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**STUDIES ON THE ECTOPARASITES OF SEALS AND PENGUINS**

**I. THE ECOLOGY OF THE LOUSE *LEPIDOPHTHIRUS MACRORHINI* ENDERLEIN ON THE  
SOUTHERN ELEPHANT SEAL, *MIROUNGA LEONINA* (L.)**

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*Summary*

Although the southern elephant seals, *Mirounga leonina*, that breed on Macquarie I., come ashore for only 3-5 weeks twice a year, the hind flippers of most of them are infested with the blood-sucking louse *Lepidophthirus macrorhini*.

*L. macrorhini* does not oviposit, and eggs do not hatch, in water. Reproduction occurs when the elephant seal is ashore on the beach or in the adjacent tussock. The life cycle can be completed in c. 3 weeks and, because 6-9 eggs are laid daily, multiplication can be rapid. Temperatures greater than 25°C are required for rapid multiplication, and these temperatures occur more frequently on the hind flippers than elsewhere on the body. The number of *L. macrorhini* on a hind flipper however rarely exceeds 100. The principal causes of mortality of the lice are failure to survive the seal's prolonged stay at sea, the moult of the seal, and transmission to unfavourable sites on the seal.

When an elephant seal goes to sea its skin temperature falls to nearly that of the sea. The reduction in the metabolic rate of the louse at low temperatures results in the amount of oxygen obtained from the sea by cutaneous respiration being sufficient for survival. The lice do not enter into a state of complete suspended animation, and a blood meal is required at least once a week to enable sufficient to survive to repopulate the seal.

The skin temperature of a seal at sea rises more frequently on the flippers than elsewhere on the body because of the increased rate of blood flow to the flippers after diving and whenever it is necessary to dissipate heat. Consequently, there are more opportunities for the lice on the hind flippers to feed.

*L. macrorhini* burrows into the stratum corneum, thus reducing losses to the population when the elephant seal annually sheds the outer layers of the stratum corneum attached to the hair, because only the roof of the burrow is lost. Lice do not reproduce on the older seals that moult in muddy wallows, and consequently fewer lice are found on these animals.

Pups are infested within a few days of birth, and the gregarious habits of the elephant seal spread infestations through the seal population. Lice transfer to all parts of the bodies of seals but it is the multiplication of those on the flippers that maintains the louse population.

The abundance of *L. macrorhini* is determined largely by the frequency and duration of opportunities to reproduce when the elephant seal is ashore, and to feed when the elephant seal is at sea.

**I. INTRODUCTION**

The mammals which spend much of their life in water may be divided into those whose hair coat traps an air-blanket around the body, and those whose hair coat becomes wet as water permeates through the pelage to the skin surface. Thus,

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on mammals of the first type such as the water-vole, *Arvicola terrestris*, the lice, like those of penguins (Murray 1964), still live in air even when their host is leading an aquatic existence. Many species of seals, however, conform to the second type of aquatic mammal described, and the lice are exposed to a fully aquatic existence when the seal is at sea.

*Lepidophthirus macrorhini* Enderlein is a blood-sucking louse of the family Echinophthiriidae of the order Anoplura, a family which is only found upon marine carnivores of the Suborder Pinnepidia. It is the sole member of the genus, and is most distinctive as its body is thickly beset with scales and flattened setae of various sizes, and there is a poorly marked constriction between the thorax and abdomen (Plate 2, Fig. 3).

*L. macrorhini* infests the southern elephant seal, *Mirounga leonina* (L.), on which it survives prolonged immersion in the sea, and preliminary investigations suggested that the louse may enter into a state of suspended animation during these periods (Murray 1957, 1964). Furthermore, it appeared that lice only bred when the elephant seal was ashore, and they had to multiply sufficiently during this short period to ensure the survival of the species. The ease with which lice were found on the southern elephant seal on Macquarie I., 54° 30' S., 159° E., (Murray 1957) clearly demonstrated that *L. macrorhini* had successfully adapted itself to this environment.

This paper reports the results of the first of a series of studies on the ectoparasites of seals and penguins, the field work of which has constituted part of the biological programme of the Australian National Antarctic Research Expeditions.

## II. METHODS

Many hundreds of elephant seals may be ashore at Macquarie I. (Plate 1, Fig. 1). They do not move away when approached quietly, and it is possible without methods of restraint to observe the degree and incidence of infestation with *L. macrorhini*, the influence of moulting on louse populations, and to record the skin temperature of the seals (Plate 1, Fig. 2).

The methods of restraint used when necessary varied with the age of the animal. Pups\* were restrained manually or given 20g of choral hydrate orally in a gelatine capsule as a sedative. The capsule was placed well to the back of the throat with a modified veterinary balling gun to ensure that it was swallowed immediately. Older animals were immobilized with succinylcholine chloride as described by Ling and Nicholls (1963).

Seals to be studied in the laboratory were tied in a cargo net after immobilization, lifted with a hoist, and transported with a tractor. In the laboratory the seal was strapped to a table (Plate 1, Fig. 3) which facilitated the examination of the hind flippers (Plate 2, Fig. 1). To prevent transference of lice during experiments, each flipper was placed in a hessian bag. The temperature of water around a flipper was controlled by placing the flipper in a plastic bag through which water at a selected temperature flowed (Plate 2, Fig. 2). Feeding of the seal was not necessary as they fast for the whole period they are ashore.

\* A pup is a seal of up to c. 3 months old which has not left land for its first prolonged period at sea.

Temperatures were measured with probe thermistors, using recording ammeters when continuous records were required. The skin temperature of elephant seals on land was measured whilst they were resting or asleep on the beach. When seals were in water they were restrained by a rope which was placed around the neck and tied to a nearby offshore rock. One person waded into the sea beside the seal to place the thermistor on the skin of the seal while another remained ashore to adjust and to read the bridge.\* In the laboratory the thermistor was attached to the flipper within the hessian or plastic bag.

Hind flippers were usually removed from a seal carcass to count the number of lice, and were examined in the laboratory with a stereoscopic microscope. When handling living lice special care was necessary to avoid rupturing the cuticle.

Lice could be kept at 0–5°C for many days, and this enabled some experiments to be performed at the McMaster Laboratory up to 6 weeks after the lice had been collected at Macquarie I.

Lice were examined with transmitted light under a stereoscopic microscope to observe the disposition of air bubbles on their setae and the movements of the spiracular atria. The oxygen consumption of lice at different temperatures was measured with a Warburg apparatus. Skin for histological examination was fixed in 5% formol saline, embedded in paraffin, sectioned in the usual manner, and stained with haematoxylin, eosin, and picric acid.

