

# The Structure of Whale Blubber, and a Discussion of its Thermal Properties

BY

D. A. PARRY

(From the Department of Zoology, University of Cambridge)

With one Plate

AS a warm-blooded animal, a whale must be adapted not only to prevent an excessive loss of heat but also to control the rate of heat loss in relation to changes in its metabolic activity and in the temperature of its surroundings. This paper contains an account of whale blubber considered from this point of view. The first part is devoted to the morphology of blubber, particular attention being paid to the blood circulation which does not appear to have been previously described; and the second part contains a discussion of the efficacy of blubber as a thermal insulator of controllable conductance. The results are based on a study of the Common Porpoise (*Phocaena phocaena*), and the Blue and Fin Whales (*Balaenoptera musculus* and *B. physalus*).

The term 'blubber' is in popular and commercial use to denote the superficial tissues of whales and seals, which form a compact layer loosely fastened to the underlying muscle and easily stripped off for commercial purposes. Blubber comprises the animal's epidermis, dermis, and hypodermal tissues; and in the following account the word will always be used in this sense. The term 'integument' is used to refer to these tissues in other mammals.

## GROSS MORPHOLOGY

### Area

The surface area of whales and porpoises was found by measuring the circumference or semi-circumference at intervals down the body and finding the area contained by the smooth curve drawn through these values plotted against length. Flukes, dorsal fin, and flippers (measured for the porpoise only) were traced on squared paper.

*Phocaena phocaena*. One male, 155 cm. long, was measured, the circumference being taken at intervals of 15 cm. The results were:

Area of body only . . .	9,950 cm. <sup>2</sup>
„ flukes . . .	820 „
„ fin . . .	250 „
„ flippers . . .	540 „
Total area . . .	11,560 „

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Assuming that the surface area is proportional to the square of the length, that is to say,  $A = Kl^2$ , we have:

$$K = 0.45 \text{ for the total area,}$$

$$K_1 = 0.39 \text{ for the body area alone.}$$

The value for  $K$  is in good agreement with that calculated from Gray's data (Gray, 1936) which gave  $K = 0.44$ .

*Balaenoptera physalus*. Measurements were made of one adult whale and several foetuses, the results being as follows. The figures refer to the body area alone, excluding fin, flukes, and flippers.

Length	Measurement interval	Area	$K_1$
19.8 m.	3 m.	137 m. <sup>2</sup>	0.35
308 cm.	25 cm.	32,330 cm. <sup>2</sup>	0.34
245 cm.	„	20,280 cm. <sup>2</sup>	0.34
240 cm.	„	20,710 cm. <sup>2</sup>	0.36

These figures give a mean value for  $K_1$  of 0.35. This compares favourably with the value of  $K_1 = 0.37$  derived from Laurie's data (1933) which were based on the assumption that a whale can be regarded as two cones fastened together at their bases.

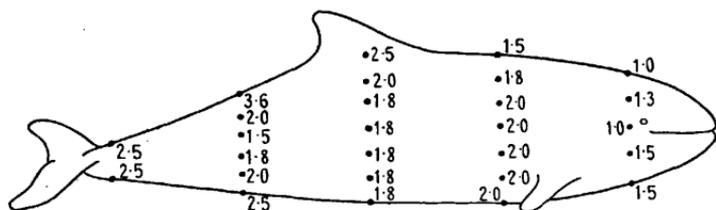
#### Thickness

*Phocaena phocaena*. The blubber thickness of a 155-cm. male was found both by direct measurement and indirectly from the area, weight, and density. The results of direct measurement are shown in Text-fig. 1 and give a mean thickness of 1.8 cm. The same figure was obtained by the other method, the density having been determined as 0.98 gr./c.c.

*Balaenoptera physalus*. It is difficult to study the distribution of blubber thickness under the conditions on board a factory ship, but from personal observations and those kindly made by Dr. M. Begg (Biologist, Factory Ship *Balaena*, 1946-7) I found that the thickness on the flank, level with the dorsal fin (the standard measuring-point of the Discovery Investigations), was approximately the mean value for the whole surface. It is now possible to amplify this conclusion as I have the advantage of a personal communication from Dr. E. J. Slijper embodying the results of extensive measurements made during 1946-7 and 1947-8. From these measurements I have calculated the mean thickness in two ways. Firstly, the outline of a whale was drawn on graph-paper so that it was divided into about eighty squares. Blubber thicknesses were marked in or interpolated, and the mean found from the sum of the product of areas and thicknesses. This gave a mean of 1.1 times the thickness at the standard place. The method may be suspected of error owing to the foreshortening of the dorsal and ventral surfaces, but as both the thickest and thinnest blubber is to be found on these surfaces (dorsal and ventral surfaces of the tail, and ventral surface of the throat and chest, respectively), the

resultant error is unlikely to be great. This contention is supported by the fact that the second method of calculation gave the same result as the first. This method was to find the mean of an equal number of thicknesses measured or interpolated along the dorsal, lateral, and ventral lines, and effectively allots equal areas to the dorsal, ventral, and lateral surfaces.

