Thermal Adjustment and Respiratory Exchange in Monotremes and Marsupials. A Study in the Development of Homaeothermism

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PHILOSOPHICAL TRANSACTIONS.

I. *Thermal Adjustment and Respiratory Exchange in Monotremes and Marsupials.—A Study in the Development of Homœothermism.*

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Some isolated observations have been made from time to time upon the temperatures of the Monotremes.[*] More recently Sutherland[†] has published an important series of observations upon the temperatures of Echidna and several Marsupials, and upon the variation in their body-temperature with changes in that of the air. These observations of Sutherland have been referred to in some detail by Vernon,[‡] in whose paper, and in Pembrey's chapter "On Animal-heat" in Schäfer's 'Text-book of Physiology,' and in Richet's article "Chaleur" in the 'Dictionnaire de Physiologie,' the literature of the subject is so fully collected that it will merely be necessary for me to refer to those papers directly bearing upon the present work, when discussing the experimental results.

Without doubt, as pointed out by Sutherland,[§] Monotremes and Marsupials present a stage of physiological development intermediate between the fairly accurate homœothermism of the higher mammals, and the rudimentary indications in this direction which, according to Vernon,[||] occur in lower vertebrates, but the conclusion of both Sutherland and Vernon that *Ornithorhynchus* "is nearly a cold-blooded animal," which conclusion is based upon some observations of Macleay's,[¶] is very far from being sustained by my experiments.

The present paper is an attempt to locate more precisely the position of

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[*] Miklouho-Macleay, 'Linn. Soc. N.S. Wales Proc.,' vol. 9, 1st series, p. 1204; Semon, 'Arch. f. d. ges. Physiol.,' vol. 58, p. 229, 1894.

[†] 'Roy. Soc. Victoria Proc.,' 1896, vol. 9, New Series.

[‡] "The Physiological Evolution of the Warm-blooded Animal," 'Science Progress,' 1898, vol. 7, p. 378.

[§] *Loc. cit.*

[||] *Loc. cit.*

[¶] *Loc. cit.*

Monotremes and Marsupials in this ascending scale of physiological superiority to the temperature of environment.

SUTHERLAND made his observations upon Echidnas and Marsupials kept in confinement during an extended period, in which the temperature of the air varied from 14 to 36° C. I also have done this, and my observations entirely confirm SUTHERLAND'S. My range was somewhat more extensive, viz., 4—35°, and, in some cases, 40° C. I found further that during the winter Echidna abandons all attempts at homœothermism, and hibernates for 4 months.

The present investigation was not primarily concerned with recording the variations in the temperature of the animals with that of the environment, but with ascertaining to what extent the different groups of animals utilised variation in production and variation in loss for purposes of adjustment. With this end in view I have measured the respiratory activity of specimens from the different groups of mammals. CO_2 production, and not the amount of oxygen consumed, has been taken as indicating oxidation, because the former is so much simpler. The respiratory quotient for Echidna does not appreciably vary when the animal is submitted to an environment varying 18° C., provided that the diet is the same and adequate in quantity.

In order to measure the CO_2 produced, it was necessary to inclose the animals in a receptacle, which was placed in a bath of varying temperature and supplied by a current of air at the temperature of the bath. As it was necessary to conduct observations at the whole range of temperature in one day, I was obliged to limit the experiment at any particular temperature to from $1\frac{1}{2}$ to 2 hours. Consequently the variations found in the animal's own temperature do not necessarily indicate the extent of variation which might be produced by a longer sojourn, as under the conditions of SUTHERLAND'S experiments.

The animals experimented with were—

I. Reptiles.—Blue-tongue lizards (*Cyclodus gigas*) 5 .		weight	1865	grammes.
II. Monotremes	(1).—*Ornithorhynchus*	,,	693	,,
	(2).—*Echidna*	,,	3120	,,
	(3).—*Echidna*	,,	1670	,,
	(4).—*Echidna*	,,	2300	,,
III. Marsupials	(1).—Opossum (*Trichosurus Vulpecula*)	,,	2160	,,
	(2).—Rat-kangaroo (*Bettongia Cuniculus*)	,,	1630	,,
	(3).—Native Cat (*Dasyurus maculatus*)	,,	650	,,
IV. Higher Mammals	(1).—Cat	,,	1150	,,
	(2).—Rabbit	,,	750	,,

The respiratory activity of the cat and rabbit have been investigated frequently. I made observations on them and also on the lizards to obtain data in a precisely similar manner, to place in line with those obtained with Monotremes and Marsupials. The temperature to which the animals were submitted ranged from 5 to 35° C., and in some cases 40° C.

Only one experiment was made with *Ornithorhynchus.* It is easy to shoot these animals, but extremely difficult to catch them alive. I have waited two years since this investigation commenced, but have not been successful in securing another live specimen.

Most of my earlier experiments showed less regular results than those detailed below—for instance, the production of CO_2 might be, in some cases, greater at 25° C. than it was at 20° C. In order to obtain results which would give regular curves I found it necessary to adopt the following precautions :—

(1.) To accustom the animals to confinement in the chamber by keeping them in it for a while on two preceding days, otherwise they often displayed considerable activity in efforts to escape during the earlier part of the experiment, thereby sending up the production of CO_2 in a way independent of the external temperature.

(2.) To conduct the observations in a regular order, beginning with either the lowest or the highest temperature.

When I first began I did not take these precautions. I soon found, however, that the CO_2 produced was not only a function of the temperature of the environment at the time being, but also depended upon whether this temperature was warmer or colder than the one the animal had been previously submitted to. For instance, the respiratory activity at 20° C. was invariably greater when the animal had been previously at 35° C. than when it had just been living in an environment of 5° C. The physiological response to temperature, like conscious appreciation of it, is, to a certain extent, relative.

Experimental Method.

The animal was placed in a receiver A (fig. 1). The broad end was rendered air-tight by screwing it up against a rubber washer. This was inserted in a tank containing 100 litres of water. The temperature of the bath was maintained at the desired point by ice or else a small flame. It was constantly mechanically stirred. With this bulk of water there was no difficulty in keeping the temperature constant within ·1° C. by adjusting the flame or adding or removing ice from time to time. The thermometer* was graduated in $\frac{1}{10}$th of a degree.

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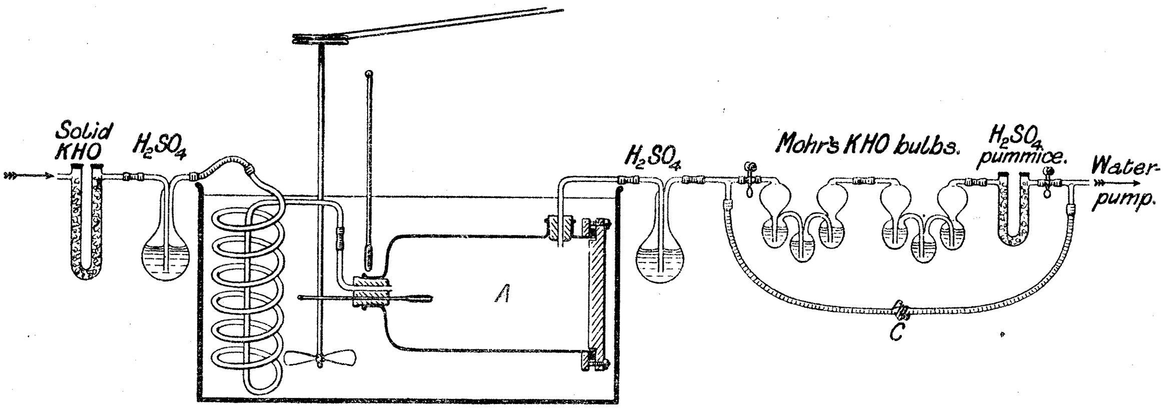
* All thermometers used throughout the experiments had their errors determined by reference to a standard.

