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An allometric comparison of the mitochondria of mammalian and reptilian tissues: The implications for the evolution of endothermy

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Summary. The effects of body size and phylogeny on metabolic capacities were examined by comparing the mitochondrial capacities of 6 mammalian and 4 reptilian species representing 100-fold body weight ranges. The mammals examined included 3 eutherian, 2 marsupial and a monotreme species and the reptiles 2 saurian, 1 crocodilian and 1 testudine species. The tissues examined were liver, kidney, brain, heart, lung and skeletal muscle. Allometric equations were derived for tissue weights, mitochondrial volume densities, internal mitochondrial membrane surface area densities, tissue mitochondrial membrane surface areas both per gram and per total tissue and summated tissue mitochondrial membrane surface areas.

For the mammals and reptiles studied a 100% increase in body size resulted in average increases of 68% in internal organ size and 107% in skeletal muscle mass. Similarly, total organ mitochondrial membrane surface areas increase in mammals and reptiles by an average 54% and for skeletal muscle by an average 96%. These values are similar to increases in standard (54 and 71%) and maximum (73 and 77%) organismal metabolism values found by other authors for mammals and reptiles respectively.

Although the allometric exponents (or rates of change with increasing body size) of the mitochondrial parameters in mammals and reptiles are statistically the same, in general the total amount of mitochondrial membrane surface area in the mammalian tissues are four times greater than found in the reptilian tissues. These differences were not the result of any single 'quantum' factor but are the result of the mammals having relatively larger tissues with a greater proportion of their volume occupied by mitochondria and to a lesser extent increases in the internal mitochondrial membrane surface area densities. Mitochondrial volume density from this present study would appear to be the major factor involved in changing weight specific metabolism of tissues both as a result of changes in body size and in the evolution of endothermy in mammals from reptiles.

Introduction

Two of the major determinants of how much oxygen an animal will consume under standard conditions are its body size and its phylogeny. An increase in body size of 100% increases an animal's total oxygen consumption by 68%. This is generally true for both mammals (Kleiber 1961; Dawson and Hulbert 1970) and ectothermic vertebrates (Hemmingsen 1960; Bennett and Dawson 1976; Taigen 1983) and is described by the relationship between metabolism (M) and body size (W) as $M = a\,W^{0.75}$. The phylogenetic differences between groups of animals lies in the level of their total organismal oxygen consumptions. Mammals consume vastly greater amounts of oxygen (5–10 ×) than similar sized ectotherms measured at the same body temperatures (Dawson and Hulbert 1970; Bennett and Dawson 1976). These differences are shown in the 'a' constants (or elevations) which are higher for mammals than for ectothermic vertebrates.

In the evolution of mammals from reptiles there has been a transition from low to high meta-

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bolic capacities. In a comparison between single mammalian and reptilian species, of similar body weight and preferred body temperature (Else and Hulbert 1981), large differences in the mitochondrial capacities of the tissues from each species were found. These differences always showed increased metabolic capacities in the mammalian tissues compared to the same reptilian tissues. In a further comparison (Else and Hulbert 1985), the mitochondrial capacities of liver, kidney, brain, heart, lung and skeletal muscle, measured by determining the mitochondrial membrane surface areas, from six diverse mammalian species over a 100-fold weight range showed allometric exponents characteristic of those for aerobic metabolism of the whole animal. In this present paper the mitochondrial capacities of the same six tissues from 4 reptilian species representing 3 reptilian subclasses and a 100-fold weight range are examined. Mitochondrial volume densities, membrane surface area densities, tissue weights, tissue specific and total tissue mitochondrial membrane surface areas are determined and compared allometrically to those values found for mammals.

Materials and methods

Animals. The reptilian species used in the comparison are the lizards, *Amphibolurus nuchalis* (body weights 29 g and 36 g) and *Amphibolurus vitticeps* (246 g and 249 g), the freshwater tortoise, *Chelodina longicollis* (575 g and 582 g) and freshwater crocodile, *Crocodylus johnstoni* (242 g and 2286 g). The lizards were maintained in temperature controlled boxes at 37 ± 2 °C. The freshwater tortoises were kept at room temperature (25 °C) in a filtered, aerated pool with access to a dry pen area. The crocodiles were obtained from Sydney University. The lizards and tortoises were fed daily on a varied fruit, meat, mealworm, diet.