Extensive data are available concerning blubber thickness at the standard place. It varies with locality, time of year, and size of whale. Mackintosh and



TEXT-FIG. 1. *Phocaena phocaena*. Depth of blubber in centimetres.  
Length of animal: 155 cm.

Wheeler (1929) give measurements made at South Georgia, while the following are taken from Dr. Slijper's communication and come from whales caught on the Antarctic pelagic whaling grounds:

	Dec.	Jan.	Feb.	March
	cm.	cm.	cm.	cm.
Blue whales, ♂ 74'-80'	11.7	10.6	12.6	12.1
" " ♀ over 80'	15.2	14.0	16.0	16.4
Fin whales, ♀ 65'-70'	7.8	9.6	11.2	12.7

## MICRO-ANATOMY AND HISTOLOGY

### *Phocaena phocaena*

#### Material

The following account is based on the blubber of a 155-cm. male porpoise which after death had spent 2-3 days in transit in Great Britain at air temperature (October) and a further 4 days in a cold room (0° C.) while a plaster cast was made, during which process local warming of the blubber must have occurred. Despite this treatment a considerable amount of cytological detail was preserved, as will be seen from the photomicrographs. The animal fortunately died with its peripheral blood-vessels dilated, and the blood remaining in the vessels enabled their course to be made out.

#### Methods

After the post-mortem delay described above, small pieces of material were fixed in Susa or in 5 per cent. formalin, both fixatives giving good results. For preparations of the epidermis, paraffin embedding was satisfactory and sections down to 4  $\mu$  were obtained; but this method was unsuitable for the

dermis and hypodermis as it hardened the connective tissue and dissolved away the fat so that the tissues were badly torn and distorted during cutting. Lendrum's method of softening with phenol (Carleton and Leach, 1938, p. 39) was tried unsuccessfully, and frozen sections were finally resorted to. Good preparations down to  $20\mu$  were obtained, and little difficulty was experienced in making up complete series by transferring each section to a slide treated with gelatin, and exposing the full slide to formalin vapour (Pantin, 1946, p. 26).

The epidermis was well stained by Heidenhain's haematoxylin. More difficulty was experienced with the other tissues, where a stain was required which would not obscure the red blood in the vessels and would show up the vessel walls so that arteries could be distinguished from veins. Mallory's triple stain, and Masson's trichrome stain, gave unsatisfactory results, and the required contrast between blood and tissues was finally obtained by staining lightly with 1 per cent. water-soluble aniline blue.

#### *Tissue Components*

The blubber of the porpoise is composed (Pl. I, fig. 1), like the integument of other mammals, of epidermis, dermis, and hypodermal tissue. Its most distinctive features are the thickness and almost exclusively fatty nature of the hypodermis, and the absence of hair, skin glands, and sense organs. The following account deals separately with the three tissue layers, and then considers the blood-supply. No sensory or vasomotor nerves have been found.

#### *Epidermis*

(i) *Micro-anatomy.* The thickness of this, the most superficial layer, varies little over the body, being 3.25 mm. or  $\times(2 \times 10^{-3})$  of the body length. It varies in colour from white to dark grey, being responsible for the colour of the animal. The deeper half of the epidermis is penetrated by upward extensions of the dermis in the form of 'dermal ridges' running parallel to the long axis of the body, from the summits of which arise the dermal papillae. The section illustrated in Pl. I (fig. 1) is cut at right angles to the long axis of the body so that the ridges are cut transversely; the second ridge from the right-hand side has been cut between two papillae while all the others have papillae rising from them so that the distinction between the two is not evident. Pl. I, fig. 3 shows a transverse section through the ridges, and fig. 2, cut more superficially, shows the papillae which have arisen from the ridges. This arrangement differs from the condition found in most mammals where the papillae arise directly from the base of the epidermis.

There are approximately 25 papillae per sq. mm., which is about half the mean density found in man (Lewis, 1927, p. 253).