Air was aspirated through the chamber as shown in the figure. It was first freed from CO_2 by passing over KHO, and dried by bubbling through H_2SO_4, then warmed or cooled to the temperature of the bath by passing through 8 metres of metal tube. After leaving the chamber the air was dried by the H_2SO_4 bottle and passed through two extra large Mohr's bulbs, filled with 30 per cent. KOH_1 and a U-tube containing H_2SO_4 on pumice. Between the H_2SO_4 bottle and the KHO bulbs was a T-piece leading to a by-pass which communicated again with the aspirating tube beyond the tube containing H_2SO_4 and pumice (see fig. 1). Air could be drawn through the by-pass or through the bulbs by opening or closing the clamp C.

Fig. 1.



The CO_2 produced in a given time was found by the difference in the weight of the Mohr's bulbs and U-tube before and after the experiment.

The observations were made upon animals which had received no food since the previous day. They were weighed and their rectal temperatures taken before inserting in the chamber. At the end of an experiment at each particular temperature they were removed and their temperatures taken. They were immediately re-inserted in the chamber and gradually warmed up or cooled down to the temperature at which it was desired to make the next observation.

This warming up and adjustment usually took about 1 hour.

Details of Experiments.

I.—*Blue-tongued Lizards* (Cyclodus gigas).

As the CO_2 production of these reptiles is so small, and in order to get an average result with a minimum of trouble, I used five specimens simultaneously.

Their respective weights and surfaces[*] were—

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[*] The surfaces were reckoned as described on p. 21.

No. 1	411 grammes.	551 sq. centims.
No. 2	413 ,,	554 ,,
No. 3	421 ,,	562 ,,
No. 4	358 ,,	504 ,,
No. 5	265 ,,	412 ,,
Total . .	1868 ,,	2583 ,,

These lizards are not very active at any time—unless irritated. No observations upon their number of respirations were made. On cooling down to 5° C. they became quite inactive, and, as they were warmed up, displayed more and more activity until 30° C. was reached. Above this temperature their activity diminished. The following table represents the results of eight experiments. In each experiment the CO_2 was collected for one hour. At the expiration of the hour the animals were removed, their rectal temperatures taken, and replaced. About three-quarters to one hour was occupied in adjusting the temperature of the bath for the next experiment. The temperatures of individual lizards varied as much as ·4° C. The figures in the table represent the average of the five.

Temp. of bath.	Temp. of lizards (average).	CO_2 produced in one hour.
5·0° C.	5·5° C.	·0246
9·0	9·2	·0790
15·0	15·2	·0981
20·5	20·4	·1023
25·0	24·5	·1193
30·0	29·3	·1440
35·0	34·8	·1814
39·0	38·5	·5454

II.—MONOTREMES.

1. *Ornithorhynchus.* Female; weight, 693 grammes; cloacal temperature, 32°·5 C. external temperature, 14°·5 C.

Exp. i. Temperature of bath, 5° C.

The animal was in the bath 43 minutes before CO_2 was estimated. CO_2 estimated during 30 minutes.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	5·0	29	Experiment started.
5	5·0	20	Deep irregular gasps, animal very active.
10	4·9	24	,, ,,
15	4·9	24	,, ,,
20	4·9	22	,, ,,
25	5·0	26	,, ,,
30	5·1	21	,, ,,

Rectal temperature after 70 minutes at 5° = 31·8° C.

CO_2 produced in 30 minutes, ·545 gramme.

Exp. ii. Temperature of bath, 10° C.

The animal was in bath 30 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	10	29	Lively, moving about.
10	10	—	,,
20	10·1	31	,,
30	10·2	28	,,

Rectal temperature after 60 minutes at 10° = 32° C.
CO_2 produced in 30 minutes, ·361 gramme.

Exp. iii. Temperature of bath, 20° C.

Animal remained in bath 35 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration	Remarks.
0	20·1	33	Animal apparently asleep.
10	20·1	30	,,
20	20·0	23	,,
30	20·0	26	,,

Rectal temperature after 65 minutes at 20° = 32·7° C.
CO_2 produced in 30 minutes, ·2032 gramme.

Exp. iv. Temperature of bath, 32° C.

Animal remained in bath 30 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	31·9	32	Quiet.
10	31·9	25	,,
20	32·0	21	,, sighing occasionally.
25	32·0	24	,, ,,
30	32·1	20	,, ,,

Rectal temperature after 60 minutes at 32° = 33°·6 C.
CO_2 produced in 30 minutes, ·168 gramme.

Exp. v. Temperature of bath, 35° C.

The animal after its temperature was taken at the termination of Experiment iv. was replaced in bath, which was heated up to 35° C. As soon as this temperature became steady, the CO_2 was estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	35·1	20	Quite still.
10	35·1	24	Sighing respiration.
15	35·0	30	Lying on back.
16	35·1	16	,,
17	3·51	—	Fainted.

The animal was immediately removed and its rectal temperature found to be 35°·3 C. It recovered immediately after removal.

CO_2 produced in 17 minutes, ·107 gramme.

2. *Echidna hystrix.* No. 1. Old male; weight, 3120 grammes; cloacal temperature, 28·1° C.; external temperature, 19° C.

Exp. i. Temperature of bath, 4° C.

Animal remained in bath 42 minutes previous to estimation of CO_2.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	3·9	20, very deep	Shivering violently, huddled up.
10	3·9	20 ,,	,, ,,
20	4·0	19 ,,	,, moving.
30	4·0	20 ,,	,, ,,
45	4·1	21 ,,	,, ,,
60	4·0	20 ,,	,, ,,

Rectal temperature after 102 minutes at 4° = 25°·5 C.

CO_2 produced in 60 minutes, 2·464 grammes.

Exp. ii. Temperature of bath, 10° C.

Animal remained in bath 30 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	10·1	20, deep	Active, shivering.
10	10·1	20 ,,	,, ,,
20	10·0	19 ,,	,, ,,
30	10·0	20 ,,	,, ,,
40	9·9	21 ,,	,, ,,
60	10·1	20 ,,	,, ,,

Rectal temperature after 90 minutes at 10° = 27°·3 C.

CO_2 produced in 60 minutes, 2·004 grammes.

Exp. iii. Temperature of bath, 20° C.

Animal remained in bath 32 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	20	19	Active.
10	20·1	19	,,
20	20·1	20	,,
30	20·2	20	,,
45	20·1	20	,,
60	20·0	19	,,

Rectal temperature after 92 minutes at 20° = 28°·6 C.
CO_2 produced in 60 minutes, 1·306 grammes.

Exp. iv. Temperature of bath, 30° C.

Animal in bath 36 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	30·1	19	Asleep.
10	30·0	19	,,
20	30·1	20	,,
30	29·9	18	,,
45	29·9	18	,,
60	30·1	19	,,

Rectal temperature after 96 minutes at 30° = 30°·9 C.
CO_2 produced in 60 minutes, ·598 gramme.

Exp. v. Temperature of bath 35° C.

Animal in bath 30 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	35·0	18	Asleep.
5	35·1	18	,,
10	34·9	20	,,
20	35·0	19	,,
30	35·1	18	,,

Rectal temperature after 60 minutes at 35° = 34°·8 C.
CO_2 produced in 30 minutes, ·406 gramme.

3. *Echidna.* No. 2. Young half-grown male; weight, 1670 grammes; cloacal temperature, 30°·2 C.; external temperature, 18° C.

Exp. i. Temperature of bath, 5° C.

The animal remained in bath 47 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks
0	5·0	25, gasping	Shivering violently and active.
10	5·1	26 ,,	,, ,,
20	5·1	24 ,,	,, ,,
30	5·0	24 ,,	,, ,,

Rectal temperature after 77 minutes at 5° = 27°·6 C.
CO_2 produced in 30 minutes, ·854 gramme.

Exp. ii. Temperature of bath, 10° C.

Animal remained 37 minutes in bath before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	10·1	24	Moving, shivering.
10	10·0	24	,, ,,
20	9·9	23	,, ,,
25	10·1	25	,, ,,
30	10·1	24	,, ,,

Rectal temperature after 67 minutes at 10° = 30° C.
CO_2 produced in 30 minutes, ·733 gramme.

Exp. iii. Temperature of bath, 20° C.

Animal remained in bath 36 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	20·0	20	Restless.
10	20·0	21	,,
20	20·1	20	,,
30	20·1	22	,,

Rectal temperature after 66 minutes at 20° = 31°·4 C.
CO_2 produced in 30 minutes, ·4435 gramme.