### III. NATURAL HISTORY OF THE SOUTHERN ELEPHANT SEAL ON MACQUARIE I.

Macquarie I. (54° 30'S., 159° E.) lies isolated in the Southern Ocean, and is the southernmost of a group of subantarctic islands to the south of New Zealand. The climate is wet, windy, and cold, and throughout the whole year the temperature is usually between 0 and 8°C. The coastline is rocky but there are many beaches, particularly on the eastern shores. Adjacent to the beaches and on the slopes, which rise 800–1000 ft to the plateau, is the tussock, a rich growth of tussock grass, *Poa foliosa*, up to 4 ft high (Plate 1, Figs. 1 and 2). Erosion and seal traffic between the clumps of tussock grass create large muddy pools where seals wallow.

The elephant seal of Macquarie I. has been studied since 1949, and a detailed account of methods of aging the seal, its annual cycle, breeding and development, and its population dynamics has been given by Carrick, Csordas, and Ingham (1962), Carrick *et al.* (1962), Carrick and Ingham (1962*a*, 1962*b*, 1962*c*). The seals come ashore twice a year; mature† seals haul out to moult or to breed, and immature‡

\* This technique had been tested previously on 10 persons who placed their hand and arm into a bath of water at 0°C. The temperatures of the skin were taken with the same thermistors which were immersed with much of their flex in the water throughout the experiment. The temperatures of the skin were consistently many degrees centigrade higher than that of the surrounding water demonstrating that it was the approximate temperature of the skin and not that of the water which was being recorded.

† A seal is mature when it commences to come ashore at the breeding season.

‡ A seal is immature until it commences to come ashore at the breeding season.

seals to moult or to "rest". The times of the year when seals come ashore vary with their age and degree of maturity. The following is an abstract from the publication describing in detail the annual cycle (Carrick *et al.* 1962).

(a) *Breeding*

From the first week in August, bulls come ashore in increasing numbers, the older breeding bulls taking up station on the more open and favoured breeding beaches and the younger "bachelors" occupying less attractive beaches or lying in the adjacent tussock. Breeding cows begin to come ashore in the last week of August and gather in harems which are appropriated by the beachmasters. Each cow is ashore for about 5 days before pupping and for about 23 days afterwards until the pups are weaned. After copulation in the harems, about the time of weaning, bulls and cows return to sea in late October and November.

(b) *Pups*

The pups are about 3 weeks old when weaned. They move first to the adjacent tussock and less crowded beaches, and then disperse over the whole area as the breeding adults depart (Plate 1, Fig. 1). After fasting for 5–6 weeks during which they learn to swim, the pups begin to leave the island in December and by mid January none remains.

(c) *Moulting*

Immature seals of both sexes come ashore for 3–4 weeks during November to January in order to moult. Breeding cows moult in January and February, and the bulls that are present during the breeding season from January to April.

The younger immature seals and the breeding bulls moult on the beach. Older immature males may remain on the beach in groups (Plate 4, Fig. 3), enter the tussock or use wallows. Adult cows tend to segregate from bulls and lie in wallows (Plate 4, Fig. 2) or the tussock (Plate 1, Fig. 2).

(d) *Autumn and Winter Haul-out*

Between mid-February and September some immature seals and occasional pregnant cows come ashore and lie on the beach or in the tussock for some days or weeks "resting". The significance of this haul-out is obscure. Adult bulls do not come ashore in the winter.

(e) *Annual Cycle*

During their first autumn and winter, elephant seals of both sexes come ashore irregularly between mid-February and late September. They lie singly on the beaches and do not congregate like older seals.

Second year seals stay at sea during the breeding season and come ashore to moult during November and December until about mid-January. They haul out again in autumn and winter mainly in April and May, and tend to huddle together either on the beaches or in the tussock.

The behaviour of the third year seals resembles that of the 2-year-old seals except that the main winter haul-out is in early May.

Fourth year cows moult during November–January whether mated or not. Males follow their previous pattern with the main winter haul-out in late May, and more prolong the moult into January.

Fifty year primiparous females come ashore to pup in September and their moult is postponed to January and February. Other cows moult with the immature seals in December and January but many move into wallows to moult. Males continue to haul out in late May, and moult from November–January.

Most 6-year-old cows are mature. Males keep to the immature pattern with a reduction in the winter haul-out, and there is an increased use of wallows for moulting.

All 7-year-old cows are mature. Some bulls appear during the breeding season, and for the first time their moult is postponed until February.

#### (f) *Other Activities*

Seals may be completely inactive for long periods when ashore and are often asleep (Plate 1, Figs. 1 and 2). Much time is spent scratching themselves, and all parts of the body except the middle of the back can be reached with ease. The dexterity of the digits is remarkable, and one hind flipper can be scratched thoroughly by the other (Plate 3, Fig. 4). Apart from first-year seals, which lie singly on the beach, there is a pronounced gregariousness both in wallows and on open beaches (Plate 4, Fig. 3). Seals may be seen at sea around the shores floating with the body partially submerged, and only the head and hind flippers breaking the surface (Plate 4, Fig. 4).

### IV. HABITAT OF *L. MACRORHINI*

#### (a) *General*

The habitat of *L. macrorhini* is the skin and pelage of the elephant seal. The epidermis of the skin, particularly the stratum corneum, is thick (Plate 3, Fig. 1), and hair covers most of the body but is sparse on the webs of the hind flippers. The hair fibres are only a few millimetres in length, they are flattened and lie parallel to one another and closely adpressed to the skin (Plate 3, Fig. 2). Consequently, the depth of the pelage is usually only 1–2 mm.

There was no evidence of an air-blanket or air bubbles being maintained in the pelage of pups or older seals whilst they were in the sea. This was confirmed by anaesthetizing three pups, immersing the hind flippers and posterior part of the body in water, and examining the pelage under a stereoscopic microscope. An occasional bubble, however, was seen in the burrow made by *L. macrorhini* in the stratum corneum (see Section VI(b)). The pelage became wet when a seal was in a mud wallow.

#### (b) *Skin Temperature of M. leonina*

##### (i) *On Land*

The temperature of the skin of three pups, one 2–3-year-old and two 4–7-year-old male seals were measured at several sites over the body and flippers whilst they

were asleep. The atmospheric temperature was 8°C, and the sun was shining. The skin temperature of their bodies ranged from 30–33°C whereas that of their flippers ranged from 24–34°C. The rectal temperatures of two of the pups were 33·5 and 36°C, and that of one of the older bulls 35°C.