(ii) *Histology.* The epidermis is composed of two layers, the superficial *stratum corneum* (unstained in Pl. I, fig. 1); and a deeper layer which on comparative grounds will be called the *stratum germinativum*, although no mitoses have been observed. The transition between the two layers is characterized by a

flattening of the cells parallel to the surface, a thickening of the cell walls or inter-cellular substance, and a reduction of nuclei and cytoplasm. There is no *stratum granulosum* or *stratum lucidum*, a condition not unusual in other mammals.

As in other mammals the *stratum germinativum* may be subdivided into 'cylindrical cells' with large nuclei, lining the dermal ridges and papillae; and polygonal 'prickle cells' with well-developed intercellular and intracellular fibrils, lying superficial to the papillae.

In the pigmented parts of the blubber, pigment granules occur in the epidermis; most densely in the cylindrical cells of the *stratum germinativum*, especially those immediately bordering the ridges and papillae; and less densely in the prickle cells. Pl. I, figs. 2-4 show the granules in unstained sections.

### *Dermis*

This consists of a mat of connective tissue fibres parallel to the surface, very dense at the base of the epidermis (Pl. I, fig. 1), and becoming less dense and invaded by fat cells at deeper levels where it merges into the underlying hypodermis. Its thickness is about 0.34 mm., or  $\times (0.22 \times 10^{-3})$  of the body length. This tissue is formed predominantly of white fibres, staining characteristically with v. Giesson's stain. No elements took up orcein, but a few elastic fibres were recognized in some preparations.

*Hypodermis* (note: only a fraction of the total thickness of the tissue is shown in Pl. I, fig. 1)

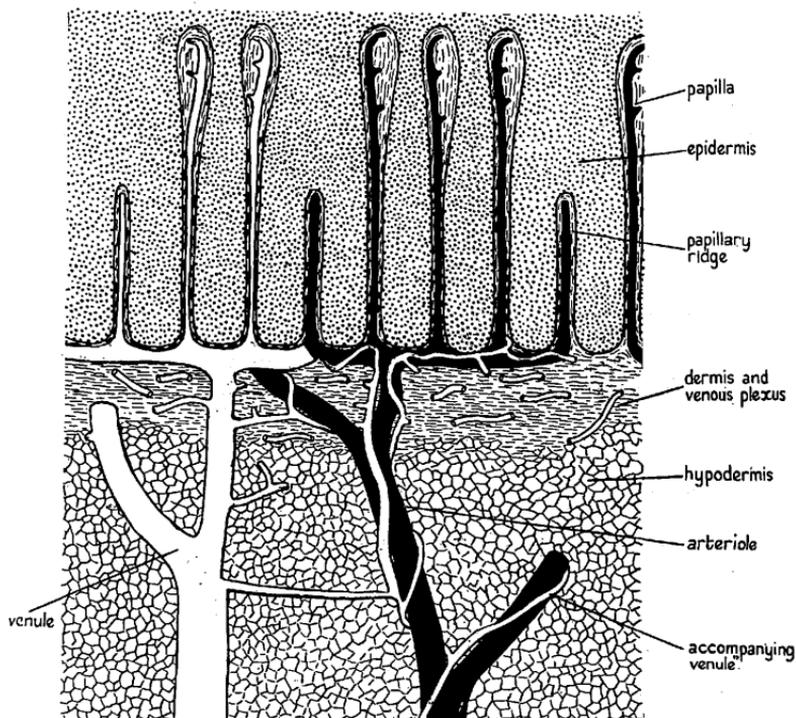
This tissue is composed almost entirely of fat cells, with occasional bundles of white fibres running irregularly among them (Pl. I, fig. 1). The great development of this layer is responsible for the thickness of blubber as a whole, and for its commercial value. It corresponds to the panniculus adiposus of that other almost hairless mammal, man; and presumably also to the thick layer of fat beneath the skin of the domestic pig.

*Blood-supply* (see Text-fig. 2, which has been constructed from a large number of serial drawings)

(i) *Arteries*. Arterioles run up through the hypodermis, branching as they do so; and through the dermis to the base of the epidermis. Here they run somewhat obliquely across the bases of the dermal ridges, giving off twigs which run up the ridges to join the capillaries in the papillae. The most careful examination has failed to show the arterioles giving rise to capillaries or forming a plexus in the hypodermis or dermis, neither are there any signs of arteriovenous anastomoses. The only course open to the blood appears to be up the twigs in the ridges to the capillaries in the papillae. Text-fig. 3 (a) shows an arteriole running through the dermis to the base of the epidermis. Pl. I, fig. 3 shows both arterial and venous twigs in the dermal ridges, running upwards, and also horizontally to supply the papillae arising from the

summits of the ridges. It is probable that even at this level, arterial and venous vessels are distinguished by the thickness of their walls.

