J. Physiol. (1975), **244**, *pp.* 223–234
With 2 plates and 2 text-figures
Printed in Great Britain

BROWN ADIPOSE TISSUE IN THE NEW-BORN CALF (*BOS TAURUS*)

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(*Received 30 May 1974*)

SUMMARY

1. Electron microscopic examination revealed that most of the adipose tissue of new-born calves had the cellular morphology of brown adipose tissue; only subcutaneous tissue had the cellular morphology of white adipose tissue.

2. The cellular morphology of the brown adipose tissue changed progressively to that of white adipose tissue as the age of the calves increased.

3. Infusion of noradrenaline (I.V.) at rates of 1 and 5 μg/kg.min into new-born calves exposed to a thermoneutral environment increased metabolic rate two- to threefold, and also increased rectal temperature and respiration rate. The responses declined as age of calf increased.

4. Approximately 2% of the body weight of new-born calves appears to be brown adipose tissue.

INTRODUCTION

Brown adipose tissue is present in a variety of new-born mammals and is concerned with non-shivering thermogenesis (Smith & Horwitz, 1969), thereby contributing substantially to their cold resistance (Hull & Segall, 1965; Alexander, 1970). The tissue is commonly distinguished from white adipose tissue on the basis of the multilocular distribution of the lipid within the cell. Animals with brown adipose tissue respond to an infusion or injection of noradrenaline with a marked increase in metabolic rate, while those with only white adipose tissue do not (Smith & Horwitz, 1969).

The new-born young of most ruminants that have been examined have at least some multilocular adipose tissue cells (Thompson & Jenkinson, 1970; Rowlatt, Mrosovsky & English, 1971; Gemmell, Bell & Alexander, 1972) but the new-born calf of domestic cattle (*Bos taurus*) is reported to be an exception (Wensvoort, 1968; Jenkinson, Noble & Thompson, 1968). Jenkinson *et al.* (1968) also found that the calf showed an insignificant

elevation in metabolic rate upon infusion with noradrenaline, and on both grounds concluded that the calf is devoid of brown adipose tissue and has no non-shivering mechanism for elevating metabolic rate in cold conditions.

Nevertheless, some workers have regarded the adipose tissue of the new-born calf to be brown (Meulen, Müller & Molnár, 1972) and for this and several other reasons the apparent difference between calves and closely related species needs to be re-assessed. First, the disposition of the lipid in the adipose cell as revealed by light microscopy is a less reliable indication of the nature of the cell, than the number and appearance of the mitochondria in the cell as revealed by electron microscopy (Smith & Horwitz, 1969); this has proved to be so in the sheep (Gemmell *et al.* 1972). Secondly, brown adipose tissue in kids (Thompson & Jenkinson, 1970) and lambs (Gemmell *et al.* 1972) is rapidly replaced by white adipose tissue within the first week of life. Most of the calves examined by Jenkinson *et al.* (1968) were several days old, and the adipose tissue from only two was examined by light microscopy. Thirdly, the infusion dose of noradrenaline used by Jenkinson *et al.* (1968) (1 μg/kg.min) was low by comparison with the dose that appears necessary to produce a maximum response in the metabolic rate of new-born lambs (10 μg/kg.min) (Alexander, 1969).

This paper reports on the results of a re-examination of new-born calves and shows that they do indeed have brown adipose tissue.

METHODS

Animals. Five calves less than 18 hr old were obtained from a commercial dairy herd close to the laboratory; all were at least half Friesian (Table 1). Two that were maintained beyond the first day of life were bottle-fed twice daily on cow's milk or milk substitutes according to appetite. Two Hereford × (Hereford × Friesian) calves were also available. They were born at the laboratory 9 and 14 days before full term (283 days), parturition having been induced by injecting the cow intramuscularly with 10 mg Flumethasone (SYNTEX) two and three days previously. These calves were reared by their mothers.