It was frequently observed that under cooler atmospheric conditions the skin over the body of an elephant seal was cool, whereas that of the flippers was warm. For example, when the atmospheric temperature was 1·8°C and snow was on the ground, the skin temperature of the back of a seal was 1–6°C, whereas that between the digits of the closed hind flippers was 29–32°C.

(ii) *In the Sea*

The skin temperatures of two pups, which were 3–4 months old and had commenced to swim, were c.30°C whilst they were asleep on the beach. They were lassoed, driven into the sea (the temperature of which was 8°C), and the skin temperatures were retaken within 5 min. The skin temperatures had dropped to 10–12°C on the body, 9–14°C on the hind flippers and 8–15°C on the fore flippers, and remained within these ranges during the 15 min the seals were restrained in the sea.

(iii) *In Mud Wallows*

The temperature of the muddy water of five wallows was taken on a day when the atmospheric temperature was 7·3°C. The mean temperatures ranged from 13·8 to 18·5°C, and the skin temperatures of the bodies of three seals within these wallows ranged from 19·2 to 28°C.

(c) *Moult of M. leonina*

The following description is abstracted from the publication of Carrick *et al.* (1962).

Elephant seal pups are normally born with a coat of long black curly hair covering the short straight first-year coat. This natal coat is usually shed at 2–3 weeks, the black hairs falling out in patches all over the body to reveal the silky grey coat beneath.

The annual moult is a dramatic process in that large patches of the outer layers of the stratum corneum are shed together with the hair (Plate 4, Fig. 1). It commences around the nose and eyes and at the base of the flippers where the outer layer of the skin splits and begins to curl. The process gradually spreads over the head, neck, shoulders, and flippers, and finally over the body. The seals hasten the process by scratching.

The moult haul-out may be divided into three phases, a premoult period of up to 13 days, a coat-shedding period of 9–26 days, and a postmoult period of up to 11 days for second- and third-year cows, up to 18 days for mature cows, up to 12 days for bulls under 5 years old, and up to 28 days for bulls 5–8 years old. Mature male seals may return to the sea for short periods during the moult but all other seals remain ashore during the whole period.

V. STAGES OF THE LIFE CYCLE OF *L. MACRORHINI*

The stages of the life cycle are the egg, three nymphal instars, and the adult male and female.

The eggs are 0.85 mm long and 0.4 mm wide, pale fawn in colour when newly laid, darkening as the embryo develops, and the posterior third of the egg is well cemented to the hair with the end of attachment near the skin.

The nymphal stages are less extensively covered with flattened setae and scales than adults, and the three stages may be distinguished by their size. Stage I nymphs are *c.* 1 mm long and *c.* 0.6 mm wide, stage II nymphs are *c.* 1.6 mm long and *c.* 0.9 mm wide, and stage III nymphs are *c.* 2.3 mm long and *c.* 1.2 mm wide.

Females are larger than males being on the average 3.1 mm long and 1.9 mm wide compared with 2.8 mm long and 1.6 mm wide.

The cuticle of each instar becomes progressively more invaginated at the union of thoracic and abdominal segments.

VI. DISTRIBUTION AND NUMBER OF *L. MACRORHINI* ON THE ELEPHANT SEAL*(a) Distribution on the Body*

The distribution of nymphal and adult lice on 21 infested seals of various ages was determined. Lice were found on the hind flippers of all, but on the body and fore flippers of only six. The principal site of infestation was the hind flippers where lice were readily found on most of 200–300 seals examined. On the hind flippers lice were present on the digits, on the webs between the digits, and frequently along the posterior margins of the flippers (Plate 2, Fig. 1).

Eggs were found on the internal lateral aspects of the digits of the hind flipper, but not on the web between the digits.

*(b) Distribution on the Skin*

Eggs, each attached to a single hair, were found in clusters of 3–15. Stage I nymphs were found mostly in the vicinity of hatched eggs, and stage II nymphs were also in groups.

Each nymph and adult was usually located within a burrow in the thick stratum corneum of the skin with only the posterior tip of the abdomen visible (Plate 3, Figs. 1–3). Erect and disturbed hair over a burrow usually indicated the presence of an adult (Plate 3, Fig. 2). Adults were also seen moving actively over the skin surface.

*(c) Number of Lice*

The number of lice found on four elephant seals whose whole bodies were infested was 88, 32, 40, and 25, and of these 41, 16, 22, and 20, respectively, were found on the hind flipper, thus further demonstrating that the hind flipper was the predilection site of *L. macrorhini*.

The number of each instar present on the hind flippers of seals of various ages was determined. Table 1 shows that only adults and eggs were found on three pups which were 1–2 weeks of age. Pups of 2–3 months of age, *i.e.* just before they would

TABLE 1  
STRUCTURE OF POPULATIONS OF *L. MACRORHINI* ON THE HIND FLIPPERS OF ELEPHANT  
SEALS OF VARIOUS AGES AT DIFFERENT TIMES OF THE YEAR

+ Indicates that a few lice were present; ++ indicates that many lice were present

Number of Seals Examined	Number of Lice					
	Eggs	Nymph II	Nymph III	Male	Female	Total
<i>Pups: 1-2 weeks; September, October</i>						
1	+			1	4	5
2	+			2	6	8
3				+	+	5
<i>Pups: 2-3 months; December, January — just before leaving for sea</i>						
1			23	13	20	56
2			33	14	17	64
3			18	9	10	37
4		3	43	0	1	47
5		4	53	3	8	68
6			28	12	25	65
7			1	12	12	25
8		4	7	10	19	40
9			10	3	5	18
10	+	11		13	12	36
11			21	28	25	74
<i>Immature Seals: 6 months to 2½ yr; May, July — winter haul-out</i>						
1 (6 months)	+	116		6	28	150
2 (6 months)				3	3	6
3 (6 months)			19	0	8	27
4 (6 months)	+	+	+	+	+	10
5 (1½ yr)		++		+	+	25
6	+	++		+	+	33
7	+			+	+	33*
8	+	+	+	+	+	41
9	+		7	4	5	16
10	+		5	3	14	22
11			3	4	8	15
<i>Immature Seal: 1-2½ yr; December, January</i>						
1				10	21	34
<i>Female: on arrival to breed after several months at sea</i>						
1				9	25	34†
<i>Female: at end of breeding in harems after 4 weeks ashore</i>						
1	+	5	6	0	1	12*
2		3	1	2	2	8
3				1	1	2
4	+		1	3	3	7
5				1	3	4