(ii) *Capillaries*. Capillaries occur in the papillae (Pl. I, fig. 2) where the terminal twigs are probably joined together by several short capillaries, as



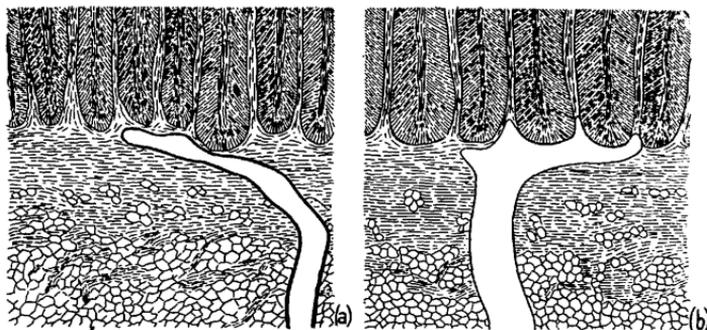
TEXT-FIG. 2. *Phocaena phocaena*. Blood circulation in the superficial regions of the blubber. To avoid confusion, arterial and venous vessels are not both shown in the same dermal ridge and papilla. Based on numerous serial drawings.

photomicrographs of living tissue have shown to be the case in man (see Lewis, 1927, p. 13). The diameter of the capillaries is about  $15\mu$ .

(iii) *Veins*. Venous twigs running down the dermal ridges are collected into venules which, like the corresponding arterioles, run obliquely across the base of the epidermis and then down through the dermis and hypodermis, joined by venules from adjacent parts of the skin. Text-fig. 3 (b) shows a vertical section through the dermis and base of the epidermis, with one of these venules running horizontally just below the epidermis collecting twigs from the ridges, and then turning to run down through the dermis. Pl. I, fig. 4, is a thick,

horizontal section through the extreme base of the epidermis, showing a collecting venule running just below it.

Unlike the corresponding arterioles, these venules are associated with an extensive plexus in the dermis and the transitional region between dermis and hypodermis. This plexus is shown in Pl. I, fig. 5. It appears to be a single network, with elements running in both the horizontal and vertical planes (see Pl. I, fig. 1), and so the short lengths of plexus shown in Text-fig. 2 must be imagined as inter-connected in planes above and below that of the drawing. This text-figure illustrates the fact that the venules preserve their identity



TEXT-FIG. 3. Vertical sections through the dermis and base of the epidermis showing (a) an arteriole, and (b) a venule, running up to supply the dermal ridges and papillae. Based on  $100\mu$  frozen sections, stained with aniline blue.

up to the base of the epidermis, connecting with the plexus by means of short branches; they do not divide up into the plexus which in turn gives rise to more superficial vessels. Thus blood from the papillae may run directly down through the dermis and hypodermis in the large venules; or it may flow through the narrow plexus vessels under the influence of small pressure differences between one part of the plexus and another. The diameter of the plexus vessels is about  $30\mu$ .

In addition to the large venules already described, which pursue an independent course through the blubber, there are much smaller venules, often not more than one, accompanying the arterioles in at least the superficial layers of the hypodermis, and in the dermis up to the base of the epidermis but not entering the dermal ridges (see Text-fig. 2). These vessels, like the large ones, contribute to the venous plexus, and are occasionally connected with the large ones by branches in the hypodermis.

#### *Balaenoptera*

The sample of the blubber of *Balaenoptera physalus* brought to England in a hard-frozen state for heat-conductivity measurements (see below) also

afforded material for histological examination. The peripheral blood-system could not be followed as it did not contain blood, but the micro-anatomy of the three tissue layers—epidermis, dermis, and hypodermis—was similar to that of *Phocaena* with the exception of a peculiar vacuolation in the epidermis which we suspect to be an artifact due to freezing (see next paragraph).

We have also examined a sample of the blubber of *Balaenoptera musculus* kindly supplied by Dr. Michael Begg, who fixed it in formalin shortly after the capture of the whale. The micro-anatomy of the tissue layers was also similar to that of *Phocaena*, and the vacuolation noted above did not occur. The blood-system has not been traced out in detail, but the main elements found in *Phocaena* were all present: arterioles running through hypodermis and dermis to give off twigs to the dermal ridges; collecting venules receiving twigs from the ridges and running down through dermis and hypodermis; and plexus in the dermis.