Exp. iv. Temperature of bath, 30° C.

Animal remained in bath 42 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	30·0	20	Quiet.
5	30·0	21	,,
10	30·1	20	Moving occasionally.
20	29·9	20	,,
30	29·9	21	Quiet.

Rectal temperature after 72 minutes at 30° = 33°·4 C.
CO_2 produced in 30 minutes, ·171 gramme.

Exp. v. Temperature of bath, 37° C.

Animal in bath 41 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	37·1	19	Uneasy.
5	37·0	18, sighing	,,
10	37·0	18 ,,	Lying on back.
20	36·9	18 ,,	,,
25	37·0	19	Quiet.
28	37·0	19	Fainted.
30	37·0	19	Taken out.

Rectal temperature after 71 minutes at 37° = 40° C. Animal died 10 minutes later.
CO_2 produced in 30 minutes, ·180 gramme.

4. *Echidna.* No. 3. Three-quarter grown male; weight, 2300 gramme.

Exp. i. Temperature of bath, 8° C.

The animal was in the bath 63 minutes before CO_2 was estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	8·1	23	Active, shivering violently.
5	8·1	20	,,
10	7·9	18	,,
20	8·0	21	,,
30	8·1	20	,,

Rectal temperature after 93 minutes at 8° = 29°·1 C.
CO_2 produced in 30 minutes, 1·183 grammes.

Exp. ii. Temperature of bath, 15° C.

The animal remained in bath 38 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	15·0	24	Very restless.
10	15·0	18	Moving about.
20	15·1	17	,,
25	15·1	22	,,
30	15·0	23	,,

Rectal temperature after 68 minutes at 15° = 29°·9 C.
CO_2 produced in 30 minutes ·8575 gramme.

Exp. iii. Temperature of bath, 20° C.

Animal in bath 30 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
5	20·0	19	Restless.
10	19·9	19	,,
22	19·9	21	,,
27	20·0	20	,,
30	20·1	20	,,

Rectal temperature after 60 minutes at 20° = 30°·4 C.
CO_2 produced in 30 minutes ·6454 gramme.

Exp. iv. Temperature of bath, 25° C.

Animal in bath 42 minutes before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	25·1	12	Quiet.
5	25·1	12	,,
10	25·1	15	,,
15	25·1	14	,,
25	25·1	12	,,
30	25·1	16	,,

Rectal temperature after 72 minutes at 25° = 31°·6 C.
CO_2 produced in 30 minutes, ·480 gramme.

Exp. v. Temperature of bath, 30° C.

Animal remained 37 minutes in bath before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	30·1	12	Quiet.
4	30·1	15	,,
10	30·0	14	,,
15	29·9	11	,,
20	29·9	12	,,
30	29·9	12	,,

Rectal temperature after 67 minutes at 30° = 33°·0 C.
CO_2 produced in 30 minutes, ·359 gramme.

Exp. vi. Temperature of bath, 35° C.

Animal remained 35 minutes in bath before CO_2 estimated.

Minutes.	Temp. of bath.	Respiration.	Remarks.
0	35·0	8	Absolutely still.
5	34·9	9	,,
10	35·0	6	,,
20	35·0	7	,,
25	35·0	7	,,
30	34·9	6	,,

Rectal temperature after 65 minutes at 35° = 37°·1 C.
CO_2 produced in 30 minutes, ·444 gramme.

III.—MARSUPIALS.

1. Native Cat (*Dasyurus maculatus*). Male; weight, 650 grammes; rectal temperature, 36°·3 C.; external temperature, 15° C.

Exp. i. Temperature of bath, 35° C.

Immediately on placing the glass chamber in the warm bath, the animal went to sleep. It remained in the warm bath for 31 minutes before CO_2 was estimated.

Minutes.	Respiration.	Remarks.
0	96	Asleep.
10	134	,,
20	120	,,
30	106	,,

CO_2 produced in 30 minutes, ·2016 gramme.
Rectal temperature after 61 minutes at 35° = 40° C.

Exp. ii. Temperature of bath, 30° C.

The animal remained in bath 33 minutes before CO_2 was estimated.

Minutes.	Respiration.	Remarks.
0	75	Asleep.
10	76	,,
20	58, deep	,,
30	60 ,,	,,

CO_2 produced in 30 minutes, ·1095 gramme.
Rectal temperature after 63 minutes at 30° = 38° C.

Exp. iii. Temperature of bath, 20° C.

Animal in bath 36 minutes prior to estimation of CO_2.

Minutes.	Respiration.	Remarks.
0	120	Awake but quiet.
10	115	,, ,,
20	105	,, ,,
30	100	,, ,,

CO_2 produced in 30 minutes, ·169 gramme.
Rectal temperature after 66 minutes at 20° = 36°·6 C.

Exp. iv. Temperature of bath, 10° C.

Animal in bath 30 minutes prior to estimation of CO_2.

Minutes.	Respiration.	Remarks.
0	105	Moving about.
10	106	,,
20	88, deeper	,,
30	84 ,,	,,

CO_2 produced in 30 minutes, ·3895 gramme.
Rectal temperature after 60 minutes at 10° = 37° C.

Exp. v. Temperature of bath, 5° C.

Animal in bath 35 minutes prior to estimation of CO_2.

Minutes.	Respiration.	Remarks.
0	70, very deep	Crouched up, shivering violently.
5	92 ,,	,, ,, ,,
10	89 ,,	,, ,, ,,
20	84 ,,	,, ,, ,,
30	90 ,,	,, ,, ,,

CO_2 produced in 30 minutes, ·4425 gramme.
Rectal temperature after 65 minutes at 5° = 37°·1 C.

2. Rat Kangaroo (*Bettongia*). Female; weight, 1630 grammes.

Exp. i. Temperature of bath, 40° C.

Placed in receiver in bath for 45 minutes prior to estimation of CO_2.

Minutes.	Respiration.	Remarks.
0	36	Asleep.
10	36	,,
15	39	Uneasy.
25	56	,,
30	33	Faint.

Directly on removal fainted; recovered in 3 minutes.
CO_2 produced in 30 minutes, ·476 gramme.
Rectal temperature after 95 minutes at 40° = 38°·6 C.
Allowed an hour's rest between Exp. i. and ii.

Exp. ii. Temperature of bath, 30° C.

33 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	40	Asleep.
10	32	,,
20	33	,,
30	30	,,

CO_2 produced in 30 minutes, ·280 gramme.
Rectal temperature after 63 minutes at 30° = 36°·2 C.

Exp. iii. Temperature of bath, 22° C.

36 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	42	Awake, but still.
10	36	,, ,,
20	35	,, ,,
30	39	,, ,,

CO_2 produced in 30 minutes, ·3135 gramme.

Rectal temperature after 66 minutes at 22° = 35°·9 C.

Exp. iv. Temperature of bath, 10° C.

32 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	36	Restless.
10	38	,,
20	49	,,
30	34	,,

CO_2 produced in 30 minutes, ·5845 gramme.

Exp. v. Temperature of bath, 5° C.

35 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	27	Restless, shivering.
10	28	Crouched up, ,,
20	20	Restless, ,,
30	32	,, ,,

CO_2 produced in 30 minutes, ·8555 gramme.

Rectal temperature after 65 minutes at 5° = 38°·2 C.

3. Opossum (*Trichosurus Vulpecula*). Large male; weight, 2160 grammes; rectal temperature, 35°·6 C.; external temperature, 16° C.

Exp. i. Temperature of bath, 35° C.

Animal remained in bath 40 minutes before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	25	Quiet, awake.
10	27	,, ,,
20	27	,, ,,
30	29	,, ,,

Rectal temperature after 70 minutes at 35° = 37°·8 C.

CO_2 produced in 30 minutes, ·3385 gramme.

Exp. ii. Temperature of bath, 30° C.

Animal in bath 30 minutes before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	21	Asleep.
10	22	,,
20	22	,,
30	20	,,

Rectal temperature after 60 minutes at 30° = 36°·6 C.

CO_2 produced in 30 minutes, ·2684 gramme.

Exp. iii. Temperature of bath, 20° C.