\* Stage I nymphs present; † Seven dead lice (five ♂, two ♀) were also found.



normally go to sea for a prolonged period, were infested with adults and many nymphs, particularly stage III nymphs, but few eggs were present. The average size of a population was 48. All instars and many egg clusters were found on immature seals (6 months–2½ yr) which were ashore during the autumn and winter, and an average of 43 lice were present. An adult female was examined just after she had come ashore to breed, after spending possibly 6–7 months at sea, and only adult lice, some of which were dead, were found whereas adults, nymphs, and eggs were found on females which had been ashore for 4 weeks in harems and had completed breeding. Fewer lice were found on the breeding females, older immature males and mature males than on the younger immature animals, but occasionally a heavily infested older animal was found. For example, a non-breeding male *c.* 8 yr old, which hauled out of the sea in the winter (June), had more than 80 lice, mostly adults, on its hind flippers.

#### (d) *Percentage of Elephant Seals Infested*

Louse infestations were found on immature and mature seals of all ages and of both sexes, and extensive observations made during 1962–63 indicated that the majority of the elephant seals on Macquarie I. were infested. An examination of 50 pups in December 1957 showed 86% to be infested within 4 months of birth.

### VII. EXPERIMENTAL

#### (a) *Activity of L. macrorhini at Various Temperatures*

In air at *c.* 100% R.H. lice were inactive at 0–5°C, sluggish movements of the antennae and legs were seen at 5–10°C, and lice were very active and able to travel several centimetres in a few minutes at 20–30°C.

Lice submerged in water at 20–30°C were much less active than those in air.

#### (b) *Time Required by L. macrorhini to Feed*

It was observed repeatedly that *L. macrorhini*, which had been removed and kept for a few days at a low temperature, became mobile within 1 min and prepared to feed shortly after being placed on the warm flipper of another seal. Nymphs and adults usually burrowed into the stratum corneum to feed, although adults often fed without burrowing where the thick stratum corneum was thinner as on the web. However, the dark setae covering the cuticle made it difficult to see the blood within the living louse, and the behaviour of the louse gave no clue as to when feeding was completed.

A starved adult female weighing 3.6 mg was placed on a hind flipper of a seal, the skin temperature of which was 30°C. After 10 min the louse was firmly attached but did not appear to have inserted its mouth parts. However, it was sucking blood after 20 min and voiding blood-stained faeces. After a further 10 min the louse was removed and weighed again, and its weight had increased by 0.8 mg, *i.e.* 22%. A typical engorged female louse removed from a seal weighed 4.6 mg. Another starved louse which weighed 2.5 mg increased its weight by 16% within 5 min of being placed on the seal.

(c) *Rate of Reproduction of L. macrorhini on an Elephant Seal on Land*(i) *Oviposition Rate*

The abdomens of 20 female lice were dissected, and the number of maturing ova, which were visible at  $\times 25$  magnification, determined. The mean number was 8.2 ova per louse (S.D.  $\pm 3.2$ ; range 5–20) of which 2.9 (S.D.  $\pm 1.6$ ; range 0–6) were well matured.

Six female lice were collected from seals and kept at 6°C for 3 days before being placed on the louse-free hind flipper of a restrained seal. The skin temperature of

TABLE 2

DAILY NUMBER OF EGGS LAID BY FEMALE *L. MACRORHINI* ON THE HIND FLIPPER OF AN ELEPHANT SEAL THE SKIN TEMPERATURE OF WHICH WAS MAINTAINED AT 25–35°C\*

Number of Days	Louse 1	Louse 2	Louse 3		Louse 4	Louse 5			Louse 6		
			a†	b†		a	b	c†	a	b	c
0	0	0	0		0	0			0		
$\frac{1}{2}$	3	13	13	5	0	5			3		
$1\frac{1}{2}$	1	5		2	0	5			8		
$2\frac{1}{2}$	Dead	Lost		1	1	8			5	6	
$3\frac{1}{2}$				6	5	4	5			12	
$4\frac{1}{2}$				4	9		0				7
$5\frac{1}{2}$				Lost	11		3				6
$6\frac{1}{2}$					Lost		10	3			6
$7\frac{1}{2}$								7			6
$8\frac{1}{2}$								7			1
$9\frac{1}{2}$								0			22
Total number of eggs in each cluster	4	18	13	18	26	22	18	17	16	18	48
Total number of eggs laid	4	18	31		26	57			82		
Mean daily number of eggs laid	2.6	12	6.9		6.5	6.7			8.6		

\* The lice had been removed from seals and kept at 6°C for 3 days prior to the commencement of the experiment.

† a, b, c, represent different clusters of eggs.

the flipper was maintained at 25–35°C. The lice were placed 5–10 cm apart to facilitate the daily determination of the number and distribution of the eggs laid. Table 2 shows that five females commenced to lay eggs within 12 hr. The number of eggs laid daily varied from 0 to 22, and the daily average production of the lice which were observed for more than  $2\frac{1}{2}$  days ranged from 6.5 to 8.6 eggs.

(ii) *Length of Life Cycle*

The eggs laid in the above experiment were left on the flipper, and over 90% had hatched within 5–10 days. The stage I nymphs burrowed immediately into the stratum corneum of the skin so that only the posterior tip of the abdomen was visible.

After the 11th day it was not possible to maintain the skin temperature of the flipper between 25–35°C, and it dropped to 7–15°C. Many stage II and III nymphs, but no adults, were found on the 18th day, and an accident terminated the experiment on the 19th day.

Stage II and III nymphs were collected from seals over a period of 5 days, and kept at 6°C. A total of 70 nymphs was collected, and they were placed on a louse-free hind flipper of a seal restrained in the laboratory. The skin temperature of the flipper was maintained at 25–35°C. When the flipper was examined 3½ days later the lice found were mainly adults, and eggs were present after 4½ days. A few nymphs were still present after 5½ days, but by the sixth day all of the surviving 20 lice were adults. Some 350 eggs were found on the flipper.

Thus, the life cycle of *L. macrorhini* could be completed in *c.* 3 weeks on a flipper the skin temperature of which is 25–35°C.