#### DISCUSSION OF THE MICRO-ANATOMY AND HISTOLOGY

A few previous accounts exist of the blubber tissues, excluding the vascular system. That of Bonin and Vladykov (1940) deals with the Beluga (*Delphinapterus leucas*) where the dermis is relatively better developed than in our species, so as to be of commercial importance in the manufacture of shoelaces. These authors do not mention the dermal ridges; otherwise their account is in good agreement with ours. Stiglbauer (1913: *Delphinus delphis*) also does not describe the dermal ridges, nor does he find 'prickle cells' in the epidermis. Japha (1907: *Balaenoptera* spp.) gives a clear account of the ridges, from which Schumacher (in Bolk *et al.*, 1931) has made a good perspective drawing (Fig. 248, p. 468). In other respects, too, we are in general agreement with Japha, and his account of five different layers in the epidermis, as compared with our three, seems to be a refinement of description rather than a difference of substance.

We know of no other account of the blubber vascular system. This differs from that in the integument of man (Spanholtz, in Lewis, 1927) where the plexuses are much more complicated: the arterioles break up into two separate ones at different levels, while the venules divide up into no less than four. The 'accompanying venules', which we have described as running beside the arterioles, do not occur in man.

#### THE THERMAL PROPERTIES AND FUNCTION OF BLUBBER

##### *Blubber regarded as a Heat Transmitter*

Blubber is generally thought of as a protection against cold, but the integument of a homothermous animal is much more than a mere passive insulator. It actively controls the outward passage of heat, and so preserves the deep body temperature despite changes both in the rate of production of heat by the animal, and in the thermal characteristics of the environment.

In whales, no less than in terrestrial animals, is such a control of heat loss necessary. Variation in the rate of swimming must be accompanied by a considerable variation in heat production; and whereas most whales probably undertake irregular wanderings which carry them over at least a moderate range of temperature, the rorquals undergo a twice-yearly migration between polar and tropical waters, involving a temperature change of no less than 25° C.

The difference in the environment of whales and terrestrial animals carries with it necessary differences in the methods of heat-regulation. The latter lose heat by three channels: evaporation, controlled by the sweat glands and breathing; and convection and radiation, controlled by the surface temperature which is in turn influenced by vaso-regulation. In addition, habitat selection plays an important role. A whale, on the other hand, cannot sweat or seek shelter, neither can it radiate to an environment which is within a degree or two of its own surface temperature. It can lose heat solely by 'forced' convection to the water flowing past it, and we have shown that blubber contains a blood-circulation by control of which this heat loss could be regulated. The system will now be considered in more detail.

*Minimum Heat Transmission.* It is known that in man exposed to cold the blood-flow through the skin is reduced almost to zero by constriction of the arterioles (Lewis, 1927; Forster *et al.*, 1946). It is not unreasonable to assume that this is also true of whales where similar arterioles exist, though it may be added that, if a slight flow is always necessary for purposes of nutrition, the heat loss from this might be reduced by a return stream of blood through the 'accompanying venules'. This would short-circuit some of the heat and prevent it from being lost at the surface.

When the blood-flow through the blubber is negligible, heat loss is entirely due to passive conduction through the tissues and its rate is given by the expression:

$$\text{Rate of heat transmission} = \frac{\text{Blubber conductivity}}{\text{Blubber thickness}} \times \left( \frac{\text{Body temperature} - \text{Sea temperature}}{\text{Sea temperature}} \right).$$

The conductivity and internal temperature were found as follows:

(i) *Conductivity.* A sample of whale blubber (*Balaenoptera physalus*) about 1 ft. square was hard-frozen a few hours after the capture of the whale, and maintained in this condition for about five months during transport to, and storage in, this country. It was then kept at just over 0° C. for a week to thaw out and at air temperature (October) for 3½ hours during transport to the National Physical Laboratory, where it was immediately put in the heat-conduction apparatus. The Laboratory report was as follows:

The sample of whale blubber submitted for the determination of the thermal conductivity was supplied in the form of two slabs each measuring 12 inches by 12 inches by 1½ inches approximately. For the purposes of the test, the slabs were placed one on each side of a hot plate surrounded by a guard ring, the whole being clamped between two cold plates maintained at a constant temperature. The

temperatures of the hot and cold surfaces were measured by means of thermocouples. The heat input to the hot plate was obtained by observations of the watts dissipated in its heating coil. The results given in the table below refer only to the particular sample tested.

*Whale Blubber*

(Approximate density 65 lb. per cub. ft.)

Cold face temperature:  $0^{\circ}\text{C}$ .

