Standard metabolism, body temperature, and surface areas of Australian marsupials

TERENCE J. DAWSON AND A. J. HULBERT
School of Zoology, University of New South Wales, Kensington, New South Wales 2033, Australia

EARLY REPORTS of low body temperatures of marsupials (34) prompted Martin in 1902 (21) to measure the metabolic rates of several species. He reported values that were less than one-third of those of eutherian mammals and since that time his work has been widely cited as evidence that marsupials represent a level of physiological development intermediate between the "lower" monotremes and the "higher" eutherians. Recently, however, several workers have shown that many marsupials can regulate their body temperatures efficiently over a wide range of temperatures (5, 7, 25, 26, 30) and thus marsupials should not be regarded as homeothermically inferior to the placental mammals. This work, especially that which showed that marsupials represent a level of physiological development intermediate between the "lower" monotremes and the "higher" eutherians. Recently, however, several workers have shown that many marsupials can regulate their body temperatures efficiently over a wide range of temperatures (5, 7, 25, 26, 30) and thus marsupials should not be regarded as homeothermically inferior to the placental mammals. This work, especially that which showed that marsupials represent a level of physiological development intermediate between the "lower" monotremes and the "higher" eutherians. Recently, however, several workers have shown that many marsupials can regulate their body temperatures efficiently over a wide range of temperatures (5, 7, 25, 26, 30) and thus marsupials should not be regarded as homeothermically inferior to the placental mammals.

MATERIALS AND METHODS

Animals. The species used in the study and their origins are listed in Table 1. Only mature animals in reasonable condition were used, and in almost all cases an equal sex ratio was maintained. Mean weights and ranges may be found in Tables 2 and 3. The kangaroos were weighed before the experiments on a Weddburn platform balance capable of weighing to 10 g, whereas all the other animals were weighed on a Sauter top-pan balance accurate to 0.1 g. The weights ranged from 9 g to 54 kg; that is, a 6,000-fold range between the smallest and largest animal.

Temperature measurements. Temperatures were measured with copper-constantan thermocouples, which had been calibrated to 0.1 C against a standard thermometer, and were continuously recorded on a Honeywell electronic 15 recording potentiometer. Body temperature (Tbody) was measured as deep colonic temperature. The depth of insertion of thermocouples varied from 2 to 20 cm depending on the size of the animal. To prevent biting of the thermocouple leads during continuous measurements, the animals were placed in wire cages just small enough to prevent the animals turning around. These restraining cages also served to reduce excessive movement while still allowing the animals to rest.

All experiments were carried out in a temperature-controlled room or cabinet regulated to ±0.2 C. The air temperature at which each species was examined is given in Table 2. These temperatures were judged to be above the lower critical temperatures of the various species on the basis of preliminary studies.

Metabolism. Oxygen consumption was determined using an open-circuit technique. The animals were fasted for 12–48 hr prior to measurement depending on their size. The restraining cage containing the animal was placed inside an airtight Perspex metabolic chamber through which room air was drawn at rates ranging from 200 ml/min for the marsupial mice to 60 liters/min for the kangaroos. The rate at which air flowed through the chamber was kept constant during each experiment and was measured with a calibrated gas meter. The ΔPo2 of
TABLE 1. Australian marsupial species used in present study