The mammalian species used include the mouse (*Mus musculus;* body weights 27 g and 41 g), the rat (*Rattus norvegicus*: 235 g and 298 g) and the rabbit (*Oryctolagus cuniculus*: 1870 g and 2067 g). The marsupial mammals include the brown antechinus (*Antechinus stuartii*: 18 g and 23 g) and the bandicoot (*Perameles nasuta*: 1145 and 1835 g). The monotreme species examined was the echidna (*Tachyglossus aculeatus;* 1486 g). All animals were provided with food daily, ad libitum water and a 12:12 light:dark photoperiod.

Two animals from each species were used to determine the mitochondrial volume and membrane surface area densities and tissue weights. The tissues used were the liver, kidney, brain, heart, lung and skeletal muscle (gastrocnemius muscle) except for *A. nuchalis* and *M. musculus* where only liver, kidney, brain and heart values are available. These values for *A. nuchalis* and *M. musculus* are those previously reported (Else and Hulbert 1981). Only liver, kidney and heart data is available from either one or the other of the two *A. stuartii* used. For skeletal muscle the mitochondrial parameters were measured only on the gastrocnemius muscle but muscle weight includes all skeletal muscle. The values for the mammals are those previously reported (Else and Hulbert 1985).

Determination of tissue weights and the preparation of the tissu Animals were killed either by decapitation or an injection Sagital. The six tissues: liver, kidney, brain, heart, lung a gastrocnemius muscle were quickly removed from each anin and weighed (±0.001 g). The carcasses were frozen for la complete body composition determinations. Random samp from each of the six tissues were placed in ice cold 2% glutar dehyde fixative in 0.1 M sodium cacodylate buffer overnig after which they were fixed in 2% w/v osmium tetroxide 0.1 M sodium cacodylate buffer (pH = 7.4) for 4 h and th rinsed in 2% w/v sodium acetate and bulk stained in 2% w uranyl acetate. The tissue samples were then dehydrated in a ethanol series (30–100% dry) over 3 h, transferred to 100° dry acetone (2 × 15 min) and infiltrated with 1:2 and 1:9 ac tone: Spurrs resin for 1 h and 12 h respectively. The tissu blocks were then placed in pure resin for 1 h and finally cure in fresh resin at 60 °C overnight. Sections were post staine with lead citrate (Reynolds 1963). Glutaraldehyde (10% solr and sodium cacodylate (97%) were obtained from BDH Chem cals. Ethanol, acetone, lead nitrate and sodium acetate wer all A.R. grade and supplied by Ajax Chemicals. Sodium citrat (99%) was supplied by May and Baker Laboratory Chemical and osmium tetroxide from Johnson Malthey Chemicals. Ura nyl acetate and Spurrs resin kits were purchased from Polaron

Sampling and sectioning of tissues. Ten randomly chosen tissu blocks (12 blocks in the case of the liver) were sectioned fo each tissue of every individual animal studied. Tissue block sections were cut on an ultramicrotome (LKB 8800 III) using glass knives and supported on 200 μm copper mesh grids.

Electron microscopy and stereology. Electron micrographs a magnifications of × 6,200 and 53,000 were taken from each sectioned tissue block using a JEM 100U electron microscope. The × 6,200 micrographs were used to determine relative mitochondrial volume densities and inner mitochondrial membrane surface areas. The × 53,000 micrographs were used for the determination of cristae membrane surface areas. Cristae membrane surface densities (S_{vc}) were measured from orthodox (state 4) mitochondria.

Relative volume densities of the mitochondria (V_v) were estimated by projecting electron micrographs onto a 28 cm square screen with a 100 point lattice test system. The surface area densities (S_{vi}) of the mitochondrial membranes were found from the projection of electron micrographs onto similar screens and counting the number of intersections (I_i) of the membranes with six diameters of known length within a circular test grid, using the equation

$$S_{vi} = 2I_i / LT \quad (1)$$

where S_{vi} equals the surface area per volume ratio ($m^2 \cdot cm^{-3}$), from Weibel (1969). Cristae membrane surface areas (S_{vc}), determined from within the mitochondria using the × 53,000 electron micrographs are in units of m^2 of cristae membrane per cm^3 of mitochondria. Inner membrane surface areas (S_{vim}) determined from the × 6,200 micrographs and therefore relative to the tissue volume, were in units of m^2 of inner mitochondrial membrane per cm^3 of tissue and are a function of both the size, shape and number of the mitochondria. The mitochondrial membrane surface area per cm^3 (S_v) for each tissue was determined using the following equation