Hot " " :  $35^{\circ}\text{C}$ .

Thermal conductivity : 0.00050 gr.-cal. per sq. cm. per sec. for  
1 cm. thickness and  $1^{\circ}\text{C}$ . diff. in  
temp.

(ii) *Internal Temperature.* That of a Blue Whale (*Balaenoptera musculus*) was measured 60 minutes after death, the thermometer being placed in a deep cut in the epiaxial muscle, level with the flipper, immediately after the blubber had been removed from that part. Three readings all gave the same result:  $35.5^{\circ}\text{C}$ ., which is likely to be nearer the true value than Laurie's figure (1933) of  $35.1^{\circ}\text{C}$ ., based on the measurement of twenty whales at a land station.

Substituting these values for the conductivity and internal temperature in the above expression, we have:

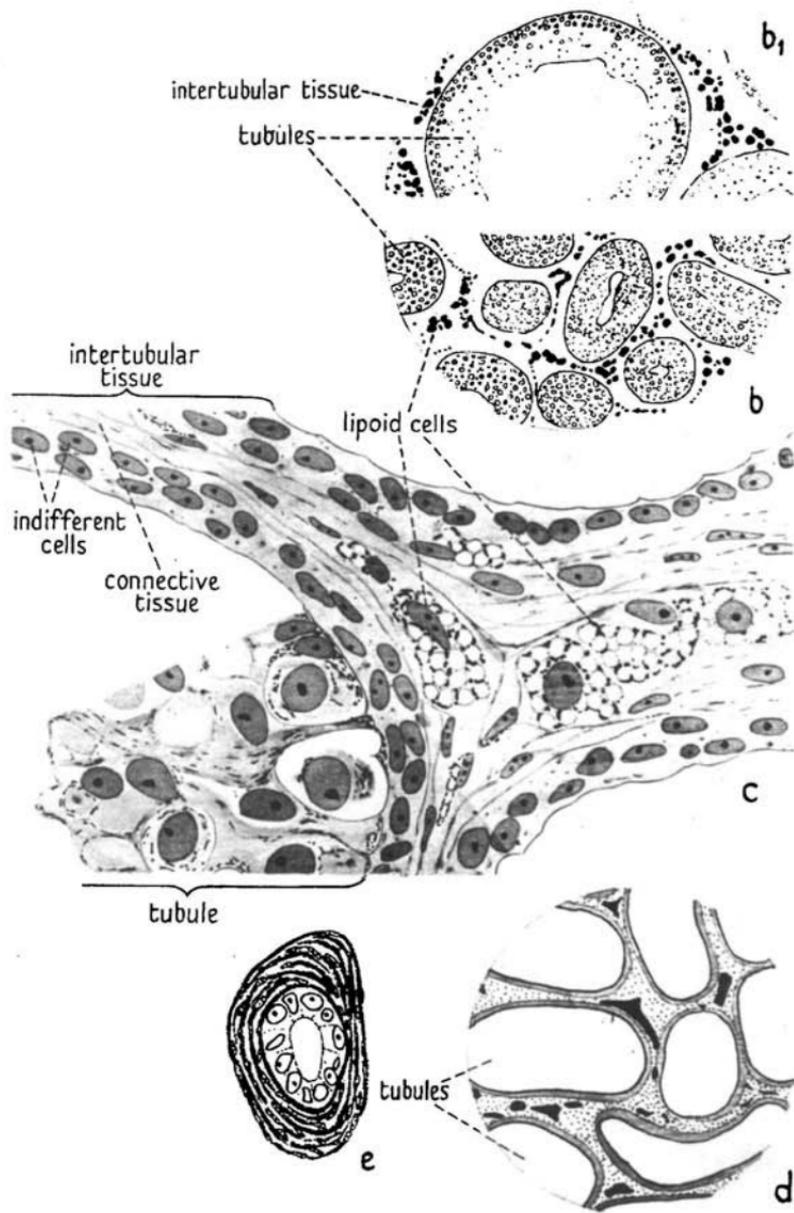
$$\text{Heat transmission (cal./sq. cm./sec.)} = \frac{5 \times 10^{-4}}{d} (36 - t_e),$$