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dasyuridae</td>
<td>Fat-tailed marsupial mouse (Sminthosipris crassicaudata)</td>
<td>Western NSW and eastern South Australia</td>
</tr>
<tr>
<td></td>
<td>Brown marsupial mouse (Antechinus stuartii)</td>
<td>Central NSW coast</td>
</tr>
<tr>
<td>Phalangeridae</td>
<td>Sugar glider (Petaurus breviceps)</td>
<td>Northeastern NSW</td>
</tr>
<tr>
<td></td>
<td>Brush-tailed possum (Trichosurus vulpecula)</td>
<td>Sydney, NSW</td>
</tr>
<tr>
<td>Peramelidae</td>
<td>Long-nosed bandicoot (Peramelis nasuta)</td>
<td>Sydney, NSW</td>
</tr>
<tr>
<td></td>
<td>Short-nosed bandicoot (Isoodon macrourus)</td>
<td>Central NSW coast</td>
</tr>
<tr>
<td>Macropodidae</td>
<td>Tammar wallaby (Macropus eugenii)</td>
<td>Kangaroo Island, South Australia</td>
</tr>
<tr>
<td></td>
<td>Potoroo (Potorous tridactylus)</td>
<td>Sydney, NSW</td>
</tr>
<tr>
<td></td>
<td>Red kangaroo (Megaleia rufa)</td>
<td>Western NSW</td>
</tr>
</tbody>
</table>

* Used only in energy metabolism study. † Used only in surface-area study.

As a check on our equipment, the standard metabolic rates of several laboratory rabbits were determined and compared with the values that Lee (20) obtained during his extensive studies. Our results were all within 1% of those predicted from Lee's work.

Surface area. Surface area was determined immediately after the animals were killed and weighed. Parts of the body with excess hair were shaved with clippers and the body surface area was then divided into four major regions: head, tail, trunk, and limbs (in the sugar gliders the limbs and trunk were treated as one). These areas were then skinned, the pieces of skin were pinned out on drawing paper, without excessive stretching, and their outlines traced. Usually there were about 16-24 individual pieces of skin per animal. Parts like the ears, glider's membranes, and the feet of the very small animals were pinned out, traced, and the areas within these outlines doubled.

TABLE 2. Resting body temperature and standard metabolism of some Australian marsupials

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Weight, g</th>
<th>Mean Air Temperature, °C</th>
<th>Body Temperature, °C</th>
<th>Oxygen Consumption, ml/hr</th>
<th>Standard Metabolic Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>kcal/hr</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>cal/g·hr</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>kcal/mg·kg per hr</td>
</tr>
<tr>
<td>Sminthosipris crassicaudata</td>
<td>6</td>
<td>14.1±3.0</td>
<td>32</td>
<td>33.6±0.0</td>
<td>10.7±3.0</td>
<td>0.090±0.018</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.067-0.112)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(5.91-7.13)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(40.4-59.2)</td>
</tr>
<tr>
<td>Antechinus stuartii</td>
<td>6</td>
<td>36.5±12.2</td>
<td>30.5</td>
<td>34.4±0.9</td>
<td>36.6±10.2</td>
<td>0.174±0.031</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.115-0.229)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(4.19-5.66)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(40.9-56.5)</td>
</tr>
<tr>
<td>Petaurus breviceps</td>
<td>6</td>
<td>128.1±19.1</td>
<td>30</td>
<td>36.4±0.7</td>
<td>88.7±11.0</td>
<td>0.424±0.003</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.392-0.480)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(3.14-4.14)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(45.1-56.7)</td>
</tr>
<tr>
<td>Perameles nasuta</td>
<td>6</td>
<td>686±143</td>
<td>28</td>
<td>36.1±0.7</td>
<td>322±65</td>
<td>1.54±0.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(1.01-1.87)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(2.11-2.46)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(45.9-55.1)</td>
</tr>
<tr>
<td>Isondon macrourus</td>
<td>6</td>
<td>880±301</td>
<td>28</td>
<td>34.7±0.9</td>
<td>393±80</td>
<td>1.85±0.40</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(1.51-2.60)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(1.79-2.30)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(42.2-57.4)</td>
</tr>
<tr>
<td>Trichosurus vulpecula</td>
<td>6</td>
<td>1,983±154</td>
<td>27</td>
<td>36.2±0.5</td>
<td>625±62</td>
<td>2.99±0.29</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(2.62-3.50)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(1.21-1.65)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(35.3-47.1)</td>
</tr>
<tr>
<td>Macropus eugenii</td>
<td>6</td>
<td>1,796±141</td>
<td>25</td>
<td>36.4±0.5</td>
<td>1,382±125</td>
<td>6.64±0.60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(3.85-7.44)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(1.31-1.30)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(46.9-53.7)</td>
</tr>
<tr>
<td>Megaleia rufa</td>
<td>6</td>
<td>32,490±12,680</td>
<td>26</td>
<td>35.9±0.5</td>
<td>5,791±3,294</td>
<td>26.78±3.29</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(17.61-42.15)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(0.781-0.926)</td>
</tr>
</tbody>
</table>

