that it normally does so, even in subsistence economies. Such large quantities of adipose tissue may be critical to successful reproduction only in severe famine.

Frisch's ideas are not consistent with other basic aspects of human ecology: the tropical or warm temperate terrestrial habitat of early hominids, exploitation of many different food sources, social cooperation in hunting and gathering, migration over long distances, food storage and the lack of seasonal breeding. All these features suggest that, far from being vulnerable to the failure of a single food source, humans and their hominid ancestors had omnivorous, cooperative habits which buffered

✓ Good

them against severe, prolonged starvation. Many other large mammals reproduce successfully, and often more prolifically, with much less adipose tissue; it is difficult to see why an omnivorous, non-hibernating species should require so much adipose tissue to produce such relatively small quantities of low-fat milk for so few, slow-growing offspring. When the physiology and ecology of humans are compared to those of other large mammals, the conclusion that the high adipose tissue content of women is an adaptation to the energetic cost of maternity is untenable.

Sex differences in the distribution of adipose tissue

When correlated for differences in body composition, stature and skeletal proportions, sex differences in the distribution of human adipose tissue are relatively minor and are most marked in small depots, particularly those on the calf, breast, thigh and buttock (Bailey and Katch, 1981), and in younger, lean individuals (Schaefer, 1977). In contrast to most mammals, sex differences in the distribution of adipose tissue in humans are influenced by sex hormones throughout adult life (Krotkiewski *et al.*, 1983). Such features have few parallels in other mammals (Pond, 1987b, 1987c) and have been exhaustively studied and discussed during the last thirty years.

Few issues have been the focus for a wider range of speculation based on so few facts than the evolutionary origin and physiological function of the mammary adipose tissue. Morris (1967) suggested that pectoral swellings promoted frontal intercourse. Morgan (1982) believed that the enlargement of the breast occurred during the aquatic phase of human ancestry as an adaptation to the transport of infants in deep water. Gallup (1982), much influenced by the writings of Frisch and McArthur (1974), concluded that prominent breasts were an indicator of sexual status that became necessary following the elimination of an overt oestrus phase. Cant (1981) was also persuaded by the critical energy store hypothesis, and suggested that both the breast and the buttock adipose depots were indications of the woman's nutritional status and hence of her fecundity and competence as a mother.

The facts of the matter are as follows. In most mammals, the mammary glands are associated with the adipose tissue in the groin and/or the posterior abdominal wall, and the mother nurses while standing or lying down. In all higher primates the single pair of nipples is pectoral, and nursing takes place while the mother is sitting or carrying the infant under her belly. Mammary adipose tissue forms from the posterior and medial part of the bilaterally symmetrical depot on the thorax, that is present, albeit in much smaller quantities, in other mammals (see Figure 12.2). In spite of the importance attributed to them, the breasts are normally a relatively small depot, typically about 0.5 l (Campaigne *et al.*,

1979), which is about 4 per cent of the total adipose tissue in young women. Rebuffé-Scrive (1987) expressed surprise that, in lactating women, lipids seem to be more readily mobilised from the 'femoral' (groin) depots than from the adipose tissue in the breast itself. However, this situation is to be expected from the comparative anatomy.

The reduction of body hair makes the enlargement of the breast before and during lactation much more conspicuous than in furred mammals. In most mammals, the mammary glands do not mature until towards the end of pregnancy. But in girls, growth of the mammary adipose tissue is among the earliest major anatomical changes in puberty, preceding the menarche by about two years. The breasts may be almost full-size before fertility and adult sexual and maternal behaviour have developed. From early childhood, girls are fatter than boys on a similar diet, and adolescence begins earlier and is completed sooner in fatter, taller girls (Marshall and Tanner, 1986). Regression of mammary adipose tissue occurs sometime after fertility has declined, and is not necessarily accompanied by a change in total body composition (Lanska *et al.*, 1985). Breast adipose tissue has no special physiological relations with the mammary gland (Rebuffé-Scrive, 1987), and it does not necessarily enlarge disproportionately with parity (Lanska *et al.*, 1985). These facts suggest that mammary adipose tissue in women and girls is not solely, or even primarily, related to its role in the energetics of lactation. It simulates and exaggerates the form of the lactating breast, generating the appearance of fertility in girls long before they are actually capable of successful reproduction.

Expansion of muscle and adipose tissue on the hip and thigh begins early in adolescence, but maximum growth of the pelvic skeleton occurs after that of the long bones, and the birth canal does not reach adult dimensions until up to five years after the menarche (Moerman, 1982). Thus, in spite of its importance to successful reproduction, the maturation of the pelvic skeleton is not complete until long after the development of the conspicuous secondary sexual characters. In women, femoral and buttock adipose tissue has properties that may enable it to be mobilised selectively in lactation (Rebuffé-Scrive, 1987), but the process has never been demonstrated in other mammals. Far from being an accurate indicator of total body composition, the thickness of buttock adipose tissue correlates very weakly with that of other depots (Harrison, 1985).