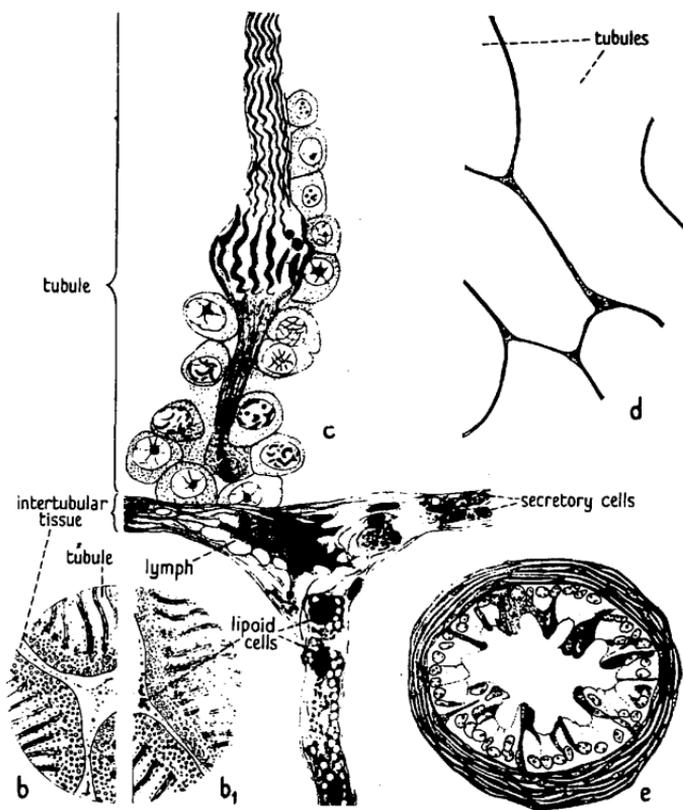
where  $d$  = thickness of blubber (cm.) and  $t_e$  = environmental temperature ( $^{\circ}\text{C}$ .).

Two examples may now be considered. For a porpoise in which  $d = 1.8$  cm., living in a sea at  $t_e = 10^{\circ}\text{C}$ . (e.g. around the British coast):

$$\begin{aligned} H &= \frac{5 \times 10^{-4}}{1.8} (36 - 10) \\ &= 72 \times 10^{-4} \text{ gm.-cal./sq. cm./sec.} \\ &= 260 \text{ kilo-cal./sq. m./hr.} \end{aligned}$$

For a rorqual in which  $d = 8$  cm., living in a sea at  $t_e = 0^{\circ}\text{C}$ ., the heat loss is 81 kilo-cal./sq. m./hr. The significance of these figures will appear when it is recalled that the basal metabolism of a wide range of terrestrial animals (including horse, man, pig, dog, and hen) is almost constant and equal to 45 kilo-cal./sq. m./hr.—a figure which has come to be regarded as generally applicable though its physiological basis is unknown (see Krogh, 1941). If this figure also applies to the whale then we must conclude that neither the porpoise nor the rorqual, in the environments considered above, can afford to remain at rest: despite their blubber they would suffer a net loss of heat. It also follows that for the heat loss to be reduced to 45 kilo-cal./sq. m./hr. in any whale at rest (independent of size or species), a layer of blubber with an average thickness of 14 cm. would be required, a thickness which is





J. W. SLUITER AND G. J. VAN OORDT—PLATE III

actually encountered in the largest rorquals, and in the right whales (*Balaenidae*), whose 'rightness' as a target for the harpoons of an earlier age was in part due to their sluggishness compared with the rorquals. We are, of course, aware that some authorities are unwilling to grant to the above figure for basal metabolism the dignity of a physiological constant. Benedict (1938) puts forward a relation making metabolism per unit area increase with length, quoting figures as low as 12 kilo-cals./sq. m./sec. for the dwarf mouse, and as high as 85 kilo-cal./sq. m./sec. for the elephant. His conclusion may be criticized on the ground that it is based on very few data from animals at the two extremes of size; but even if it is correct it quite fails to endow a small whale such as a porpoise with a basal metabolism nearly large enough to compensate for its heat loss in temperate seas.

*Maximum Heat Transmission.* This will be achieved when the blubber arterioles are fully dilated and the mass flow of blood to the surface is maximal. Then it is most likely that much more heat is lost from the blood than through the blubber, so the latter can be ignored in comparison. The interesting consequence is that maximum and minimum heat losses are virtually independent: the achievement of a low minimum by the development of a thick layer of blubber does not affect the maximum which will depend on the maximum mass flow of blood through the superficial vessels and their spacial arrangement. This arrangement may be contrasted with that found among the majority of terrestrial homotherms where the insulation (fur or feathers) overlies the vascular tissue, so that an increase in the thickness of the former must reduce the maximum as well as the minimum heat loss.