Animal 30 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	20	Asleep.
10	23	,,
20	21	,,
30	24	,,

CO_2 produced in 30 minutes, ·3425 gramme.

Rectal temperature after 1 hour at 20° = 36°·2 C.

Exp. iv. Temperature of bath, 10° C.

Animal 35 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	25	Quiet, shivering occasionally.
10	22	,, ,,
20	22	,, ,,
30	20	,, ,,

CO_2 produced in 30 minutes, ·551 gramme.

Rectal temperature after 65 minutes at 10° = 36°·5 C.

Exp. v. Temperature of bath, 5° C.

40 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	26	Moving about, continuously shivering.
10	24	,, ,,
20	28	,, ,,
30	19	,, ,,

CO_2 produced in 30 minutes, ·786 gramme.

Rectal temperature after 70 minutes at 5° = 36°·1 C.

IV.—*Higher Mammals.*

1. Rabbit, half-grown ; weight, 750 grammes.

Exp. i. Temperature of bath, 40° C.

28 minutes in bath before CO_2 estimated.

Minutes.	Remarks.
0	Still. Panting like a dog ; respiration over 200 per minute.
10	,, ,, ,, ,,
20	,, ,, ,, ,,
30	,, ,, ,, ,,

CO_2 produced in 30 minutes, ·4485 gramme.
Rectal temperature after 58 minutes at 40° = 41°·6 C.

Exp. ii. Temperature of bath, 35° C.

30 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	140	Panting.
5	147	,,
10	195	,,
20	197	,,
30	192	,,

CO_2 produced in 30 minutes, ·383 gramme.
Rectal temperature after 60 minutes at 35° = 40°·5 C.

Exp. iii. Temperature of bath, at 20° C.

34 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	41	Animal quite quiet.
10	37	Scratching.
20	46	Moving about.
30	33	Quiet.

CO_2 produced in 30 minutes, ·456 gramme.
Rectal temperature after 64 minutes at 20° = 38°·7 C.

Exp. iv. Temperature of bath, 10° C.

31 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	36, deep	Quiet, shivering.
10	37 ,,	Moving about.
20	30 ,,	,, shivering.
30	38 ,,	,, ,,

CO_2 produced in 30 minutes ·519 gramme.
Rectal temperature after 61 minutes at 10° = 38°·0 C.

Exp. v. Temperature of bath, 5° C.

33 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	35, very deep	Very restless, shivering, tucked up.
10	31 ,, ,,	Deep gasping respiration.
20	29 ,, ,,	,, ,,
30	37 ,, ,,	,, ,,

CO_2 produced in 30 minutes, ·713 gramme.
Rectal temperature after 63 minutes at 5° = 37°·5 C.

2. Half-grown Cat; weight, 1150 grammes; rectal temperature, 39°·7; external temperature, 21° C.

Exp. i. Temperature of bath, 40° C.

40 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	120	Distressed, panting with tongue out.
10	111	,, ,, ,,
20	100	,, ,, ,,
30	156	,, ,, ,,

CO_2 produced in 30 minutes, ·726 gramme.
Rectal temperature after 70 minutes at 40° = 39°·9 C.

Exp. ii. Temperatnre of bath, 30° C.

32 minutes before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	33	Asleep.
10	34	,,
20	34	,,
30	31	,,

CO_2 produced in 30 minutes, ·582 gramme.

Rectal temperature after 62 minutes at 30° = 39°·7 C.

Exp. iii. Temperature of bath, 20° C.

30 minutes at 20° before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	49	Sitting still.
10	48	,,
20	60	Moving about.
30	48	Still.

CO_2 produced in 30 minutes ·713 gramme.

Rectal temperature after 60 minutes, at 20° = 39°·5 C.

Exp. iv. Temperature of bath, 10° C.

35 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	68, deep	Still.
10	60 ,,	Lively.
20	60 ,,	,,
30	61 ,,	,,

CO_2 produced in 30 minutes, ·824 gramme.

Rectal temperature after 65 minutes at 10° = 39° C.

Exp. v. Temperature of bath, 5° C.

32 minutes in bath before CO_2 estimated.

Minutes.	Respiration.	Remarks.
0	54, deep	Restless, shivering.
10	60 ,,	,, ,,
20	60 ,,	,, ,,
30	58 ,,	,, ,,

CO_2 produced in 30 minutes, 1·1745 grammes.

Rectal temperature after 62 minutes at 5° = 38°·5 C.

The Respiratory Quotient in Echidna.

The Echidnas were fed whilst in confinement upon milk containing either egg beaten up or very finely divided cooked meat. They do very well, however, for a month or two upon a diet of milk only.

Observations upon the respiratory quotient were made when they were upon a milk diet. The animal respired through a T-piece provided with gut-valves, one opening inwards, the other outwards. The expiratory valve was connected with an air meter the resistance of which was compensated for by a weight passing over a pulley and geared to the axis of the meter. A sample representative of the whole of the air breathed was obtained by the ingenious arrangement of GEPPERT and ZÜNTZ,* by which the meter operates as a motor, and by appropriate gearing lowers the level of the out-flow tube of the gas-burette and takes a sample of the air into the burette in amount exactly proportionate to the particular expiration moving the meter. An analysis of the air in the burette gave the respiratory quotient. This was done in duplicate. The animal breathed through the meter for ten minutes at a time. The amount of air breathed varied between 4000 and 5000 cub. centims.

Respiratory quotient at 10°·4 C.

	CO_2 per cent.			O_2 per cent.			$\frac{CO_2}{O_2}$
	(1)	(2)	Mean.	(1)	(2)	Mean.	
1	2·61	2·70	2·66	3·14	3·01	3·07	·87
2	3·54	3·52	3·53	3·02	3·12	3·07	1·15
3	2·04	2·11	2·07	2·81	2·81	2·81	·74
4	4·06	4·12	4·09	5·38	5·40	5·39	·75

Average $\frac{CO_2}{O_2}$ for four experiments, ·88.

Respiratory quotient at 28°·9 C.

	CO_2 per cent.			O_2 per cent.			$\frac{CO_2}{O_2}$
	(1)	(2)	Mean.	(1)	(2)	Mean.	
1	2·70	2·68	2·69	3·62	3·62	3·62	·75
2	3·51	3·49	3·50	3·90	3·89	3·90	·90
3	2·90	2·95	2·92	3·15	3·20	3·17	·92
4	3·62	3·55	3·58	4·21	4·15	4·18	·85

Average $\frac{CO_2}{O_2}$ for four experiments, ·88.

The respiratory quotient calculated from the combustion of the milk = ·84.

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* The apparatus in an improved form is described (with illustration) by MAGNUS-LEVY, 'PFLÜGER'S Arch.,' vol. 55.

Discussion of Results.

Before discussing the results of the experiments detailed above, I will place them in tabulated form. I have also expressed them in curves (figs. 2, 3, 4, 5). In order that the amount of CO_2 produced by the different animals of varying size, can be compared, they must be reduced to some common term. Rübner* and Richet† have shown that this term is surface. I have accordingly calculated the experimental results in terms of 1000 sq. centims. surface.

The surface of an animal is proportional to the $\sqrt[3]{}$ of its volume, or $S = k\sqrt[3]{v}$ where k is a constant. Assuming that the specific gravity of the different animals does not vary, weight can be substituted for volume—k of course assuming a different value. The value of k in this case was determined by Meeh‡ and also by Rübner,§ and found to be 11·2 for mammals. I have used this value for all the animals except the lizards.

In their case I determined the value of the constant by direct measurement of the skin after removal from the body. Before skinning, the girth was taken in several parts of the body and limbs, and the spread-out skin was stretched slightly to coincide with these measurements. I found the value of k for these animals to be 9·95, and have in the calculations used 10.

Series A.—Lizards (*Cyclodus gigas*). Five individuals, total weight 1868 grammes.

Temperature of bath ° C.	Temperature of lizards (average).	CO_2 per 1000 grammes per hour.	CO_2 per 1000 sq. centims. per hour.
5·0	5·5	·0132	·0095
9·0	9·2	·0423	·0306
15·0	15·2	·0525	·0380
20·5	20·4	·0548	·0396
25·0	24·5	·0637	·0462
30·0	29·3	·0771	·0557
35·0	34·8	·0971	·0702
39·0	38·5	·2919	·2112

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* 'Zeitschr. f. Biol.,' vol. 19, p. 535.