$$S_v = (S_{vc} \cdot V_v / 100) + S_{vim} \quad (2)$$

where S_{vc} equals cristae surface area densities ($m^2 \cdot cm^{-3}$ of mitochondria), S_{vim} equals inner membrane surface area densities ($m^2 \cdot cm^{-3}$ of tissue) and V_v equals mitochondrial volume densities (% of tissue volume). The units of S_v equal the m^2 of mitochondrial membrane per cubic centimetre of tissue. To-

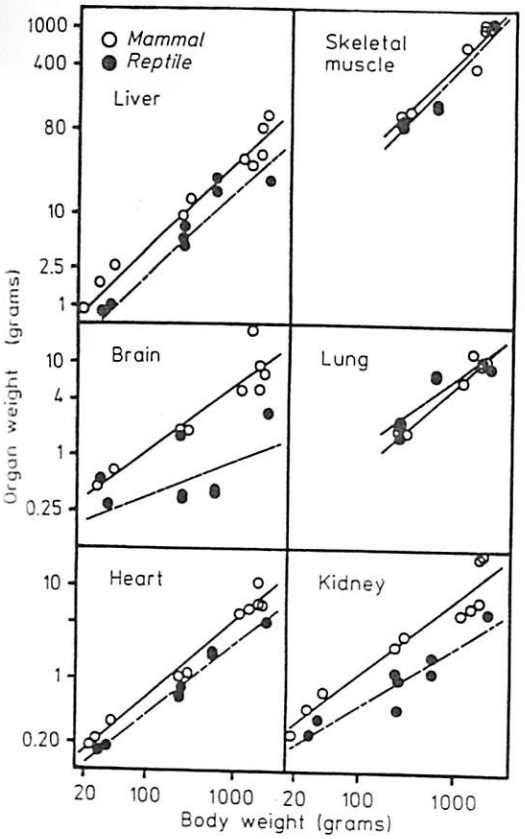


Fig. 1. A comparison of mammalian (o) and reptilian (•) tissue weights

tal tissue mitochondrial membrane surface areas (m^2) were derived by multiplying S_V by respective tissue weights (assuming the specific weight of the tissues to be that of water).

Statistics. Equations used for the biostatistical analysis were obtained from Zar (1974). Mammalian and reptilian allometric slopes were tested for significant differences. In the two only cases where the slopes of the mammalian and reptilian regressions were found to be different no further statistical analysis was performed. When the mammalian and reptilian slopes were found to be parallel (i.e. statistically the same slopes), the elevations were tested for significant differences. Percentage differences (Table 3) between the mammalian and reptilian mitochondrial parameters were calculated from common slopes (where slopes statistically parallel) and adjusted mean scores.

Results

The liver, kidney, brain, heart and skeletal muscle tissues are all larger in mammals than in reptiles. These results are shown in Fig. 1 and the corresponding allometric equations for the reptiles are given in Table 1 and for the mammals in Table 2. In all figures each point represents the data from a single animal.

The lung is the only organ to have a similar weight in both the mammals and reptiles, although the reptiles include two aquatic species. The reptilian lung allometric exponent of 0.73 is less than 1.0 found by Tenney and Tenney (1970). The allometric exponent for the heart weight of the reptiles,

Table 1. The allometric equations for tissue weights, mitochondrial volume density and mitochondrial membrane surface areas in tissues of reptiles