Tissue sampling and examination. Samples of adipose tissue were collected from various sites at various times after birth (Table 1). Some samples were taken at laparotomy with the calf under pentobarbitone anaesthesia; these samples were restricted to the perirenal and mesenteric sites. More extensive samples were taken from calves 1, 2, 3 and 6 following terminal anaesthesia. Sampling sites were the perirenal, abdominal, omental, intestinal mesenteric, pericardial, cardiac groove, cervical, prescapular, popliteal, orbital, and the subcutaneous areas on the midside and sternum. Quantitative dissection of major adipose tissue depots (Table 2) was done on calves 1, 2 and 6.

Samples for examination under the light microscope were fixed in buffered 10% formalin, and embedded in paraffin wax; sections 7 μm thick were stained with haematoxylin and eosin.

Tissue for examination with the electron microscope (Hitachi HU-11C) was cut into pieces approximately 1 mm^3 and fixed at 4° C in 1·3% (w/v) osmium tetroxide in 0·067 M-S-collidine buffer at pH 7·2 (Bennett & Luft, 1959). The fixed tissue was

embedded in epoxy resin (Araldite); all sections were stained sequentially with uranyl acetate (Watson, 1958) and lead citrate (Reynolds, 1963).

Measurement of metabolic rate and infusion of noradrenaline. O_2 consumption and CO_2 production were measured with an open circuit mask system while the calf rested in a large climatic chamber held at approximately 26° C, 1·3 kPa water vapour pressure. Under these conditions, metabolic rate of young calves should be minimal (Jenkinson *et al.* 1968). The calves were allowed to settle down in the chamber for at least an hour before measurements commenced, but they were not fasted deliberately as a preliminary to the tests. Calves more than two days old were subjected to periods of training, with the mask in place, in the chamber during the several days prior to each test.

TABLE 1. Breed of calves and age when adipose tissue sampled

Calf no.	Breed	Age when sampled (days)
1	at least ¾ Friesian	0·25
2	Friesian	1·7
3	Friesian	0·6*
		7
4	at least ¾ Friesian	8*
		15*
		30*
5 (Prem)	¾ Hereford ¼ Friesian	1·25*
		15*
6	½ Friesian ½ Jersey	< 0·5
7 (Prem)	¾ Hereford ¼ Friesian	2·6*
		12*
		30*

* Samples taken at biopsy.

The open-circuit system used was almost identical with that described by Bennett (1972). O_2 was analysed paramagnetically (analyser model E2, Beckman Instruments Inc.) and CO_2 was analysed by an infra-red analyser (Lira 300, M.S.A. Co.). Recordings were taken manually at 2 min intervals. Metabolic rate was measured over a control period of 30 min during which saline (0·9 % NaCl) was infused into the recurrent tarsal vein via a polyvinyl chloride cannula. Measurements were then continued over test periods of 30 min each during which noradrenaline was infused. Usually 1 μg/kg.min was given during the first test period, and 5 μg/kg.min was given during the second (Table 3), and with some animals metabolic rate was also measured during a recovery period of a further 30 min. Priming doses of noradrenaline equivalent to 2 min of infusion were given at the start of the respective periods. The noradrenaline was given as the hydrochloride (Sigma) and was freshly prepared by dissolving in 0·9 % NaCl containing 0·03 % of ascorbic acid as preservative. Infusions were given at the rate of 0·14 ml./min, and the dose of noradrenaline was calculated as noradrenaline base.

During these measurements, activity was noted, respiration rate was determined by direct counting of chest movement, and the animal's temperature was recorded by means of a thermocouple probe extending 9 cm into the rectum.

Calf 2 stood throughout the measurements but the other calves lay quietly for

most of the time. Since metabolic rate and respiration rate were transiently elevated by movement and depressed during periods of apparent sleep, the results presented are confined to periods of at least 10 min of 'standard activity' when the animal scarcely moved but was awake.

RESULTS

Histology of adipose tissue

The adipose cells in tissues from ten of the twelve sites examined in calves less than 2 days old, appeared under the light microscope to be dominated by a large locule of lipid approximately 30 μm in diameter although some small locules of lipid were observable in the marginal cytoplasm of a proportion of the cells (Pl. 1, fig. 1). The tissue from the remaining two sites, the midside and sternal subcutaneous regions, contained few adipose cells and these were almost all unilocular and approximately 20 μm in diameter; the marginal cytoplasm was not apparent (Pl. 1, fig. 2).