† 'Travaux du Laboratoire,' vol. 1, p. 181, 1893.

‡ 'Zeitschr. f. Biol.,' vol. 15, p. 425.

§ *Loc. cit.*, p. 549.

SERIES B.—*Monotremes.*

1. *Ornithorhynchus.* Weight, 693 grammes; surface, 876 sq. centims.

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per hour per 1000 sq. centims., in grammes.
5	31·8	26·8	1·090	1·244
10	32·0	22·0	·722	·825
20	32·6	12·6	·405	·463
32	33·6	1·6	·336	·383
35	35·3	·3	·377	·430

2. *Echidna.* No. 1. Weight, 3120 grammes; surface, 2390 sq. centims.

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per hour per 1000 sq. centims., in grammes.
4	25·5	21·5	2·464	1·031
10	27·3	17·3	2·004	·838
20	28·6	8·6	1·306	·545
30	30·9	·9	·598	·250
35	34·8	– ·2	·812	·341

3. *Echidna.* No. 2. Weight, 1670 grammes; surface, 1407 sq. centims.

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per hour per 1000 sq. centims., in grammes.
5	27·6	22·6	1·708	1·214
10	30·0	20·0	1·466	1·042
20	31·4	11·4	·887	·631
30	33·4	3·4	·342	·243
37	40·0	3·0	·360	·256

4. *Echidna.* No. 3. Weight, 2300 grammes ; surface, 1956 sq. centims.

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per hour per 1000 sq. centims., in grammes.
8	29·1	21·1	2·366	1·210
15	29·9	14·9	1·715	·872
20	30·4	10·4	1·291	·661
25	31·6	6·6	·96	·491
30	33·0	3·0	·718	·367
35	37·1	2·1	·888	·454

Series C.—*Marsupials.*

1. Native Cat (*Dasyurus maculatus*). Weight, 650 grammes.

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per 1000 sq. centims., in grammes.
5	37·1	32·1	·895	1·050
10	37·0	27·0	·779	·69
20	36·6	16·6	·338	·390
30	38·0	8·0	·219	·261
35	40·0	5·0	·403	·481

2. Rat-Kangaroo (*Bettongia*). Weight, 1630 grammes.

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per 1000 sq. centims., in grammes.
5	36·2	32·2	1·711	1·104
10	—	—	1·169	·754
22	36·0	14·0	·627	·404
30	36·2	6·2	·560	·361
40	38·6	–1·4	·952	·614

3. Opossum (*Trichosurus*). Weight, 2160 grammes ; surface, 1870 sq. centims

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per hour per 1000 sq. centims., in grammes.
5	36·1	31·1	1·571	·840
10	36·5	26·5	1·102	·589
20	36·2	16·2	·685	·367
30	36·6	6·6	·537	·282
35	37·8	2·8	·677	·362

SERIES D.—*Higher Mammals.*

1. Cat ; half grown. Weight, 1150 grammes.

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per hour per 1000 sq. centims., in grammes.
5	38·5	33·5	2·349	1·910
10	39·0	29·0	1·648	1·34
20	39·5	19·5	1·426	1·16
30	39·7	9·7	1·163	·946
40	39·9	−0·1	1·452	1·180

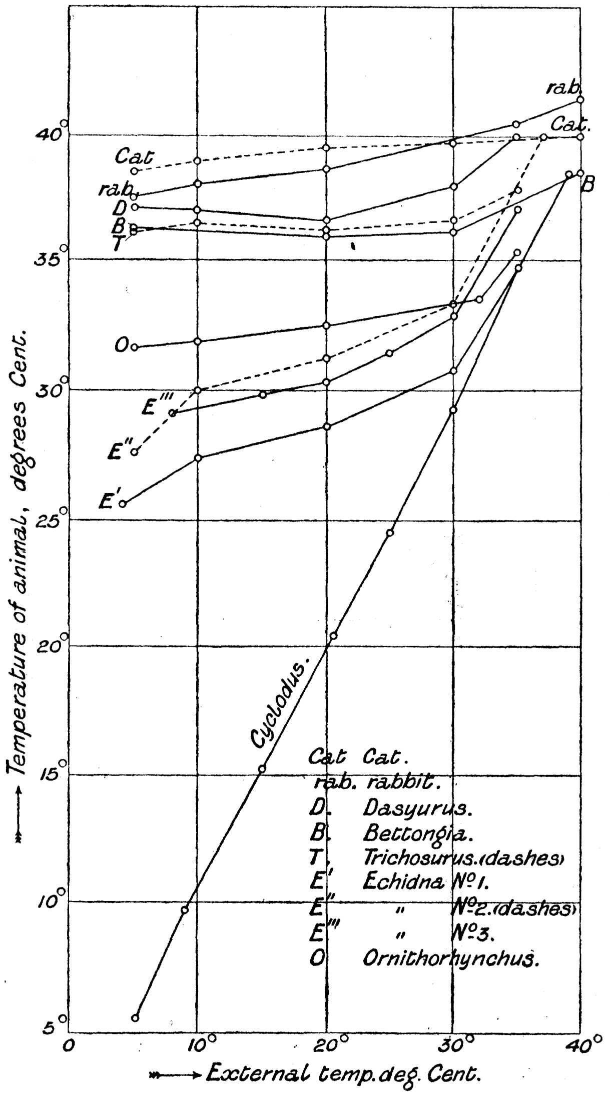
2. Rabbit. Weight, 750 grammes.

Temperature of environment.	Temperature of animal.	Difference in temperature, animal and environment.	CO_2 per hour, in grammes.	CO_2 per hour, per 1000 sq. centims., in grammes.
5	37·5	32·5	1·426	1·543
10	38·0	28·0	1·038	1·124
20	38·7	18·7	·912	·987
35	40·5	5·5	·766	·829
40	41·6	1·6	·897	·971

I.—*Variations in the Body Temperature of Monotremes, Marsupials, and Mammals.*

On examining the figures setting forth the temperature of animals corresponding with variations in the temperature of environment under the conditions of the experiments, or better by glancing at the curves (fig. 2) wherein these relationships are graphically represented, it will be seen that the lizards I was working with are truly poikilothermic. The curve of variation of body-temperature with change in temperature of environment from 5° to 39° C., is nearly a straight line.

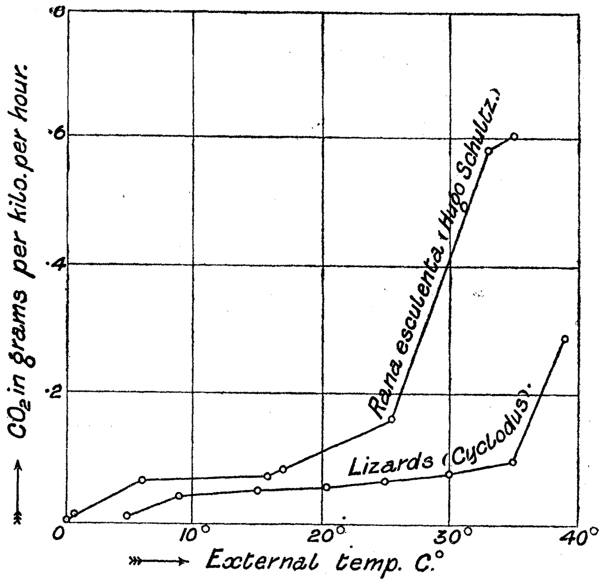
Fig. 2.



The experiment was begun at the highest temperature employed (39°·1 C.). Notwithstanding that I kept the animals in an environment of between 39 and 40° C. for $2\frac{1}{2}$ hours, I could not get their mean temperature above 38·5. The air supplied was dry, so that this difference was probably due to some small amount of transpiration.

On lowering the temperature, this difference between animal and environment gradually diminished until, at 20° C., there was only a difference of 0°·1 C. between them. As the temperature of environment was further lowered the animal's temperature sank with it, keeping, however, two or three tenths of a degree in excess, and at 5° C. their temperature was 5·5. In these temperature curves no attempt on the part of the animal in the direction of resisting the fall of temperature of their bodies is manifested, nor on glancing at the figures showing their CO_2 production, or the curve (fig. 3) is there any indication of the increased heat formation observed by VERNON in frogs.