(d) *Rate of Reproduction of L. macrorhini on an Elephant Seal in Water*

A seal was restrained in the laboratory and one of the hind flippers placed in a plastic bag. Seven female lice, four male, and one stage III nymph were placed on the flipper which was kept dry for 1½ days. During this period the skin temperature of the flipper was 25–30°C. All the lice were still alive after 1½ days, and 46 eggs had been laid. Seawater at 4–7°C was then circulated around the flipper for 3 weeks, and the skin temperature of the flipper dropped to 6°C, at which it was maintained for most of the time. No more eggs were laid, and of those already laid 29 died and 17 were lost. Six female lice, one male, and the stage III nymph were still alive after 3 weeks. During the last 24 hr of the experiment, when the flipper was again kept warm and dry, the females resumed laying eggs.

Ten female lice, three male, and one stage III nymph were placed on the other hind flipper as a control for the above experiment. During the first 1½ days, when the skin temperature of the flipper was 25–30°C, 26 eggs were laid. During the next 3 weeks the flipper was intermittently cool or warm depending upon contact with the other flipper around which cold seawater was being circulated. The flipper was re-examined after 3 weeks, but only 1 dead and 2 living female lice, and 2 dead males were found. However, an additional 42 eggs had been laid of which 15 had hatched.

In other experiments (Section VII (e) (iii)) where lice were placed on hind flippers immersed in water at *c.* 15, 20, or 25°C the lice did not oviposit. An additional 150 eggs, collected from other seals, died when submerged in seawater and kept at 6°C.

(e) *Survival of L. macrorhini in Water*

(i) *Mode of Respiration*

The spiracles are used when the louse is in air. Lice were immersed in seawater, and examined under a stereoscopic microscope. A plastron was not visible between the setae or scales and the cuticle. Small bubbles of air were occasionally attached to any of the setae on the body, and these were easily removed by gently stroking the setae with a dissecting needle. Air bubbles were not regularly attached to the setae

surrounding a spiracle so they were not in direct communication with the tracheal system except when occasionally trapped around a louse within its burrow. When the spiracular opening was surrounded by an air bubble, regular contractions of the spiracular atrium commenced, and ceased within a few hours after the bubble was removed. After the bubble was removed the atrium admitted no water but occasionally expelled a bubble. No other structures which might have a respiratory function were detected on the lice.

When immersed in fresh seawater at 5–10°C, completely wetted and with no bubbles of air attached to their setae, lice remained alive for several weeks. Thus, it was concluded that oxygen was obtained from seawater by diffusion through the cuticle.

(ii) *Oxygen Consumption at Low and High Temperatures*

The oxygen consumption of four groups of nymphs or adult lice was measured with a Warburg apparatus. Two groups were exposed to 33°C for 30 min, then to

TABLE 3  
AMOUNT OF OXYGEN\* CONSUMED BY *L. MACRORHINI* WHEN EXPOSED  
ALTERNATELY FOR ½ HR TO 10–12°C AND 33°C

Number of Lice	Temperature			
	10–12°C	33°C	10–12°C	33°C
1 adult (♀)	2.0	11.2	0.7	—
3 stage III nymphs	4.0	14.3	1.3	—
3 stage III nymphs	—	14.1	0.7	10.4
3 stage III nymphs	—	16.5	4.6	14.6

\* In microlitres.

10–12°C for 30 min and finally returned to 33°C for 30 min. The remaining two groups were exposed to 10–12°C for 30 min, then to 33°C for 30 min and finally returned to 10–12°C for 30 min. Table 3 shows that considerably less oxygen was consumed at 10–12°C than at 33°C.

(iii) *Survival at Different Temperatures*

A group of 88 lice, predominantly adults, was placed in moist air at 5–10°C. Another group of 72 lice was submerged in seawater, and also exposed to 5–10°C after all the visible bubbles of air were removed from them and the water. Groups of lice were removed at fortnightly intervals to determine the survival rate over the subsequent 8 weeks, and Figure 1 shows that there was little difference between the two groups. About 70% of the lice survived 2 weeks, less than 50% of the lice survived 4 weeks, and a few lice survived longer than 6 weeks in moist air. The similar mortality rate in both groups indicated that death of the lice submerged in water was not due to lack of oxygen. As both groups were unable to feed, the cause of death was probably starvation.

Seals were restrained in the laboratory, and water at 15°C, 20°C, or 25°C was circulated around one hind flipper of each seal. The temperature next to the skin of the flippers was maintained within  $\pm 5$  degC of that required throughout the experiments. Groups of adults and stage III nymphs were placed on the flippers, and 65 lice were exposed to 15°C, 33–20°C, and 44–25°C. The intervals at which samples were removed were determined by observation of the mortality rate at each temperature. In addition on each seal 13 lice were placed on the other hind flipper which was kept dry to act as a control.

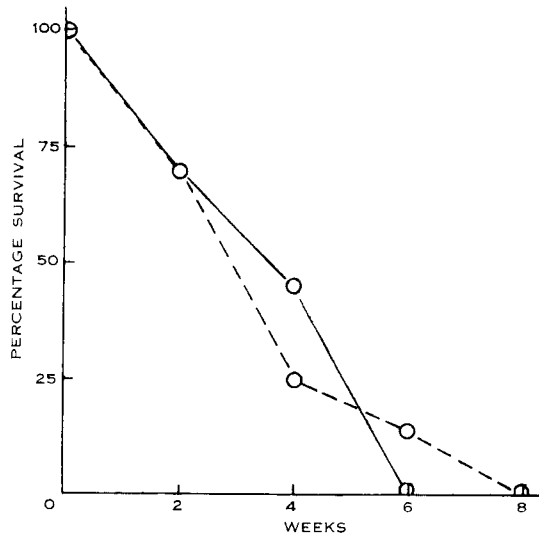


Fig. 1.—Percentage survival of *L. macrorhini* when exposed to 5–10°C in moist air or seawater. (— — —) Moist air; (———) seawater.

The lice on the flippers in seawater were retrieved at the site where they had been placed, and those which were alive were plump and their stomachs contained blood. Survival, however, decreased as temperature increased (Fig. 2). No eggs were laid at any of the temperatures. Only the control lice on the seal whose immersed flipper was kept at 15°C were recovered, and all had survived. The other control lice were not recovered but many lice have survived 1–2 weeks on dry flippers at 25–35°C in other experiments (see Section VII (c)).

As lice were able to feed, the results suggest that at the higher temperatures death of the lice submerged in water was due to their inability to obtain sufficient oxygen rather than to starvation.

(f) *Influence of the Moulting of the Elephant Seal on Numbers of L. macrorhini*

Patches of moulting hair and stratum corneum were removed from over 30 moulting seals as they lay asleep on the beaches. An occasional louse was found attached to the moulted skin, but most of them remained on the seal as only the roof of their burrow had been removed.