When examined with the electron microscope, all the adipose cells, with the exception of those from the two subcutaneous sites had morphological features typical of brown adipose tissue. The cells were multilocular, there being a large central lipid locule and many small locules in the relatively meagre cytoplasm. In addition there were numerous closely packed mitochondria in contact with lipid locules and the mitochondrial cristae were arranged in parallel rows (Pl. 1, fig. 3). The subcutaneous adipose cells were mainly unilocular and had the typical appearance of white adipose cells. There was a single large lipid locule, the cytoplasm formed a thin layer, restricted to the cell periphery, and contained a few small lipid locules, the mitochondria were sparse and had few cristae, and the mitochondria and lipid locules were not in contact (Pl. 1, fig. 4).

The morphology of the adipose cells changed with the age of the calf. Under the light microscope, the small locules in the non-subcutaneous adipose tissue appeared to diminish as age increased (Pl. 2, figs. 5 and 6), but the morphology of the adipose cells from the subcutaneous sites did not change. Examination of the non-subcutaneous adipose cells with the electron microscope revealed a continuous range of cell types in the older calves, the features of brown adipose tissue being progressively replaced by those of white adipose tissue (Pl. 2, figs. 7 and 8). These changes occurred earliest in the cardiac, cervical and popliteal regions. All the adipose cells in calf 4 examined at 30 days showed the morphological features of white adipose tissue but in calf 7 examined at 30 days, there were some cells with characteristics of brown adipose cells.

Distribution and amount of adipose tissue

Post-mortem examination of calves 1, 2 and 6 killed 6, 40 and < 12 hr after birth, revealed a large amount of adipose tissue in the abdominal cavity (Table 2), surrounding the kidney and extending from the diaphragm into the inguinal canal. There was also a substantial deposit on the intestinal mesentery and omentum. There were smaller amounts surrounding the prescapular lymph nodes and extending into the cervical

TABLE 2. Weight of adipose tissue depots in three young calves

Region	Calf no., age and weight: 1 (6 hr) (28 kg)	2 (40 hr) (40 kg)	6 (< 12 hr) (31 kg)
	(g)	(g)	(g)
Perirenal/abdominal	146	267	149
Inguinal	49	65	62
Pericardial	*	19	23
Prescapular/cervical	34	82	21
Popliteal	*	*	8
Orbital	*	*	23
Lumbar (extra-abdominal)	*	*	9
Stomach complex including omentum	*	75†	73†
Large intestinal mesentery	*	216†	15†
Small intestinal mesentery	*		86†
Total	> 229	> 724	469
% of body weight	> 0·82	> 1·81	1·51

* Region not examined.
† Included some large blood vessels and mesentery.

region, and also, in the orbit of the eye, on the pericardium, along the cardiac groove on the surface of the heart, around the other lymph nodes and along the major blood vessels. When the calves were skinned, patchy sheets of subcutaneous adipose tissue less than 1 mm thick were observed on the shoulder and anterior abdomen. The perirenal, abdominal, inguinal, prescapular and cervical adipose tissue depots together amounted to about 1 per cent of total body weight (Table 2). Dissection of adipose tissue associated with the gut was attempted in calves 2 and 6; it was not possible to separate the adipose tissue from the blood vessels and mesentery but most of the dissected tissue appeared to be adipose and the dissected mass was equivalent to about 0·6 per cent of body weight. The total adipose tissue dissected from calves 2 and 6 appeared to be close to the total that