	n	Tissue weight (g)	Mitochondrial volume density (% of cell volume)	Mitochondrial membrane surface area (m^2)		
				per centimetre^3 of mitochondria$^+$	per centimetre^3 of tissue	per total tissue
Liver	8	$0.05\ W^{0.85\,*e}$ (±0.28, 0.95)	$11.03\ W^{-0.11e}$ (±0.49, 0.21)	$15.28\ W^{-0.01}$ (±0.21, 0.31)	$2.58\ W^{-0.10e}$ (±0.47, 0.22)	$0.14\ W^{0.74\,*e}$ (±0.48, 0.84)
Kidney	8	$0.03\ W^{0.63\,*e}$ (±0.25, 0.93)	$18.33\ W^{-0.09e}$ (±0.21, 0.39)	$21.49\ W^{0.05}$ (±0.15, 0.29)	$6.05\ W^{-0.07e}$ (±0.14, 0.43)	$0.18\ W^{0.56\,*e}$ (±0.30, 0.88)
Brain	8	$0.11\ W^{0.31e}$ (±0.47, 0.54)	$2.51\ W^{0.09}$ (±0.27, 0.30)	$32.05\ W^{0.03s}$ (±0.14, 0.22)	$0.92\ W^{0.15}$ (±0.40, 0.54)	$0.10\ W^{0.45\,*e}$ (±0.43, 0.73)
Heart	8	$0.01\ W^{0.77*e}$ (±0.12, 0.99)	$39.99\ W^{-0.17e}$ (±0.19, 0.61)	$30.10\ W^{0.07s}$ (±0.10, 0.56)	$15.62\ W^{-0.12e}$ (±0.20, 0.52)	$0.18\ W^{0.65*e}$ (±0.23, 0.94)
Lung	6	$0.04\ W^{0.73\,*}$ (±0.59, 0.86)	$0.38\ W^{0.24}$ (±0.48, 0.56)	$89.61\ W^{-0.17}$ (±0.39, 0.53)	$0.55\ W^{0.02}$ (±0.82, 0.04)	$0.04\ W^{0.69\,*}$ (±0.65, 0.82)
Skeletal muscle	6	$0.19\ W^{1.09\,*}$ (±0.43, 0.96)	$0.89\ W^{0.20}$ (±0.66, 0.39)	$93.23\ W^{-0.14}$ (±0.29, 0.53)	$1.17\ W^{0.05}$ (±0.63, 0.09)	$0.22\ W^{1.14\,*}$ (0.37, 0.97)

n = number of animals
( ) Within brackets firstly there is the ±95% confidence limit for each exponent and secondly the correlation coefficient
* Denotes exponents statistically significant from 0 ($P<0.05$)
e Denotes statistically different elevations between mammals and reptiles ($P<0.05$)
s Denotes statistically different slopes between mammals and reptiles ($P<0.05$)
\+ Refers to cristae membranes
W in grams

Table 2. The allometric equations for tissue weights, mitochondrial volume density and mitochondrial membrane surface areas in tissues of mammals

	n	Tissue weight (g)	Mitochondrial volume density (% of cell volume)	Mitochondrial membrane surface area (m^2)		
				per centimetre^3 of mitochondria $^+$	per centimetre^3 of tissue	per total tissue
Liver	10	$0.09\ W^{0.87}$ * (±0.13, 0.98)	$27.51\ W^{-0.13}$ * (±0.12, 0.70)	$35.01\ W^{-0.15}$ * (±0.07, 0.88)	$11.42\ W^{-0.24}$ * (±0.09, 0.91)	$0.98\ W^{0.64}$ * (±0.10, 0.98)
Kidney	10	$0.03\ W^{0.78}$ * (±0.17, 0.97)	$37.97\ W^{-0.14}$ * (±0.13, 0.64)	$53.15\ W^{-0.11}$ (±0.12, 0.56)	$21.71\ W^{-0.22}$ * (±0.20, 0.66)	$0.76\ W^{0.55}$ * (±0.28, 0.85)
Brain	9	$0.05\ W^{0.69}$ * (±0.24, 0.93)	$5.38\ W^{0.00}$ (±0.08, 0.03)	$69.37\ W^{-0.12}$ * (±0.09, 0.79)	$4.65\ W^{-0.11}$ * (±0.10, 0.71)	$0.21\ W^{0.59}$ * (±0.19, 0.94)
Heart	10	$0.01\ W^{0.83}$ * (±0.09, 0.99)	$42.23\ W^{-0.09}$ * (±0.06, 0.73)	$74.95\ W^{-0.08}$ (±0.10, 0.56)	$33.61\ W^{-0.16}$ * (±0.12, 0.72)	$0.45\ W^{0.67}$ * (±0.18, 0.95)
Lung	7	$0.01\ W^{0.90}$ * (±0.26, 0.97)	$5.89\ W^{-0.11}$ (±0.42, 0.30)	$98.79\ W^{-0.17}$ (±0.26, 0.60)	$1.52\ W^{-0.07}$ (±0.62, 0.14)	$0.07\ W^{0.66}$ * (±0.39, 0.89)
Skeletal muscle	7	$0.42\ W^{1.01}$ * (±0.36, 0.96)	$8.16\ W^{-0.09}$ (±0.41, 0.25)	$110.03\ W^{-0.13}$ (±0.34, 0.40)	$12.39\ W^{-0.23}$ (±0.61, 0.41)	$5.16\ W^{0.78}$ (±0.81, 0.74)