(g) *Transmission*

The transmission of infestations was studied in a small isolated harem consisting of one bull and three cows. Each cow gave birth to a pup, the hind flippers of which were examined subsequently to determine the stage of the life cycle which was transferred. Five adults were seen on one pup when it was 4 days old. At the first examination of another pup when it was 7 days old, eggs were present and three males and six females were found 10 days later. One adult was found on the third pup when 7 days old, five when 12 days old, and four when 17 days old. An additional five adults and one stage III nymph were found on the bodies of these pups. Thus, it was mainly adult lice which transferred from the cows to their pups.

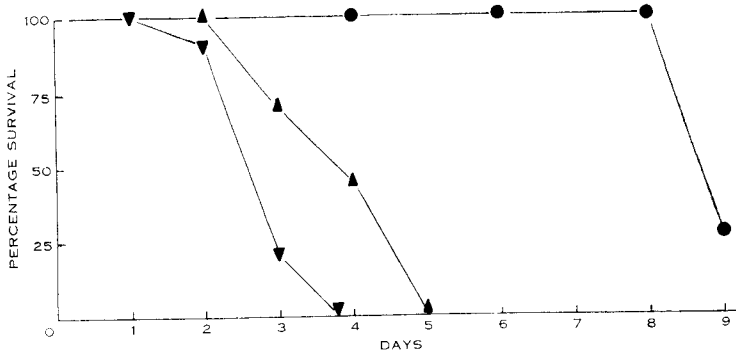


Fig. 2.—Percentage survival of *L. macrorhini* on the hind flipper of an elephant seal in water at various temperatures. ● 15°C; ▲ 20°C; ▼ 25°C.

## VIII. DISCUSSION

The southern elephant seals of Macquarie I. come ashore only twice a year, yet the majority of them are infested with lice. The younger seals are the more heavily infested, and the predilection site of *L. macrorhini* is the hind flipper. To understand the population dynamics of *L. macrorhini* it was necessary initially to determine the factors responsible for its occurrence in greatest densities on the hind flippers.

*L. macrorhini* did not oviposit when placed on hind flippers surrounded by water at temperatures which ranged from 4–25°C, and eggs submerged in water at 6°C failed to hatch. The lice reproduced only in air, and only rapidly when the skin temperatures of the flippers exceeded 25°C. Thus, any increase in the numbers of *L. macrorhini* takes place when the elephant seal is ashore on the beach or in the tussock, and not when it is at sea or submerged in a muddy wallow.

The skin temperature of the elephant seals was influenced greatly by the environmental temperature, and approximated it when they were in the sea or when the atmospheric temperatures were cold. The skin temperatures of the flippers were the most variable and frequently, they were warm (> 25°C) when those of the body were cold. These observations, together with the evidence that the insulating capacity of the blubber is probably adequate to maintain the body temperature of the seal at 36°C when it is at rest in an environmental temperature of 0°C (Bryden 1964), indicate that the physiology of thermoregulation of the southern elephant seal is very likely

similar to that of other seals. Irving and Hart (1957) and Hart and Irving (1959) have studied the adaptations to life in a cold environment of the harbour seal, *Phoca vitulina concolor* DeKay, and the harp seal, *Phoca groenlandica* Erxleben. In the cold, the temperature of the skin of the body drops to that of the environment, and temperature gradients become established through the blubber to the body core. The skin temperatures of the flippers are more variable because of their role in heat dissipation. *L. macrorhini* become more abundant and their populations densest on the hind flippers, therefore, because suitable temperatures for rapid multiplication occur more frequently on the hind flippers than on the body.

The life cycle of *L. macrorhini* can be completed in *c.* 3 weeks so at least one generation can be produced on each of the two occasions the seals come ashore. Females lay an average of 6–9 eggs a day, and up to 22 eggs on occasions. Thus, *L. macrorhini* has a great potential rate of multiplication. However, the average number of lice found on the hind flippers of pups was only 48 and of immature seals 34. Even fewer lice were found on the flippers of mature animals. Evidently, there is a considerable mortality. The principal causes of these losses are most likely, the seal's prolonged stay at sea, the moult of the seal, and the transmission of the lice to unfavourable sites on the seal's body. Grooming may play a minor role.

The external morphology of *L. macrorhini* (Plate 2, Fig. 3) is very different from other Anoplura, and it is to be expected that there are features essential for the aquatic existence of the louse. The cuticle of *L. macrorhini* becomes progressively more invaginated between the thoracic and abdominal segments with each stage of development to the adult, thus increasing the surface area, and assisting cutaneous respiration. The stout spines stand erect from the cuticle in the living louse, and, in addition to anchoring the louse within a burrow, probably prevent the burrow from collapsing around the louse when the seal dives. Thus, a bubble of air trapped within the burrow would be maintained and act as a gill, or water would still be retained around the cuticle of the louse and enable gaseous exchange with the sea to take place. The function of the scales may be to protect the delicate cuticle which is required for oxygen absorption, and which is easily ruptured if the louse is handled carelessly.

When lice were exposed to 5–10°C in air, or submerged in water, there was a steady mortality until all were dead after 6–8 weeks. Thus, they did not enter into a state of complete suspended animation. At 5–10°C they were inactive, their metabolic rate was low, and apparently no fatal oxygen debt was incurred by those in water. Death was due to starvation. It will be apparent, therefore, that to survive lice must feed during the period of 4–5 months when the elephant seal is at sea.

As 25% of the lice exposed to 5–10°C died within 2 weeks, it seems that a blood meal is necessary at least once a week if the density of the surviving population is to be adequate to repopulate the seal. *L. macrorhini*, which does not have a large stomach (Plate 3, Fig. 1), was capable of imbibing a blood meal within 4–10 min, and lice fed on warm hind flippers submerged in water in the laboratory. *L. macrorhini*, therefore, could feed during short periods of increased skin temperature while the seal is at sea.

The temperature of the skin of the flippers of a seal at sea is likely to be much more variable than that of the skin of the body. Little blood circulates through a

hind flipper whenever a seal dives but the increased blood flow which occurs immediately the seal surfaces (Scholander 1940), and whenever heat has to be dissipated, will cause a rise in skin temperature which could activate the louse to feed. Thus, more lice survive on the hind flippers than elsewhere on the body because they have more opportunities to feed when the seal is at sea. Elephant seals resting at sea float with their noses and hind flippers protruding (Plate 4, Fig. 4), and this may further assist lice to survive.