Values are means ± sd. Figures in parentheses show ranges. N = numbers of animals.
area of each tracing was determined by the use of a Coradi planimeter (accuracy ± 0.2%).

To reduce errors due to the stretching or shrinking of the skin, pieces of graph paper of known areas were glued onto the animal's trunk and limbs before skinning and outlined. These areas were cut out, planimetered, and species correction factors for the surface area of the limbs and trunk were calculated. In the smallest species, due to their size, it was possible to carry out this procedure only on the trunk.

RESULTS

**Body temperature and standard energy metabolism.** The standard metabolic rates, expressed per animal, per unit weight and per unit of metabolic body size are shown in Table 2 together with the resting body temperatures of the eight species. Most of the animals were found to have body temperatures lower than those previously reported in the literature and considerably below the temperatures usually given for eutherian mammals. Morrison (26) gave minimum daily rectal temperatures of 37.1 and 37.0°C respectively for *Sminthopsis crassicaudata* and *Antechinus stuartii*. Morrison's measurements were made while the animals were being handled, however, and at air temperatures which were probably below their lower critical temperatures. The difference in T

The relationship between body weight (W) and standard metabolism (SMR) for eight species of marsupials is shown in Fig. 1, in which the data are plotted on a double logarithmic scale. Examined in this manner, the data gave a correlation coefficient of 0.9997 and were best represented by the regression line (least-squares method):

$$\text{SMR (cal/hr)} = 12.30 \times W^{0.737} \text{(g)}$$

This equation is similar to that found in a preliminary study (8). The broken line drawn in Fig. 1 is the line representing the same relationship for eutherians as determined by Kleiber (17):

$$\text{SMR} = 16.4 \times W^{0.76}$$

Expressed in units of metabolic body size, i.e., to $W^{3/4}$, the marsupial's mean standard metabolism was found to be 48.6 kcal/kg$^{3/4}$ per day. A Student *t* test showed a highly significant difference ($P < 0.0001$) between this result and the value for eutherians of 70 kcal/kg$^{3/4}$ per day (17).

**Surface area.** The ratio surface area : volume$^{3/4}$ is a constant when one considers different sizes of the same shape. Using this fact, Mech (23) assumed all animals to have approximately the same specific gravity and obtained the equation:

$$\text{SA} = K \cdot W^{3/4}$$

where $\text{SA}$ is the animal's surface area (cm²), $W$ is its weight (g), and $K$ is a constant now known as the Mech factor. The value of $K$ depends on the shape of the animal and is normally calculated empirically for different species. Table 3 contains the mean weight, surface area, and Mech factor for each species studied and a double logarithmic plot of the data appears in Fig. 2.

A Mech factor of 10 is commonly used for animals without a known value and, as can be seen from Fig. 2, this is a reasonable approximation for some of the animals. For other species, however, it is not so accurate, and the surface area of these animals may be some 20–30% more than that given by the line $\text{SA} = 10 \cdot W^{3/4}$. This is particularly the case for the small marsupial mice which have relatively very large membranous ears. The sugar gliders, due to their unusual shape, have a surface area (and $K$ value) more than double that of a normal animal. This can be explained by the fact that the gliding membranes contribute about 51% of the animal's total surface area.

The proportion of the total surface area that each body region contributes is shown in Table 4.