n = number of animals
( ) Within the brackets firstly there is the ±95% confidence limit for each exponent and secondly the correlation coefficient
* Denotes exponents statistically significant from 0 ($P<0.05$)
\+ Refers to cristae membrane only
W in grams

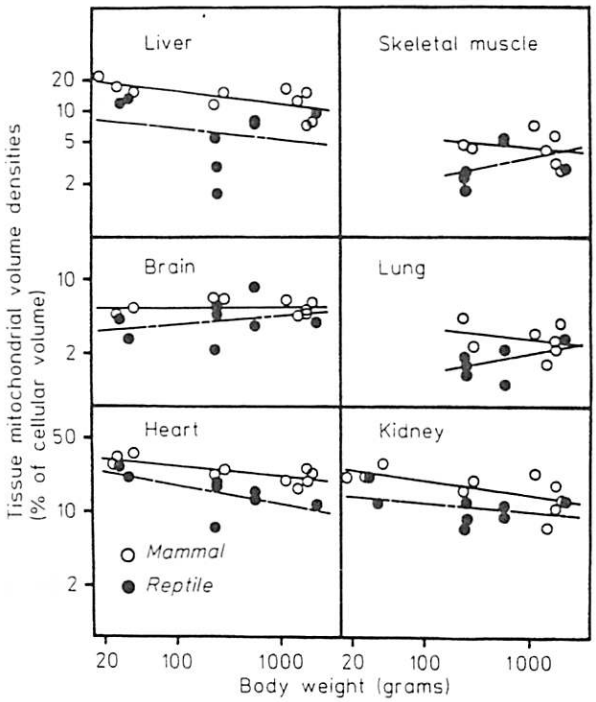
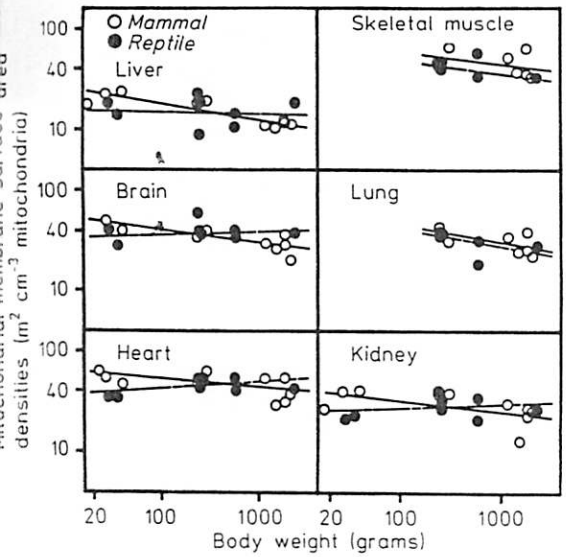


Fig. 2. A comparison of mammalian (○) and reptilian (●) tissue mitochondrial volume densities