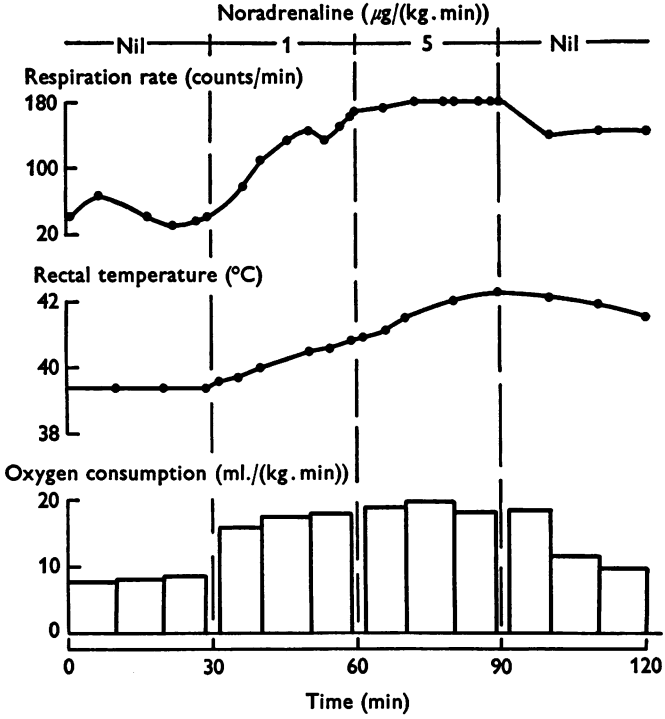
TABLE 3. Effect of noradrenaline infusion on oxygen consumption, rectal temperature, and respiration rate in calves during the first weeks of life

Calf no.	Age (days)	Body weight (kg)	Oxygen consumption ml./kg.min			Rectal temperature (°C) (At end of 30 min period)			Respiration rate (breaths/min)		
			Control	1 μg/kg.min (test minus control)	5 μg/kg.min (test minus control)	Control	1 μg/kg.min (test minus control)	5 μg/kg.min (test minus control)	Control	1 μg/kg.min (test minus control)	5 μg/kg.min (test minus control)
2	0·9	40·0	8·3	—	+9·7	38·9	—	+2·3	28	—	+105
3	0·5	41·9	4·3	+5·9	+7·3	38·4	+0·7	+1·7	29	+86	+111
	6	43·5	6·3	+2·5	+4·4	39·2	+0·3	+1·1	95	+33	+80
4	0·5	34·3	4·4	+4·2	+7·1	39·0	+0·2	+1·0	49	+59	+88
	7	37·7	8·0	+0·4	+1·9	39·4	−0·3	+0·3	113	+13	+33
	15	42·2	9·1	+1·5	+3·6	39·3	+0·3	+0·7	80	+28	+16
	30	51·7	7·9	−0·1	+1·4	39·2	0·0	+0·1	72	+2	−18
5	1·3	34·9	8·7	+7·2	+9·4	39·5	+0·9	+2·2	83	+61	+49
	15	52·7	8·0	+2·1	+4·7	39·0	+0·1	+0·7	96	+30	+42
	37	75·2	6·9	+1·9	+2·3	39·3	0·0	0·0	74	−8	−2
7	2	31·1	8·1	+9·9	+9·8	39·4	+1·5	+2·9	43	+117	+137
	12	44·5	8·0	+5·0	+6·8	39·6	+0·6	+1·5	116	+49	+56
	30	66·1	6·9	+1·8	+3·3	39·7	0·0	+0·5	93	+20	+59

could be dissected and was equivalent to 1·81 and 1·51 per cent of body weight respectively.

Effect of noradrenaline on metabolic rate, rectal temperature and respiration rate

The five calves examined within 2 days of birth all showed an increase of about two- or threefold in metabolic rate during infusion of noradrenaline (Table 3; Text-figs. 1 and 2) and the response during infusion of 5 μg/kg.min was almost always greater than that during the preceding 30 min. of infusion of 1 μg/kg.min. The responses declined as age of calf increased, but some response was still apparent in calves about a month old (Text-fig. 2).