*L. macrorhini* burrows into the stratum corneum to feed, and nymphs probably remain within the burrow until they grow into adults. This behaviour enables nymphs and adults to survive the moult which removes only the roof of the burrow, but there must be a loss of the eggs, which are invariably attached to the bases of the hairs. The habitat selected by the seal for the moult influences its effect on louse numbers. No multiplication occurs on seals in liquid muddy wallows (Plate 4, Fig. 2), and as the temperature of wallows tends to be higher than that of the sea, there is probably a mortality of lice due to their inability to obtain sufficient oxygen. Cutaneous respiration is adequate only when the metabolic rate of the louse is low. Thus, with increasing age of the seal the effect of the moult becomes more severe because older seals prefer to moult in mud pools and wallows, whereas the younger seals moult on the beaches and in the tussock. *L. macrorhini*, therefore, has more opportunities to reproduce on the younger seals, which are thus more heavily infested.

Lice are transferred from cows to the bodies and flippers of their pups within a few days of birth. Gregarious seals lie close together in all attitudes (Plate 4, Fig. 3), so transference of lice from flippers to all parts of the body undoubtedly occurs. However, because the skin temperature of the body is influenced greatly by environmental temperature, there are fewer opportunities for rapid reproduction of lice on the body than on the flippers. Furthermore, it is doubtful if any of the lice on the body survive the long stay of a seal at sea. Consequently, the lice on the body of an elephant seal probably contribute little to the maintenance of a population of *L. macrorhini*.

The life history of *L. macrorhini* on the elephant seals on Macquarie I. may be summarized as follows. Adult lice transfer from the cows to any part of the bodies of their pups soon after they are born in the spring. Oviposition occurs, the eggs develop and hatch, and the nymphs develop to adults thus completing the first generation. During this time the pup may moult, and some lice be lost but numbers increase again before it goes to sea. No eggs survive the period at sea, and more of the nymphs and adults survive on the flippers, particularly the hind flippers, than elsewhere because they have more opportunities to feed. Thus, when the seal comes ashore in winter the density of lice is greatest on the hind flippers. Reproduction recommences particularly on the hind flippers, which provide suitable temperatures more frequently, many eggs are laid, and another generation of lice is produced. The seal returns to the sea, to come ashore several months later to moult in December. Eggs are lost with the shed hair and skin but most of the lice remain as only the roofs of their burrows have been removed. This annual cycle of events is repeated, and, as the elephant seals are gregarious, lice are spread throughout the seal population. With increasing age more seals moult in wallows, and lice do not reproduce while



their hosts are in these mud pools. Thus, there may be little or no increase in the number of lice on these seals before they return to the sea. Consequently, there will be fewer lice than usual to survive the period at sea, and even fewer to repopulate the seal when it hauls out on land again. This leads to a decline in the severity and incidence of infestations on older seals.

*L. macrorhini* lives in a habitat which alternates abruptly from terrestrial to aquatic, or from warm to cold. Its biology has evolved to utilize any opportunity to multiply rapidly when the elephant seal is ashore, and to feed when the elephant seal is at sea. The frequency and duration of these opportunities determines both the distribution of the blood sucking louse *L. macrorhini* on the southern elephant seal, *M. leonina*, and the incidence and severity of the infestations.

#### IX. ACKNOWLEDGMENTS

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## EXPLANATIONS OF PLATES 1-4

## PLATE 1

- Fig. 1.—Buckles Bay beach, Macquarie I. looking south. Many hundreds of elephant seals may lie along the beaches and in the adjacent tussock. (A.N.A.R.E. photograph by M. D. Murray.)
- Fig. 2.—Examination of the hind flipper of a female elephant seal. It is frequently possible to examine a hind flipper thoroughly for lice provided it is done quietly and slowly. (A.N.A.R.E. photograph by J. Ling.)
- Fig. 3.—Immature elephant seal on table in biology laboratory of the A.N.A.R.E. station at Macquarie I. The elephant seal fasts for 3-4 weeks when it comes ashore, and thus it is possible to carry out short-term experiments in the laboratory. (A.N.A.R.E. photograph by R. Cooke.)

## PLATE 2

- Fig. 1.—The extended hind flipper of an elephant seal. The digits are well covered with hair which is absent from the webs. A common oviposition site of *L. macrorhini* is indicated with the forceps. (A.N.A.R.E. photograph by R. Cooke.)
- Fig. 2.—Controlling the temperature around a hind flipper. The right hind flipper was placed in a plastic bag through which water at a selected temperature was circulated. The water was allowed to overflow to remove excrement from the bag. A sack has been placed around the flipper to protect the plastic bag. (A.N.A.R.E. photograph by D. G. Nicholls.)
- Fig. 3.—Ventral aspect of male *L. macrorhini*. The abdomen is covered with many stout spines, and the intersegmental regions of the thorax and abdomen are more invaginated than in lice from terrestrial mammals. (Photograph by I. Roper.)