EXPLANATIONS: SEXUAL SELECTION AND LIFE HISTORY STRATEGY

Many observers, starting with Darwin (1871), have tried to explain differences in human behaviour and appearance as having arisen under sexual selection. Sexual selection normally involves competition between

males for females, and/or active choice of one sex, normally the male, by the other. In species in which the first process predominates, reproductive males are normally much larger than the females, are physically stronger, grow more rapidly and have shorter life spans. They may also have characters that enhance their apparent size, and possess horns or other adaptations to fighting. When the latter mechanism operates, the choosing sex is drab and undertakes most of the parental care; the 'selected' sex contributes much less to raising the offspring, and has conspicuous secondary sexual characters and elaborate courtship behaviour, both of which appear at the time of sexual maturity. Secondary sexual characters usually originate as indicators of physiological state, particularly in species in which the rate of reproduction is low and parental investment is high, but they may be augmented and elaborated by sexual selection to the extent that mortality from both predation and physiological malfunction is increased (Halliday, 1987). Sexual selection, particularly male/male competition for females, occurs in several different families of primates, and may account for sexual dimorphism in body size and some features of the skin and hair of the adult males. Some of the best studied examples are plains-living species such as hamadryas baboons, in which females remain in their natal troop throughout life, while males leave before sexual maturity and later compete to 'take over' harems of females (Dunbar, 1984).

Compared to other species, humans show few features of typical sexual selection: the sexes are only slightly (about 8 per cent) dimorphic for stature and body mass. Sexual dimorphism is less pronounced in *Homo sapiens* than in pre-Pleistocene hominids (Krantz, 1982), and the modern characters seem to have arisen from the females evolving towards smaller body size rather than the males becoming larger (Willner and Martin, 1985). Some of the male secondary sexual characters, including facial and body hair, deep voice and maximum physical strength, are not fully developed until long after boys achieve adult levels of fertility (Marshall and Tanner, 1986), and such characters vary considerably between individuals and their form changes with age.

In its typical form, sexual selection acts mainly on males, and so produces greater divergence from the ancestral condition in males than in females. However, the limited information available shows that it is the anatomy of adipose tissue in men and elderly women that most closely resembles that of other primates, and the distribution of adipose tissue in young women that seems to have changed most from the ancestral condition (Pond and Mattacks, 1987b). What features of human reproductive strategy could have promoted the evolution of such specialisations in young females only?

Adipose tissue in women

Low fecundity, prolonged infant dependency and extensive parental care

would promote selection for maximal physiological and social fitness for reproduction. In rhesus monkeys (Vessey and Meikle, 1987), gelada baboons (Dunbar, 1984) and probably other social primates including hominids, a female's social rank and reproductive success are closely correlated; the offspring of low-ranking rhesus females have higher mortality and occupy lower status as young adults than those born to high-ranking mothers. Rank is determined by the female's relationship to the dominant male and by her interactions with other females. In an *ad-lib*-fed, captive troop of rhesus monkeys, rank was found to be correlated with fatness (Small, 1981). Social systems like that of the gelada baboon are typical of many higher primates, but some arboreal monkeys (Moore, 1984), humans, gorillas and chimpanzees (Daly and Wilson, 1983) are atypical in that young adult females migrate between groups more than males of the same age. In such circumstances, the females must establish their eligibility to join another group, as well as maintain or advance their position in the dominance hierarchies.

Bipedalism was among the earliest and most significant developments in hominid evolution, preceding and probably promoting important changes in diet and habits that led to the intellectual capabilities and the social organisation of modern humans (Lovejoy, 1981). Once started, the rate of enlargement of the cranial capacity of hominids was exceptionally rapid. Although most of the fossil data come from adult and sub-adult remains, it is likely that dimensions of the neonatal head also increased rapidly in evolutionary time. These evolutionary changes would promote selection for females in which the shape of the pelvis permitted successful parturition, which, together with the upright posture, have promoted much more extensive sexual dimorphism of the pelvis and femur than in other primates (Schultz, 1949). Until about 3 million years ago, sexual dimorphism in hominids was most striking in the dentition, but between 1.5 and 0.1 million years ago, pelvic dimensions and stature became the most divergent features (Krantz, 1982). Sex differences in the development of the buttock and femoral adipose depots exaggerate the contrasts in the shape of the adult pelvis and femur, and hair reduction makes the body contours much more conspicuous. These depots, together with the breast adipose tissue and the minimisation of intra-abdominal and superficial 'paunch' depots (Pond and Mattacks, 1987b), generate the 'hour-glass figure' by which young women are easily recognised at a distance (by all other members of the species). Such a body conformation correlates with *skeletal* features that facilitate reproduction, not with energy storage or other *metabolic* adaptations to fecundity. Steatopygia, greatly enlarged legs and sex differences involving adipose tissue are characteristic of negroes, among whom sexual dimorphism in stature and in features of the skin and hair are minimal (Shattock, 1909; Daly and Wilson, 1983).