Fig. 3.



The next point shown is that the body temperatures of Echidna, Ornithorhynchus, Marsupials, and higher mammals gradually rise in the order mentioned. The temperature of these animals for an environment of 15° C. deduced from the curves (fig. 2) is shown in the table below.

Temperature of Monotremes, Marsupials, and Mammals, when air temperature = 15° C.

Echidna No. 1 .	Monotremes,	average 29°·8 C.
Echidna No. 2 .		
Echidna No. 3 .		
Ornithorhynchus .		
Trichosurus . .	Marsupials,	„ 36°·5 C.
Bettongia . .		
Dasyurus . . .		
Cat	Higher Mammals,	„ 38°·75 C.
Rabbit		

The above values are for the particular individuals experimented with. They are typical, and agree with SUTHERLAND'S observations and with a number of observations I have made from time to time upon the temperature of Monotremes, either in captivity or immediately after they were shot. My observations under these circumstances happened only rarely to be taken when the external temperature was 15° C., but they indicate 28–29° as an average temperature for Echidna, and 29–30° for Ornithorhynchus, with environment at 15° C.

The temperature observed by MIKLOUHO-MACLEAY* in a single specimen of Ornithorhynchus was 24°·8 C. when the water in which the animal was kept was 22°·2 C. This has led both SUTHERLAND† and VERNON‡ to the conclusion that Ornithorhynchus is "almost a cold-blooded animal." MACLEAY'S observation is, I am convinced, unreliable. I have taken the temperature of upwards of thirty specimens either in captivity or immediately after being shot, and their temperature was always above 28° C.

Ornithorhynchus is not an amphibious animal, and only goes into the water for food or to amuse itself, and if kept too long in water its temperature falls and it dies. I imagine MACLEAY, from his remarks, kept the animal in a tub, in which it could not emerge from the water. He says the animal was in a "dying condition, and presented no chance of living much longer." These circumstances fully account for the low body-temperature. The experiments with Ornithorhynchus in this paper show that between 5° and 30° C. it is better able to adjust its temperature than a rabbit. When subjected to a temperature above 30° C. it became feverish, as the physiological limits for this animal had been exceeded. I think these results show that Ornithorhynchus has been most unjustly degraded to "almost a cold-blooded animal."

The temperatures for Echidna and Marsupials agree with SUTHERLAND'S* and SENIOR'S§ observations, but as mentioned in the introduction, they are subject to much wider variations, as the specimens I have kept in the laboratory during the last two winters hibernated from the middle of June to the middle of October. During hibernation they took neither food nor water, and their body-temperature followed that of the shed in which they lived within 0°·5 C.

The table below shows to what extent the body-temperature of the individuals of the different groups of animals varied when that of the environment changed from 5° to 35° C.

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[*] *Loc. cit.*

[†] *Loc. cit.*

[‡] *Loc. cit*

[§] *Loc. cit.*

Echidna (1) . .	25·7 to 34·8 =	9·1	average 9·3
Echidna (2) . .	27·6 ,, 38·0 =	10·4	
Echidna (3) . .	28·5 ,, 36·8 =	8·3	
Ornithorhynchus .	31·8 ,, 35·3 =	3·5	,, 3·5
Dasyurus . . .	37·1 ,, 40·0 =	2·9	,, 1·3
Trichosurus . .	36·1 ,, 37·5 =	1·4	
Bettongia . . .	36·3 ,, 37·5 =	1·2	
Cat	38·5 ,, 39·8 =	1·3	,, 2·1
Rabbit	37·5 ,, 40·5 =	3·0	

Comparison of the CO_2 Output per Unit Surface in Different Groups of Animals at all Temperatures.

The experiments with lizards (*Cyclodus gigas*) show an extremely small oxidation-coefficient throughout the whole range of temperature experimented with. These animals only produced ·0525 gramme CO_2 per kilogramme per hour at 20° C., whereas the rabbit produced 1·216 grammes at this temperature. The former is approximately $\frac{1}{24}$th of the latter. The data show two critical temperatures (see curve, fig. 3), one between 5° and 10° C., and another between 30° and 40° C. A small change in the temperature between these points occasions a rapid increase in their metabolic activity disproportionate to the effect of a similar increase in temperature between 10° and 30° C. In fig. 3 I have plotted a curve for *Rana esculenta* obtained from the data of HUGO SCHULTZ.* The two curves are similar in character, but the critical temperatures are both a few degrees higher for *Cyclodus* than for *Rana*, and the respiratory activity of these frogs is throughout more energetic than that of the lizards, and greatly so at the higher temperatures.

The sudden increase in oxidation above 30° C. occurs also in the Monotremes, Marsupials, and Mammals, and is interesting as being in the two latter independent of any visibly increased activity on the part of the animals.

In all the animals experimented with, except the lizards, the minimum production of CO_2 occurred at or about 30° C. This has been found to be the case with the higher Mammals and with man.† This minimum production calculated in relation to body suface is, as may be seen in the charts (figs. 4, 5), different in the three groups of animals. The figures are—

Monotremes (mean value) . .	·302	gramme per 1000 sq. centims. surface.
Marsupials ,, . .	·300	,, ,, ,, ,,
Mammals ,, . .	·915	,, ,, ,, ,,

At temperatures above 30° the production increased rapidly, below 30° with

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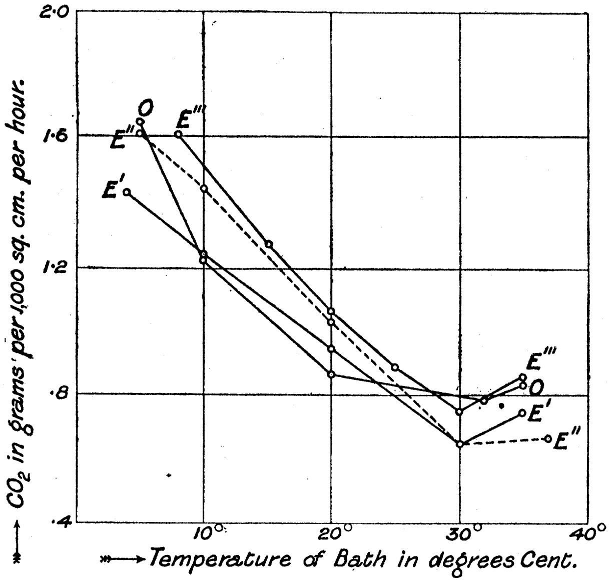
* 'Arch. f. d. ges. Physiol.,' vol. 14, p. 78.

† VOIT, *loc. cit.*; RÜBNER, "Biologische Gesetze" (Abstr.), 'Centralblatt f. Physiol,' 1887, p. 700.

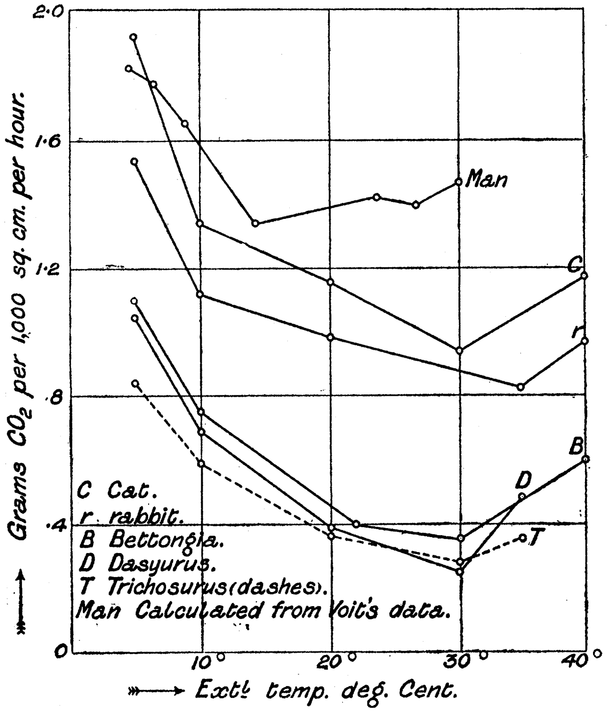
Echidnas rapidly and continuously, with Marsupials and Mammals at first slowly and afterwards more quickly (see chart, figs. 4 and 5).