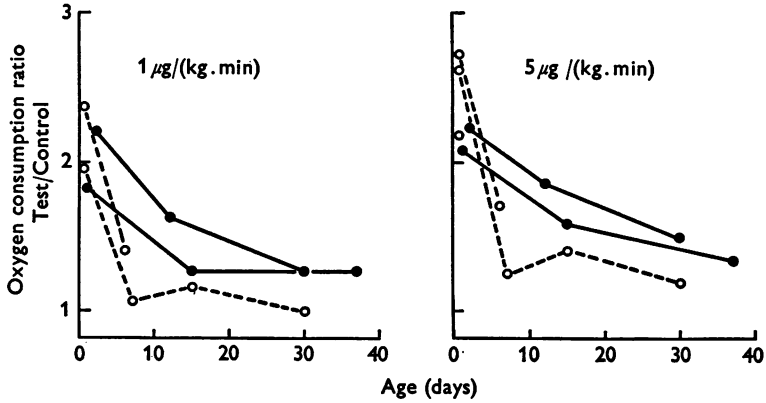


Text-fig. 1. An example of the result obtained from infusing noradrenaline into young calves. This calf (no. 7, a Hereford Friesian cross) was 2 days old. Infusion of noradrenaline produced an increase in metabolic rate, rectal temperature and respiration rate, and the responses to 1 μg/kg.min were almost as high as those to 5 μg/kg.min.

These increases in metabolic rate were accompanied by an increase in rectal temperature (Table 3; Text-fig. 1), which was most marked at the earliest ages but was almost zero in calves about a month old; rectal

temperatures during the control period ranged from 38·4 to 39·7° C, and the highest temperature recorded during the infusions was 42·3° C (calf 7).

Respiration rate also rose sharply during the infusion and usually increased further when the infusion rate was increased from 1 to 5 μg/kg.min (Table 3); however, respiration rate was very variable.



Text-fig. 2. The metabolic responses of five calves to infusions of noradrenaline. The responses are expressed as the ratio of oxygen consumption during periods of 'standard activity' within the test period to the oxygen consumption during periods of standard activity within the control period. The responses tended to be higher when the infusion was at the higher rate, and the responses clearly declined as the calves became older. The filled circles represent results for the premature calves.

When the infusion was discontinued, metabolic rate and respiration rate returned to near normal within half an hour, but rectal temperature remained elevated for longer (Text-fig. 1).

DISCUSSION

Examination with the electron microscope clearly indicated that all adipose cells of the new-born calf, except those from the subcutaneous regions, have the characteristics regarded as essential for their identification as brown adipose cells; in particular, the appearance and disposition of the mitochondria are regarded as critical (Napolitano, 1963; Smith & Horwitz, 1969). However, under the light microscope, the cells have the appearance of being unilocular rather than multilocular, and hence would be classified as white by widely used criteria. These results add to the already considerable evidence that the disposition of lipid within the adipose cell is not a reliable guide for distinguishing brown from white adipose tissue (Hull & Segall, 1966; Smith & Horwitz, 1969; Gemmell *et al.* 1972).

The results also indicate that the brown adipose tissue of the calf changes to white adipose tissue in much the same way as reported for the lamb (Gemmell *et al.* 1972). In the new-born lamb many of the adipose cells are obviously multilocular, but in the calf the majority of adipose cells possess a large dominant locule of lipid. Nevertheless, the potential for non-shivering thermogenesis in calf brown adipose tissue as indicated by a marked increase in metabolic rate due to noradrenaline infusion, appears to be as high as that in lambs in which noradrenaline infusion also produces a 2–3 fold increase in metabolic rate (Alexander & Williams, 1968).

The precise magnitude of the contribution of brown adipose tissue to this increase in metabolic rate is somewhat equivocal because the infusion of noradrenaline, particularly at the higher rate, appeared to produce discomfort and restlessness in the calves and may have also increased respiratory effort. Thus, some of the response to noradrenaline is probably not due to stimulation of brown adipose tissue and the over-estimate may be greater with 5 μg/kg.min than with 1 μg/kg.min. However, the higher values with 5 μg/kg.min than with 1 μg/kg.min do not seem to be due to the higher body temperatures reached during the second 30 min test period, because metabolic rate returned towards normal more rapidly than did rectal temperature (Text-fig. 1): further work on the optimum dose of noradrenaline is required.