**TABLE 3. Surface areas of several Australian marsupials**

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Weight, g</th>
<th>Surface Area, cm²</th>
<th>$K$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Sminthopsis crassicaudata</em></td>
<td>6</td>
<td>10.24 ± 2.56</td>
<td>88.1 ± 12.7</td>
<td>13.8 ± 1.1</td>
</tr>
<tr>
<td><em>Antechinus stuartii</em></td>
<td>6</td>
<td>30.8 ± 11.6</td>
<td>118.2 ± 29.7</td>
<td>12.3 ± 0.7</td>
</tr>
<tr>
<td><em>Petaurus breviceps</em></td>
<td>4</td>
<td>116.5 ± 28.9</td>
<td>615 ± 127</td>
<td>25.7 ± 2.7</td>
</tr>
<tr>
<td><em>Potorous nasuta</em></td>
<td>6</td>
<td>917.3 ± 523</td>
<td>956 ± 133</td>
<td>10.6 ± 1.1</td>
</tr>
<tr>
<td><em>Potorous tridactylus</em></td>
<td>2</td>
<td>1188 ± 33</td>
<td>1,201 ± 83</td>
<td>10.7 ± 0.5</td>
</tr>
<tr>
<td><em>Trichosurus vulgaris</em></td>
<td>7</td>
<td>2,054 ± 400</td>
<td>1,717 ± 162</td>
<td>10.7 ± 0.5</td>
</tr>
<tr>
<td><em>Macropus rufus</em></td>
<td>6</td>
<td>5,085 ± 733</td>
<td>3,121 ± 237</td>
<td>10.6 ± 0.3</td>
</tr>
<tr>
<td><em>Megalix rufa</em></td>
<td>6</td>
<td>28,730 ± 11,910</td>
<td>10,674 ± 5,052</td>
<td>11.6 ± 0.8</td>
</tr>
</tbody>
</table>

Values are means ± s.d. Figures in parentheses show ranges.
proportion to W^{0.75}. This theory does not, however, explain why x should represent this struggle between weight and surface proportionality. It has been seen that in the equation \( \text{SMR} = aW^{b} \), marsupials have the same value of b as eutherians, but what of the value of a for both groups? In other words, is marsupial energy metabolism at the same level as that of placental mammals? Per unit of metabolic body size, the mean level of marsupial metabolism from the present work is 48.6 kcal/kg^{0.75} per day. This is approximately 70\% of the eutherian value, 70 kcal/kg^{0.75} per day (17). Martin (21) found the mean metabolic rate of three marsupials to be less than one-third of the mean value for two eutherians of similar size. The larger difference he reported was possibly due to several factors. First, he measured carbon dioxide production, which is easier to measure than oxygen consumption, but is less satisfactory since CO₂ output may be markedly affected by changes in respiration. Martin also did not allow sufficient time for equilibration at the different ambient temperatures and, last, the eutherians used were not satisfactory for proper comparison. Both the rabbit and cat were recorded as being half-grown, and the metabolic rate of growing and immature animals is generally greater than that of fully grown, mature subjects (3).

The second report of a marsupial metabolic rate was 60 years after Martin's initial work. Bartholomew and Hudson (1) reported that the minimum oxygen consumption of the pigmy possum Cercartetus nanus was approximately 70\% of that expected for an eutherian of the same size. They explained this low value by assuming that one-third of the animal was fat. However, it is more likely that this low value was a reflection of the physiological characteristics of marsupials in general. Other recently reported marsupial metabolic rates were 30–35\% lower than the predicted eutherian values (6, 15). Indirect evidence also supports our finding of a reduced level of metabolism in marsupials (4, 6, 10, 14).