Fig. 4.



E′, E E″, Echidna; O, Ornithorhynchus.

Fig. 5.



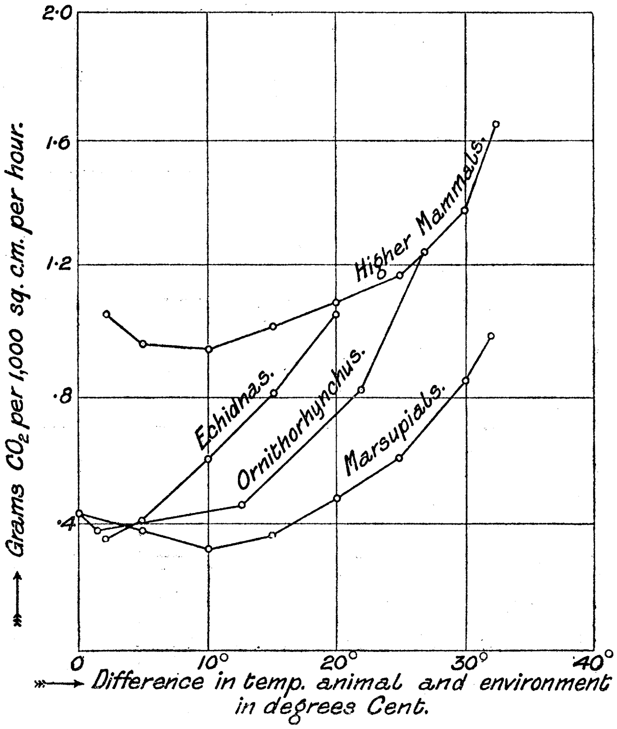
Throughout the range of temperature 5° to 35° C. oxidation is less energetic in the Monotremes and Marsupials (see figs. 4 and 5) than in the higher Mammals. This difference is most marked at the temperature at which the minimum production occurs.

Such economy can be accounted for by—

(1.) Diminished loss of heat, by better insulation, or less evaporation from skin and lungs.
(2.) A lower body-temperature.
(3.) Failure to maintain a constant body-temperature.

I have already shown that none of the animals maintained a constant body-temperature throughout the experimental range. The Marsupials, however, kept their temperature more constant than the rabbit, though less so than the cat. Imperfect homœothermic adjustment cannot explain this relative economy on their part. It is, I believe, largely due to their better insulation, though the fact that their average body-temperature is 2° lower than that of Mammals will account for it to a small extent. This explanation certainly does not explain the small heat production of Echidna, which is covered with spines and coarse hairs which do not afford a good insulation. One must accordingly look to their low temperatures (under 30°) and defective homœothermism for an explanation. Fig. 6 is a graphic representation of the relation of CO_2 production to the difference in temperature between animal and environment for the three groups of animals. By representing the experimental data in this way the effect of the comparatively low and varying body-temperature of Echidna is eliminated. In the curve for Echidnas it will be

Fig. 6.



seen that with a difference in temperature of 20–25° C. between animal and environment the production of Echidna is nearly equal to that of the Mammals.

Imperfect homœothermism is economical of energy. With a specific heat of ·8, 800 calories per kilogramme is saved to an animal by allowing its own temperature to fall 1° C. instead of maintaining it by increased production of heat.

The respiratory quotient for Echidna was found to be ·88, and I have calculated that this amount of energy (800 calories) would necessitate an amount of combustion of its food represented by about ·3 gramme of CO_2.*

Comparison of Behaviour and CO_2 production of Monotremes, Marsupials, and Mammals at Temperatures above 30° *C.*

Above 30° C. the CO_2 production increases. This is accompanied in the higher Mammals by panting. The number of respirations per minute in the cat and rabbit used in these experiments was

	20° C.	40° C.
Cat . . .	51	122
Rabbit . .	37	over 200

The respirations of the Marsupials were little affected by the warm temperatures, and the Monotremes breathed decidedly more slowly and less deeply than when in cooler air (see Details of Experiments). The increased oxidation of Monotremes and Marsupials cannot therefore be the expression of increased work done in respiratory movements, whereby the higher Mammals assist in the adjustment of their temperature (RÜBNER'S physical regulation) by operating as refrigerating machines, but must be due to the higher body-temperature which they invariably had when in air above 30° C. I imagine they have a critical temperature just as is seen in cold-blooded animals, and that when this is reached increased oxidation occurs independent of activity.

All the Monotremes and Marsupials with which I have experimented became less and less active as the temperature rose, and displayed a minimum of activity at 35 to 40°, often culminating in fainting. Nevertheless the CO_2 produced increased from 30 to 35° and from 35 to 40°.

This refrigerating mechanism is of very considerable value in animals covered with an insulating fur, and not freely supplied with sweat glands, as the dog. In one of RICHET'S† experiments a dog evaporated 11 grammes of water per kilogramme per

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* For this calculation, it was assumed that the oxygen in the foodstuffs has already oxidised the hydrogen and not the carbon. This is, of course, not the case, but gives an approximate result only. On this assumption the energy dissipated by oxidation of 1 gramme butter is 4 per cent. too high; of 1 gramme casein, 4 per cent. too low; of 1 gramme lactose, 12 per cent. low.

† 'Dict. de Physiol,' Article "Chaleur," p. 183.

hour (= 6000 calories) by the respiration, *i.e.*, three times the amount of heat normally produced.

I conclude that this power to lose heat is absent in Monotremes and little evident in Marsupials, which no doubt accounts in large measure for the fact that when heated in the chamber they so readily suffered from heat apoplexy, as their range of adaptation is thereby curtailed.

If the body-temperature rises to 35° in Platypus and 37° in Echidna they very soon die, showing that the maximum consistent with life is lower than is the case with the higher animals. In this respect I may mention an observation of CHAPMAN'S* that the muscle of Echidna, which retains its vitality after excision much as reptilian or amphibian muscle, lost its irritability immediately after its temperature was raised to 35° C.

Comparison of the Effect of Cold upon the production of CO_2 in Relation to the Minimum Production in Monotremes, Marsupials, and Mammals.

The general effect of lowering the temperature of the environment upon the CO_2 produced by the different groups of Mammals is graphically represented in the charts (figs. 4 and 5). These curves show that the oxidation in Echidna increases rapidly and in a regular manner as the external temperature is lowered. With Marsupials and Mammals this increase is less until 10° is reached, when it becomes much more marked. In many respects the curve for Platypus is between that of Echidna and Marsupials, whilst the curve for Marsupials approaches in character that of Mammals.

For comparative purposes, it is instructive if the production of CO_2 found in the experiments is plotted as ordinates against the difference in temperature between animal and environment as abscissæ. This takes into account the fact that the temperature of the different animals is itself varying, and to a different degree, in the various groups of animals.

This was done for each experiment from the data tabulated on pp. 22–24. From such curves an average curve for the three Echidnas, three Marsupials, and two Mammals was derived by taking the values for a difference of temperature of 5, 10, 15° C., &c., as indicated by the individual curves and averaging them.

These average curves are represented in fig. 6, and the data from which they were drawn are given in tabular form below.

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* "Physiol. Peculiarities of Echidna-muscle," 'Journ. of Physiol.,' vol. 26, 1901.

1. Echidnas. Average of three individuals.

Difference in temperature, animal and environment.	CO_2 produced per 1000 sq. centims. per hour		CO_2 increase per 5° C.
2° C.	·35		—
5	·41	=	·20
10	·61	=	·20
15	·81	=	·24
20	1·05		

From 5 to 20° C. difference in temperature between animal and inclosure, the production of CO_2 is approximately a linear function of the difference in temperature between animal and environment. Owing to imperfect homœothermism the difference in temperature did not exceed 20° C.