#### BLUBBER REGARDED AS AN ENERGY RESERVE

It is well known that the blubber of the southern rorquals shows a seasonal variation in thickness, being thinnest at the beginning of the southern summer when the whales are returning to high latitudes after wintering nearer the equator. This may be regarded as effecting a necessary increase in the minimum rate of heat loss corresponding to the warmer environment. But it has been suggested that the whales find little to eat in the tropics and subsist on the stored energy of their blubber. A simple calculation shows that this suggestion is quite plausible. According to Mackintosh and Wheeler (1929, p. 370) the reduction in thickness is 0.1 per cent. of the body length. Using the previously found expression  $A = 0.39L^2$  for the surface area, and assuming the density of blubber is unity and its energy content 9 kilo-cal./gm., it follows that the energy liberated during 6 months is at the rate of ( $L^3 10^{-6}$ ) watts. Now basal metabolism at 45 kilo-cal./m.<sup>2</sup>/hr. demands  $22^2 \times 10^{-3}$  watts; so it follows that a 0.1 per cent. reduction in blubber thickness would just pay for the basal metabolism of a 20-m. whale, while it would afford larger animals extra energy for movement.

This conclusion is not intended to be taken quantitatively; but it does give qualitative support to the idea that the blubber of rorquals functions as a significant energy reserve.

While this work was being done I was successively Whaling Inspector and Discovery Biologist in the Factory Ship *Empire Venture* (1945-6), and the recipient of a Senior Research Grant from the Department of Scientific and Industrial Research (1946-7). I am most grateful for the facilities which these appointments placed at my disposal. I also wish to acknowledge the willing assistance of the Director and Staff of the Scottish Marine Biological Association in securing and injecting the porpoise; and the readiness of the National Physical Laboratory to accept for conductivity measurements a specimen possessing somewhat unwelcome characteristics.

#### SUMMARY

1. The gross morphology, micro-anatomy, and histology of the blubber of the porpoise (*Phocaena phocaena*) and the rorquals (*Balaenoptera* spp.) are described.

2. If the surface area is given by  $Kl^2$ ,  $l$  being the overall length, then  $K$  is 0.39 in *Phocaena* and 0.35 in *Balaenoptera*, excluding fins and flukes.

3. Blubber consists of the whale's epidermis, dermis, and hypodermis. The hypodermis is relatively very thick and almost exclusively fatty, and in the species studied merges into the dermis which is mostly composed of white fibres. It extends into the epidermis as 'dermal ridges', from which the papillae arise. In the epidermis can be recognized: *stratum germinativum*, divided into the deep cylindrical cells and the more superficial prickle cells; and *stratum corneum*.

4. The vascular system is composed of arterioles running up to the base of the epidermis, giving rise to twigs which run up the dermal ridges to supply the capillaries in the papillae; and venules collecting twigs from the ridges and running down through dermis and hypodermis, connecting in the dermis with a venous plexus. Small 'accompanying venules' run with the arterioles to the base of the epidermis.

5. The conductivity of blubber is 0.00050 gm.-cal./sq. cm./°C./cm. and the deep body temperature is about 36° C. Thus in temperate and polar waters most whales lose heat at a greater rate than the basal metabolic rate of land homotherms, even when the blood-flow through the blubber is negligible. It is suggested that whales need to keep swimming in order to keep warm.

6. The vascular system in the blubber provides a mechanism for regulating heat loss.

7. It is shown that the energy liberated by the reduction in blubber thickness suffered by rorquals in the southern hemisphere during the winter is sufficient to meet at least a significant part of their total needs.

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## EXPLANATION OF PLATE I

(All the preparations are of *Phocaena phocaena*)

FIG. 1. Section through the epidermis, dermis, and superficial part of the hypodermis. Fixed in 5 per cent. formalin, several days *post mortem*. 100 $\mu$  frozen sections, stained with 1 per cent. aniline blue, W.S. ( $\times 29$ )

FIG. 2. Horizontal section through epidermis, showing dermal papillae with capillaries dark with blood. Fixed in 5 per cent. formalin, several days *post mortem*. 100 $\mu$  frozen sections, unstained. ( $\times 52$ )

FIG. 3. Horizontal section through epidermis, showing dermal ridges with venules dark with blood. Treatment as (2). ( $\times 52$ )

FIG. 4. Horizontal section through base of epidermis and dermal ridges, showing large venule. Fixed as (2); 200 $\mu$  frozen section, unstained. ( $\times 52$ )

FIG. 5. Horizontal section through dermis, showing venous plexus. Fixed as (2); 200 $\mu$  frozen section, unstained. ( $\times 52$ )