For many years the data of Martin (21) have been quoted as showing that marsupials are physiologically intermediate between the "lower" monotremes and the "higher" eutherians and part of a graded series from reptiles to eutherians. Whereas our results for marsupial standard metabolism differ considerably from those of Martin,

\begin{table}[h]
\centering
\caption{Contribution of various body regions to total surface area of marsupials}
\begin{tabular}{lcccc}
\hline
Species & N & Tail, \% & Head, \% & Limbs, \% & Trunk, \% \\
\hline
Sminthopsis crassicaudata & 6 & 9.7±3.0 & 26.6±2.3 & 26.2±4.1 & 38.0±4.0 \\
Antechinus stuartii & 6 & 7.7±1.7 & 19.8±2.5 & 33.2±2.2 & 73.9±3.7 \\
Petaurus breviceps & 4 & 4.7±0.4 & 9.5±1.0 & & 85.8±1.3 \\
Pteromes nasuta & 6 & 4.3±0.8 & 13.0±1.7 & 40.1±2.4 & 40.6±4.1 \\
Potorus tridactylus & 2 & 9.4±0.3 & 13.9±1.3 & 33.5±2.1 & 43.3±3.7 \\
Trichosurus vulpecula & 7 & 9.4±0.7 & 13.0±0.6 & 39.2±1.1 & 38.4±1.4 \\
Macropus eugenii & 6 & 12.0±0.3 & 10.5±0.6 & 35.9±2.9 & 41.6±2.4 \\
Megaleia rufa & 6 & 11.0±1.0 & 9.8±1.0 & 39.6±2.4 & 39.6±1.9 \\
\hline
\end{tabular}
\end{table}

Values given are means ± SD.
metabolically the marsupials are still intermediate between monotremes and eutherians; but what significance does this have from an evolutionary point of view? This point is perhaps best considered together with what is known about the metabolism of the higher vertebrates in general. A summary of this information is given in Table 5. For comparative purposes the standard metabolism also has been expressed as kcal/kg\( ^{3/4} \) per day and corrected to a common body temperature (in this case 38 °C). That the homeotherms or endotherms form a metabolic group which is distinct from the poikilothermic or ectothermic reptiles is unknown, but the differences between monotremes, marsupials, and eutherians need not show any specific evolutionary relationships in view of the current theories. One aspect of the lower metabolism of the marsupials is that it may result in a lower food requirement and an increased life of metabolic stores. A reduction of one-third in the rate of metabolism should lead to a 50% increase in the life of metabolic reserves. This would be especially advantageous for arid and semi-arid zone marsupials such as the fat-tailed marsupial mice.

Because very little information is available concerning the energy metabolism and body temperatures of American marsupials, it is not possible to say with any degree of certainty that our results apply to marsupials in general. However, the body temperatures obtained by Morrison (24) for two species of Central American opossums were similar to those we have measured in the Australian marsupials. As well, the standard metabolism of a North American opossum (Didelphis virginiana) was similar to that found in the present study (unpublished observation of T. J. Dawson, E. C. Crawford, and K. Schmidt-Nielsen). Meeh (23) suggested the equation \( SA = K \times W^{2/3} \) be used to calculate an animal's surface area where \( K \) is a constant which should be determined empirically for each species. Other powers of weight have been suggested for some species, but if one regards specific gravity as being approximately constant within a species, then these are dimensionally incorrect.

The Meeh factors for most animals fall around 10. Generally, the slimmer the species, the higher the Meeh factor; whereas, for stouter ones, it is lower. A very powerful influence on the Meeh factor is thin membranous-type areas. They add little to the weight but markedly increase the surface area and thus also \( K \). This is aptly demonstrated by the sugar gliders. Their Meeh factor is just over twice the average value for the other species with corresponding areas. They add little to the weight but markedly increase the surface area and thus also \( K \).

Meeh factors for two marsupials have been reported in the literature but both of these may be unreliable. Maxwell et al. (22) gave a value of 8.9 for kangaroos. This is similar to the value for pigs (32) but, as kangaroos appear much slimmer than pigs, the actual value should be higher.
They do not say how they determined $K$, nor on how many or what species. Reid and McDonald (28) found a factor of 12.0 for two brush-tailed possums compared to 10.7 found in the present study. The former value may be high since even the snakes have been found to have a mean value of only 12.5 (9).