2. Marsupials. Average of three individuals of different genera.

Difference of temperature, animal and environment.	CO_2 produced per 1000 sq. centims per hour.		CO_2 increase per 5° C.
0°	·43		
5	·39		
10	·32	=	·04
15	·36	=	·06
20	·48	=	·13
25	·61	=	·24
30	·85	=	·35
32	·98		

With more perfect homœothermism in Marsupials the difference of temperature reached 32° C.

3. Mammals. Average of Cat and Rabbit.

Difference of temperature, animal and environment.	CO_2 produced per 1000 sq. centims. per hour.		CO_2 increase per 5° C.
2°	1·05		
5	·96		
10	·94	=	·07
15	1·01	=	·08
20	1·09	=	·08
25	1·17	=	·21
30	1·38	=	54
32·5	1·65		

The difference in temperature reached 32°·5 C.

These tables show that the actual increase in oxidation as the difference in temperature between animal and environment increases, is at first very much less in Marsupials and Mammals than in Echidna, but reaches or exceeds that of the latter animals, when this difference becomes greater.

The contrast is more striking when expressed as the percentage increase in CO_2 produced when the difference in temperature between animal and environment varies from 10° to 20° C.

This is for Echidnas	72 per cent.
Platypus	59 ,,
Marsupials	50 ,,
Mammals	16 ,,

This indicates that the importance of variation in heat-production as a means of temperature adjustment within this range diminishes in the above order, and that whereas variation in production is uniformly employed by Echidnas, in Ornithorhynchus, Marsupials, and Mammals, other means of regulation must be utilised. A glance at the curves, fig. 6, will also show that, with the exception of Echidna, variation in production grows gradually in importance as the difference in temperature between the animal and environment increases, and, further, that in higher Mammals variation in production is comparatively trivial until the conditions become sufficiently favourable to heat loss.

The higher Mammals evidently produce a much larger quantity of heat per unit surface at all temperatures than Marsupials and Monotremes, and rely upon dissipating the balance when not wanted to keep up their body-temperature. The lower Mammals are much more economical, and tend more to increase their expenditure of energy only as required. In this respect Echidna is the most thrifty. The actual expenditure of Echidna is, for a difference of 20° between his body-temperature and the air, greater than Marsupials; but it must be remembered that his insulation is very much poorer.

According to the results of SENATOR,* SPECK,† and LOEWY,‡ *Man* utilises variation in production still less until loss of heat becomes excessive. With a very considerable variation in external temperature LOEWY found the oxygen consumed by man remained the same in more than half his experiments, and that if voluntary movements were restrained, the heat production was not increased until the loss of heat occasioned shivering and involuntary rigidity of muscles.

Apart from modifying insulation in the form of clothes, the machinery for varying heat-loss is more extensively developed in man on account of the much larger surface for sweating.

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* 'Arch. f. Anat. und Physiol.,' 1874, s. 22.

† "Normale Athmung des Menschen."

‡ 'Archiv f. d. Ges. Physiol.,' 1890, vol. 46.

In fig. 5 I have represented the CO_2 production per 1000 sq. centims. of a man with environment at different temperatures for comparison with that of Mammals and Marsupials. The curve was drawn from calculations from VOIT'S* data. These are the only figures which I know where the experiment was conducted upon the human subject under conditions similar to my experiments, viz., in a chamber supplied with cooled or warmed air. The CO_2 produced varied little when the temperature of the air was changed from 14° to 27° C.

Investigation of Echidna for Evidence of Temperature-regulation other than by Variation in Production.

Marsupials are fairly well supplied with sweat-glands. Ornithorhynchus possesses an abundant supply upon the soft snout and frill, but none elsewhere. In Echidna I could find none. To test whether Echidna varied heat-loss by vaso-motor adjustment, I shaved the coarse hair from the feet and ankles of two specimens of Echidna and secured them in two bottles, one of which I filled with water at 40° C., and the other at 0°. I could detect no difference in the colour of the two for several minutes, then the foot in the *cold* water became redder than the other.

I have tried to obtain evidence on this point in another way. I placed Echidnas in a metal box in the ice-chest (temp. 2–3° C.) for several hours. Their body temperatures slowly fell; but, notwithstanding that they stood upon the cold iron, their feet remained warm and were only 2°–3° C. lower than their rectal temperatures. When I myself grasped the metal box my fingers soon became blanched and cold.

It appears that Echidna is devoid of both sweat-mechanism and vaso-motor adjustment of superficial circulation in response to temperature. This was suggested by the fact that the production of CO_2 was so nearly directly proportional to the difference in temperature between the animal and environment, in other words, was proportional to loss of heat.

Without means of losing heat by evaporation from the skin, or of increasing evaporation from the lungs by additional respirations, Echidna is incapable of adapting itself to an environment the temperature of which is above 35°–37° C., for it cannot reduce its heat-production below a certain minimum which is itself dependent upon the body-temperature. When exposed to a temperature of 35° C. its body-temperature soon rises above the physiological maximum (about 38° C.), this causes further heat-production, and it dies of heat apoplexy.

This happened twice in the course of these experiments, and I have had unwelcome evidence of the same during the hot weather we sometimes have in Melbourne. On four occasions when the hot weather has been sufficiently prolonged for the temperature of the box in which they were kept to rise to 37° C., my Echidnas have succumbed.

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* 'Zeitschrift f. Biol.,' 1878, vol. 14.

Adjustment of temperature by variation in production is economical, but, like most economies, has its disadvantages, since it greatly curtails, as just seen, the range of temperature in which an Echidna can live. In their natural state these animals burrow several feet into the ground, and on hot days only emerge after sundown.

This curtailment of their range of temperature is not the only disadvantage attendant upon their disability to vary loss of heat. The production of heat will obviously increase with muscular work, so that their temperature is not independent of activity. I have frequently observed their temperatures rise a degree or two after digging. The following is an instance:—Echidna. Weight, 3350 grammes. Temperature of air, 19° C. Temperature of earth, 8 inches below surface, 16°·5 C. The earth was damp.

12.15. Temperature of Echidna, 32°·1 C.
Commenced to dig in a desultory way. He was kept to the task by scratching his back with a stick. He was not allowed to cover himself, but, when he had dug a hole about 10 inches in depth, he was removed to another situation and persuaded to dig again.

12.50. Temperature, 33°·7 C.
In 35 minutes his temperature had risen 1°·6 C., notwithstanding the cool damp earth in which he was working.

The amount of work necessary to raise the temperature of his body 1°·6, assuming that his specific heat = ·8° is, independent of heat lost, 1819 kilogramme metres.

CONCLUSIONS.

Echidna is the lowest in the scale of warm-blooded animals. Its attempts at homœothermism fail to the extent of 10° C. when the environment varies from 5° to 35° C.

During the cold weather Echidna abandons all attempts at homœothermism and hibernates for four months, during which time its temperature is only a few tenths of a degree above that of its surroundings.

The production of heat in Echidna is proportional to the difference in temperature between animal and environment.

At high temperatures Echidna does not increase the number or depth of its respirations. It possesses no sweat glands, and exhibits no evidence of varying loss of heat by vaso-motor adjustment of superficial vessels in response to external temperature.

Ornithorhynchus is a distinct advance upon Echidna; although its body temperature is low it maintains it fairly constant. It possesses abundant sweat glands upon the soft snout and frill but none elsewhere. The CO_2 production with varying temperature of environment indicates that the animal can modify heat-loss as well as production. Ornithorhynchus does not increase respirations at high temperatures. Marsupials show evidence of utilising variation in loss to an extent greater than Ornithorhynchus, but less than higher Mammals. Their respirations are sometimes slightly increased in number at high temperatures.

Higher Mammals depend principally upon variations in heat-loss, and do not greatly increase production of heat until subjected to an environment 25° to 30° below their own body temperatures. At high temperatures they assist in dissipating heat by rapid respiration.

Variation in production of heat is the ancestral method of homœothermic adjustment. During the evolution of the warm-blooded animal it has, through developing a mechanism by means of which it can vary production in accordance with heat lost, overcome one disadvantage of cold-bloodedness, viz., that activity is dependent upon external temperature. It has thereby increased its range in the direction of low temperatures.

Later, by developing a mechanism controlling loss of heat, it has increased its range in the direction of high temperatures, and also rendered body-temperature largely independent of activity. These advantages have been gained by a greater expenditure of energy.