Both the distribution and proportion of brown adipose tissue in the body of the new-born calf are very similar to those in the new-born lamb; in both approximately 1·5% of body weight appears to be brown adipose tissue. However, in the calf, there appears to be more of the brown adipose tissue associated with the intestines than in the lamb, in which the mesenteric adipose tissue forms a very small part of the whole (G. Alexander & A. W. Bell, unpublished data). In both species there is very little white adipose tissue at birth and this appears to be restricted to subcutaneous sites.

Since Jenkinson *et al.* (1968) used light microscopy to identify the nature of the calf adipose tissue, their conclusion that the calf had no brown adipose tissue is readily understood, but their failure to obtain significant increases in metabolic rate during noradrenaline infusion is not so readily explained. In view of the present results the anomaly does not appear to be due to a suboptimal infusion rate of noradrenaline though it may be partly due to the fact that most of their tests were conducted with calves several days old. The possibility that the difference in results is due to breed differences seems to us to be remote.

The degree to which the new-born calf can elevate its metabolic rate in response to severe cold had not been measured, although there are

suggestions that summit (or maximal) metabolism is only twice the resting metabolic rate (Gonzalez-Jimenez & Blaxter, 1962; Jenkinson *et al.* 1968) and is evoked in a dry calf in still air at about 0° C or even higher. However, in the field, calves appear to be tolerant of much colder conditions than these, and the present results indicate that the potential for non-shivering thermogenesis alone is at least equal to the resting metabolism. Indeed, from analogy with the new-born lamb (Alexander & Williams, 1968), it seems likely that shivering, coupled with non-shivering thermogenic mechanisms, provide the calf with a potential for trebling or quadrupling metabolic rate in response to cold. It seems likely that the peak observed in the metabolism curve for the calf by Gonzalez-Jimenez & Blaxter (1962) and Jenkinson *et al.* (1968) was due to a change in thermal insulation of the calf, due perhaps to piloerection. However, the physiology of cold resistance in the calf awaits elucidation.

The practice of inducing parturition prematurely in commercial dairy cattle is gaining wide acceptance but places the calf at risk (Welch, Newling & Anderson, 1973). The present experiments suggest that calves a week or two premature have a healthy non-shivering thermogenic response, similar to that of full term calves and to that of lambs a few days premature (Alexander, Nicol & Thorburn, 1973).

We are extremely grateful to Mr John Drinan for his generous permission to use calves 5 and 7, which belonged to him. Thanks are also due to Mrs Keniry and Mr Edols for painstaking technical assistance.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. Light micrograph of perirenal adipose tissue obtained from a new-born calf (no. 1). The adipose cells are dominated by a large single locule of lipid (L), though a few small locules can also be observed (× 500).

Fig. 2. Light micrograph of sternal subcutaneous adipose tissue obtained from a new-born calf (no. 1) (× 500).

Fig. 3. Electron micrograph of intestinal mesenteric adipose tissue obtained from a new-born calf (no. 6). A large locule of lipid (L) is present in each cell, though small locules of lipid (I) are also observed. The densely packed mitochondria, in close contact with the lipid locules, show many cristae (× 9200).

Fig. 4. Electron micrograph of sternal subcutaneous adipose tissue obtained from a new-born calf (no. 2). A large locule (L) and several small locules (I) of lipid are contained within the cell. A small number of mitochondria with few cristae are present (× 6000).