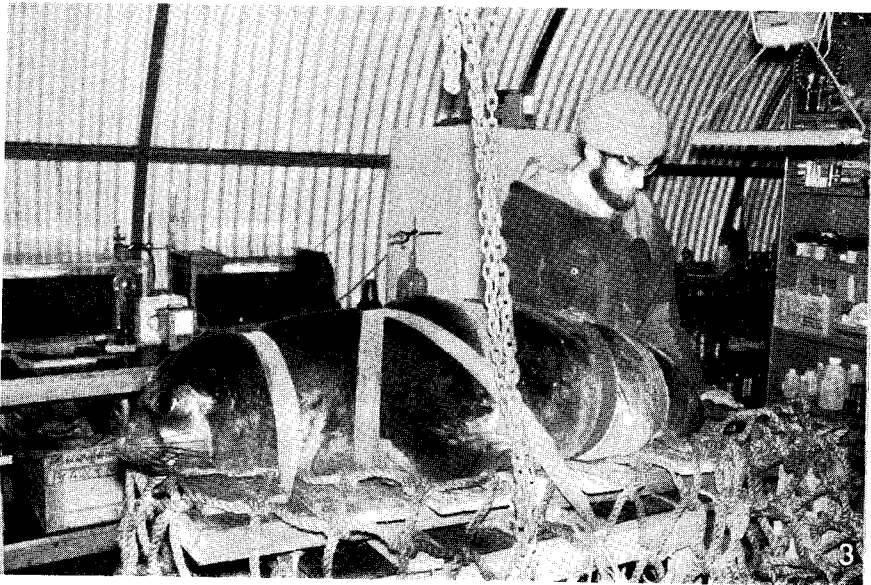
## PLATE 3

- Fig. 1.—Longitudinal section of *L. macrorhini* nymph in burrow in stratum corneum of the skin of an elephant seal. At the moult the stratum corneum and hair are shed attached together, and this removes the roof of the burrow. An inflammatory reaction to the louse is present. The stomach of the louse is not large, and is full of blood undergoing digestion. (Photograph by I. Roper.)
- Fig. 2.—*L. macrorhini* adult on the skin of an elephant seal. The posterior tip of the louse is visible, and the disarranged seal hair indicates a large louse. (Photograph by I. Roper.)
- Fig. 3.—Burrow of *L. macrorhini* in skin of the edge of a hind flipper. An adult louse has been removed to show the extent of a burrow. (Photograph by I. Roper.)
- Fig. 4.—Immature elephant seal, infested with *L. macrorhini*, rubbing one hind flipper with the other probably to alleviate the irritation. (A.N.A.R.E. photograph by D. G. Nicholls.)

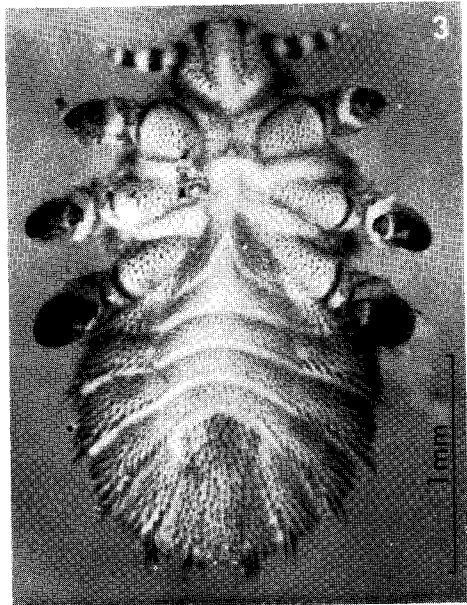
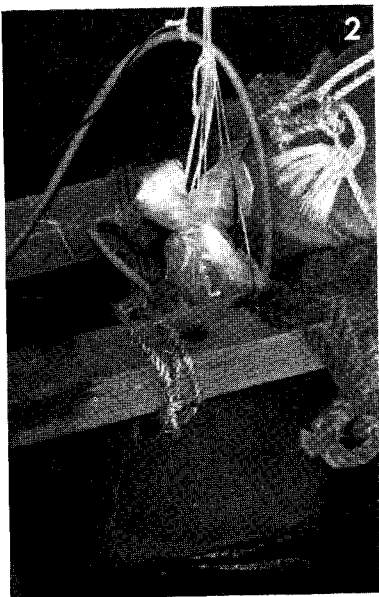
## PLATE 4

- Fig. 1.—Moulting elephant seal. The moult is nearly completed, and patches of stratum corneum and attached hair are being shed. (A.N.A.R.E. photograph by D. G. Nicholls.)
- Fig. 2.—Elephant seals moulting in wallow of liquid mud. (A.N.A.R.E. photograph by W. Vestjens.)
- Fig. 3.—Group of immature male elephant seals in which the hind flipper of one is resting on the back of another. Gregarious southern elephant seals often lie closer together than are those in this group. (A.N.A.R.E. photograph by M. D. Murray.)
- Fig. 4.—Mature male elephant seal resting with only head and hind flippers protruding out of the sea. (A.N.A.R.E. photograph by W. Vestjens.)

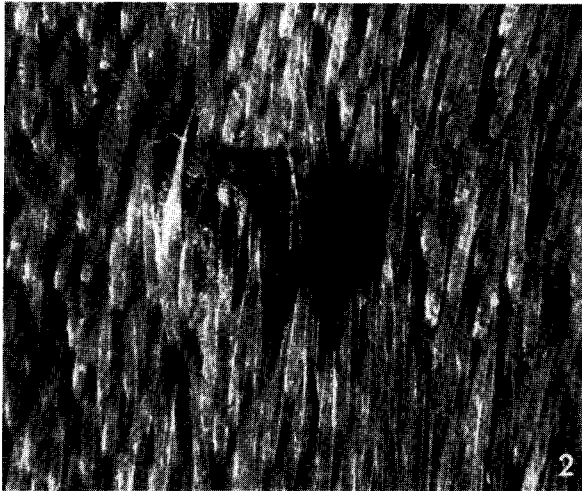
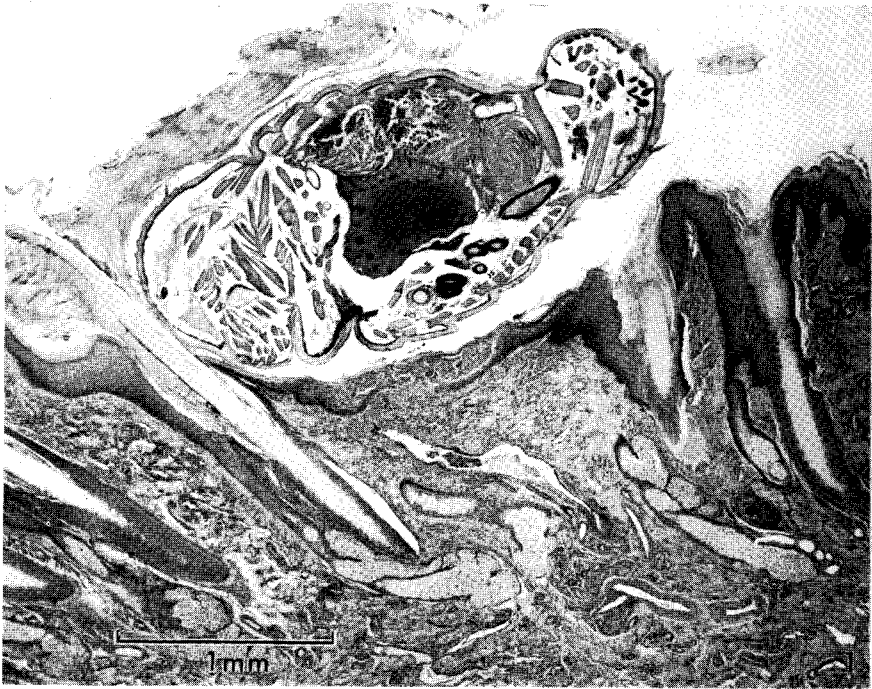
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