Although surface area is intimately involved in the heat transfer between an animal and its environment, it must be remembered that the surface area measured in this study is the total anatomic surface and need not represent the physiologically effective area, especially in the case of the gliding possum Petaurus breviceps.

We thank Mr. G. Gordon (for the Antechinus), Mr. R. Hope (for some Smilodons), Mr. P. Johnston (for the two Potorous), and the National Parks and Wildlife Service of New South Wales for permission to capture protected species.

This work was supported by a grant from the Australian Research Grants Committee.

Received for publication 29 September 1969.

REFERENCES

1. Bartholomew, G. A., and J. W. Hudson. Hibernation, estiva-
tion, temperature regulation, evaporative water loss and heart-
rate of the pigmy possum (Cercartetus nanus). Physiol. Zool. 29:

2. Bartholomew, G. A., and V. A. Tucker. Size, body temperature,
thermal conductance, oxygen consumption, and heart rate in


4. Brown, G. J., and A. R. Main. The nitrogen requirements of

5. Dawson, T. J. Temperature regulation and evaporative water
loss in the brush-tailed possum Trichosurus vulpecula. Comp.

on blood volume and haematocrit in the brush-tailed possum

balance of the macropodid marsupial Macropus eugeni. Comp.

8. Dawson, T. J., and A. J. Hulbert. Standard energy metabolism of

9. DeBoer, E. F. Basal Metabolism in Health and Disease. Philadelphia:
Lea & Febiger, 1936.

10. Fraser, E. H., and J. F. Kinneir. Urinary creatinine excretion
by macropod marsupials. Comp. Biochem. Physiol. 28: 685-692,
1969.

11. Hemmingsen, A. M. Energy metabolism as related to body size


13. King, J. R., and D. S. Farner. Energy metabolism, thermoregu-
lation, and body temperature. In: Biology and Comparative


15. Kinneir, J. E., K. C. Purkott, and A. R. Main. The ability of
the tammar wallaby (Macropus eugeni) to drink sea water. Comp.

1932.


18. Lasiewski, R. C., and W. R. Dawson. A re-examination of the rel-
ation between standard metabolic rate and body weight in birds.

19. Lillegavn, J. A. Late Cretaceous Mammals of Upper Part of
Edmonton Formation of Alberta, Canada and Review of Marsupial-
Placentan Dichotomy in Mammalian Evolution. Univ. Kansas Paleon-

18: 489-500, 1939.

21. Martin, C. J. Thermal adjustment and respiratory exchange in

dynamics of kangaroos and wallabies. Am. J. Physiol. 206: 967-
974, 1964.

23. Meiri, K. Oberflachenmessungen des menschlichen K6rpers. Z.

24. Mikkelsen, P. R. Temperature regulation in three Central Ameri-

25. Morrison, P. R. Body temperatures in some Australian mammal.

26. Morrison, P. R. Body temperatures in some Australian mammals.

27. Morrison, P. R., and F. A. Ryser. Weight and body temperature

28. Reid, J. A., and J. K. McDonald. Renal function in the mar-
supial Trichosurus vulpecula. Comp. Biochem. Physiol. 25: 1071-1080,
1968.


30. Robinson, K. W., and P. H. Morrison. The reaction to hot at-
mospheres of various species of Australian marsupial and placental

31. Runnau, M. Uber den Einfluss der K6rpergr6sse auf Stoff-und

Leipzig: Deutsche, 1902.

33. Schmidt-Nielsen, K., T. J. Dawson, and E. C. Crawford. Tem-
perature regulation in the echidna (Tachyglossus aculeatus). J. Cell.

34. Sutherland, A. The temperatures of reptiles, monotremes and