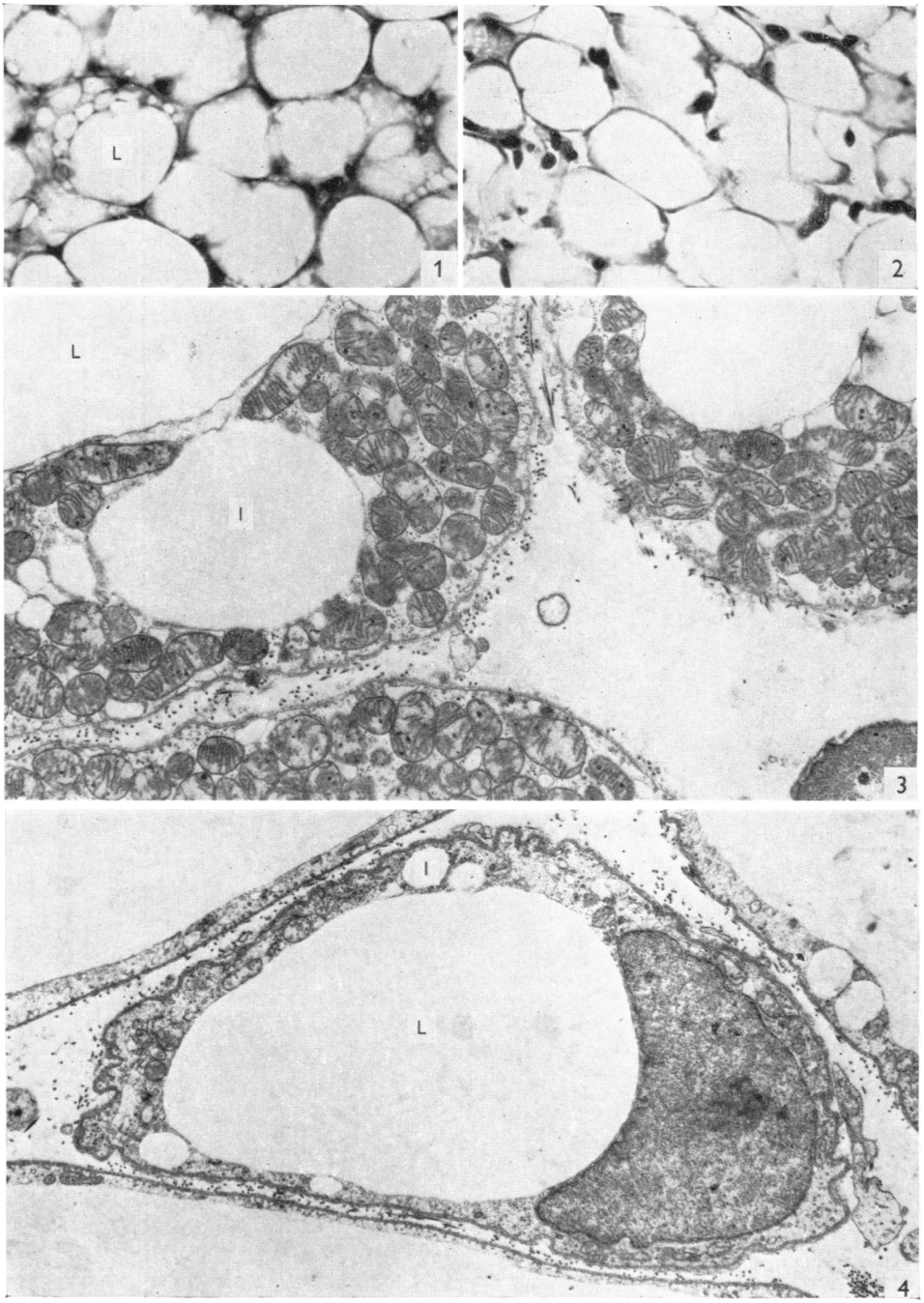
PLATE 2

Fig. 5. Light micrograph of perirenal adipose tissue obtained from a 7-day-old calf (no. 3) (× 500).

Fig. 6. Light micrograph of perirenal adipose tissue obtained from a 30-day-old calf (no. 4) (× 500).

Fig. 7. Electron micrograph of omental adipose tissue obtained from a 7-day-old calf (no. 3). Each cell is dominated by a large locule of lipid (L), but some small locules of lipid (I) are still present. The relative amount of cytoplasm and the number of mitochondria have diminished, compared with the new-born brown adipose tissue (Fig. 3) (× 6000).

Fig. 8. Electron micrograph of perirenal adipose tissue obtained from a 30-day-old calf (no. 4). Each of the three adjoining cells has a large lipid locule (L) and sparse peripheral cytoplasm almost devoid of mitochondria (× 8000).