Halliday (1980) also stressed the lack of correlation between the appearance of female secondary sexual characters and fertility, and concluded that the unusual mating habits of humans had evolved as an adaptation to minimising male rivalry and the maintenance of long-term pair bonds. These concepts can be extended to suggest that the enlarged breasts and prominent buttocks assert the female's adult status, her capacity to give birth successfully to infants with enlarged cranial capacity and hence her eligibility to enter another troop regardless of her fertility. The appearance of sexual maturity may enable a girl to join another group at a younger age, and perhaps also further her opportunities to migrate between groups several times during their reproductive life. Such migration may increase her reproductive fitness by increasing her social and sexual experience, by enabling her to achieve higher dominance rank before giving birth, and by increasing the diversity of the paternity of her offspring. Such a theory also accounts for the observations of Frisch and McArthur (1974) on the relationship between body composition, menarche and the maintenance of normal menstruation in adolescent girls. They found that disturbances or relapses in the development of sexual and maternal behaviour are associated with delayed development or regression of breasts, buttocks and other indicators of adult status as well as with menstruation and fertility. Males normally mate only with adult females, so mature breasts and buttocks may play a role in sexual behaviour, possibly according to the scenario proposed by Morris (1967), but at least the adipose tissue components of these structures should not be equated with the indicators of sexual receptivity in other primates – for instance, skin colour and texture in mandrills and gelada baboons (Dunbar, 1984).

Like other secondary sexual characters that evolve under sexual selection, body conformations that maximise the *social* components of the bearer's reproductive fitness may be irrelevant or even detrimental to his or her physiological well-being. The high degree of fatness of young women may be thus a consequence of selection for a particular body conformation, and may not itself be *physiologically* adaptive. In fact, the converse may be the case: humans, particularly women, may be evolving the ability to maintain metabolic fitness in the presence of so much adipose tissue. Indeed, obesity has fewer detectable deleterious effects on the health of women of normal body conformation than on that of men (Krotkiewski *et al.*, 1983).

Adipose tissue in men

Obesity is rarer in boys and young men than in girls and women, but is more strongly associated with genetic and endocrinological abnormalities in males (Krotkiewski *et al.*, 1983). As in women of similar body composition, much of the adipose tissue of young males is superficial, but

it becomes abundant enough to be conspicuous in only a small minority of exceptionally obese boys. During adolescence, the rate of growth of adipose tissue lags behind that of the skeleton and musculature, so that boys typically become leaner for a period in their teens and accumulate adipose tissue relatively slowly during early manhood (Marshall and Tanner, 1986). In middle-aged and elderly men and in many post-menopausal women, adipose tissue often accumulates in the intra-abdominal depots, particularly the omentum and mesentery, and in the 'paunch' on the outer wall of the abdomen, producing the characteristic 'pot-belly' and spindly limbs (Borkan and Norris, 1977). Thus sex differences in adipose tissue distribution arise in part from differences in the timing of its relative growth and in average body composition.

Large quantities of mesenteric and omental adipose tissue are very rare in wild animals, even when obese (Pond and Ramsay, 1991), and adipose tissue may be almost absent from the mesentery in some species, such as seals, dolphins, hedgehogs and moles (Pond, 1986, 1987c; Pond and Mattacks, 1985a, 1988). In badgers, the mesentery and omentum account for about half of all intra-abdominal adipose tissue, or less than 5 per cent of the total in the fattest specimens (see Figure 12.3). Thus, although the 'pot-belly' figure is very widespread among older people of both sexes, comparable body conformations are not found in wild populations. However, these depots enlarge disproportionately in some macaque monkeys (Pond and Mattacks, 1987b) and older guinea-pigs (Pond *et al.*, 1986) that have been confined in small cages and fed on an *ad-lib* diet all their lives. Characters that appear only in the elderly are not subject to natural selection in the same way as those that develop before or during reproduction and parenthood. Disproportionate accumulation of adipose tissue in the mesentery and omentum is probably not adaptive, and indeed may be a symptom or a cause of physiological malfunction (Björntorp, 1987; Bray, 1988).

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