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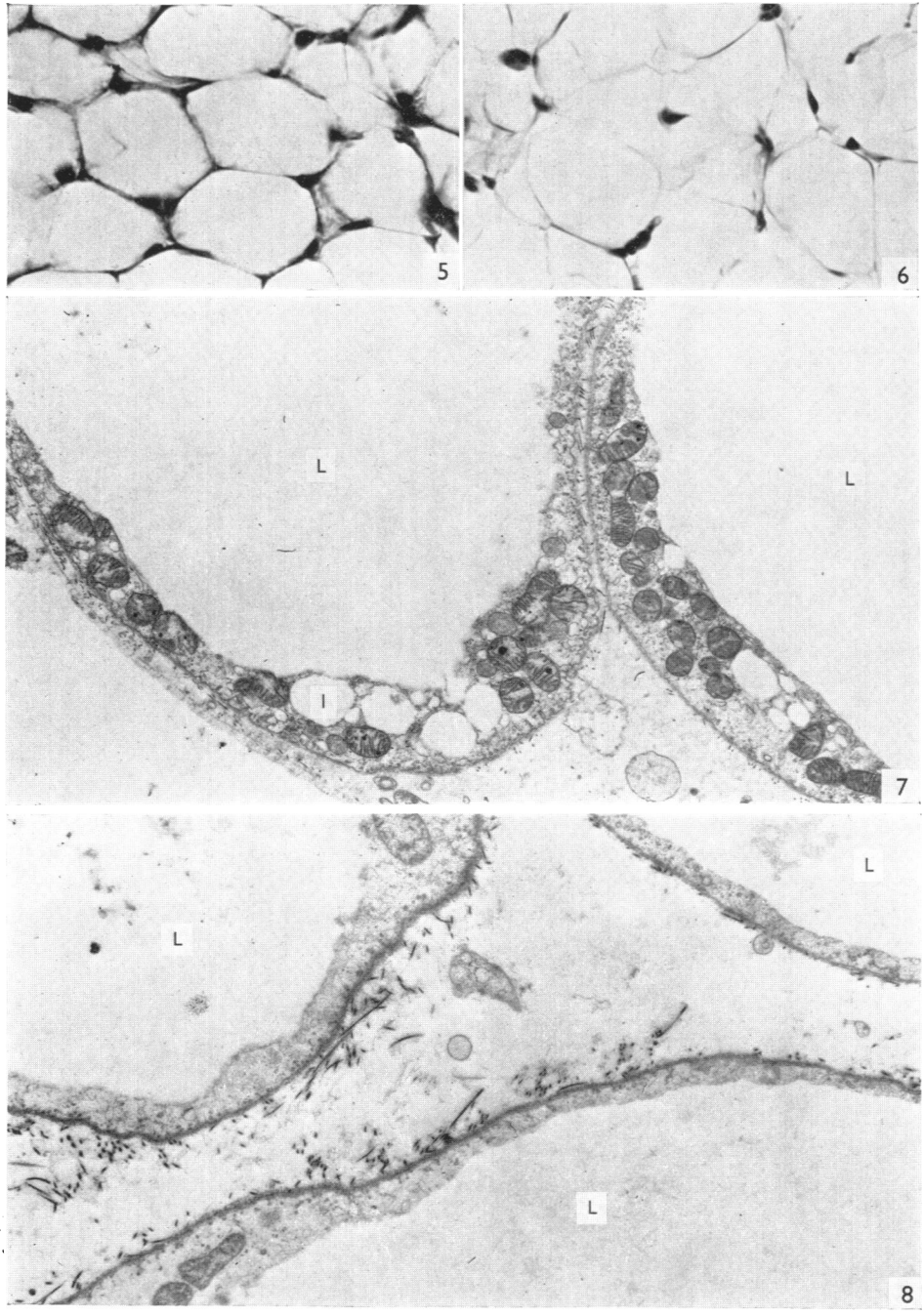

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