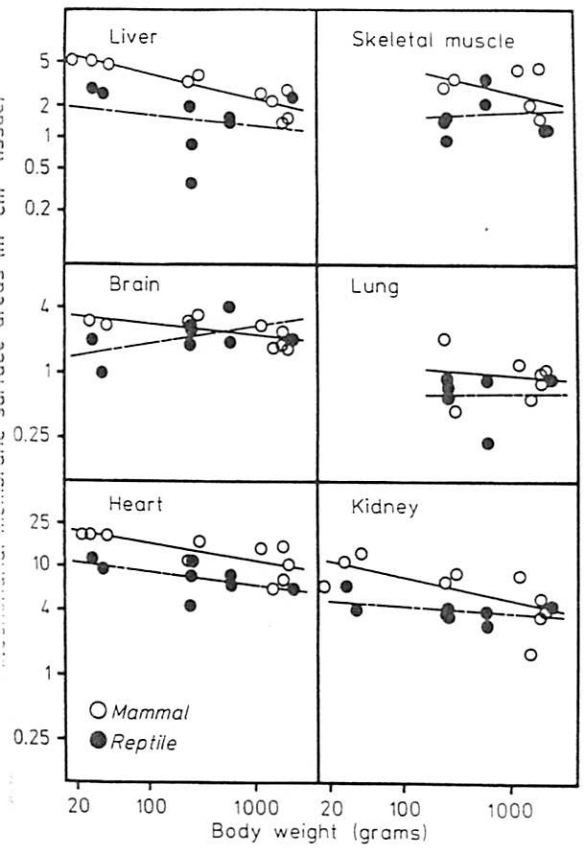
0.77 is less than that found for sea fish at 0.89 (Poupa et al. 1981). The skeletal muscle exponent of 1.09 is very similar to those found for intraspecific comparisons in teleost fish with exponents ranging from 0.90 up to 1.21 (Somero and Childress 1980). For the mammals the liver and brain exponents are the same as found by Brody (1945) and the kidney, heart, lung and skeletal muscle exponents are slightly less than values found by Brody (1945), Prothero (1979), Stahl (1967) and Heusner (1964) respectively.

The mitochondrial volume densities of the six mammalian and reptilian tissues are compared in Fig. 2 and the allometric equations for the reptilian and mammalian tissues given in Tables 1 and 2. Reptilian liver, kidney and heart tissues all scale with negative slopes as do all the mammalian tissues (except brain, slope = 0), with the mammalian liver, kidney and heart scaling with negative slopes significantly different from zero. All six tissues show statistically parallel slopes between the mammals and reptiles. The liver, kidney and heart also show significantly different elevations in mitochondrial volume densities per cm^3 of tissue between the mammals and reptiles. The average difference between the mammalian and reptilian tissues is a 60% increase in the mitochondrial volume density in the mammalian tissues.

Within the mitochondria the internal membrane surface area density (cristae membrane) differs only slightly between the mammals and reptiles. The mitochondrial membrane surface area densities per cm^3 of mitochondria for the mammalian and reptilian tissues are compared allometrically in Fig. 3, the corresponding allometric equa-



ig. 3. A comparison of mammalian (o) and reptilian (●) mito-hondrial membrane surface area densities



ig. 4. A comparison of mammalian (o) and reptilian ●) tissue itochondrial membrane surface areas

ons for the reptilian tissues are given in Table 1 nd for the mammalian tissues in Table 2. The liver nd brain of the mammals show negative slopes ignificantly different from zero whereas none of ne reptilian tissues show slopes significantly differ-

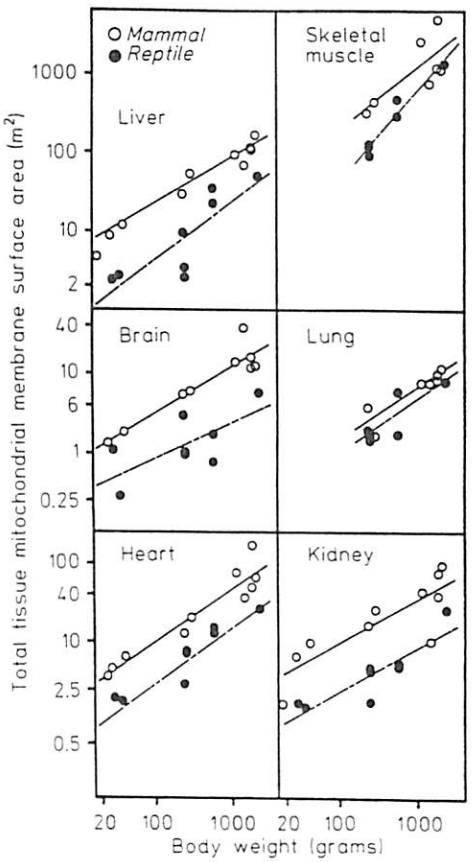


Fig. 5. A comparison of mammalian (o) and reptilian (●) total tissue mitochondrial membrane surface areas

ent from zero. The mitochondrial membrane surface area densities per cm^3 of mitochondria for the mammalian and reptilian tissues show no statistical differences in slope (with the exceptions of brain and heart mitochondria) or elevation values (Table 1).

Using data for mitochondrial volume densities, cristae and inner membrane surface area densities, the mitochondrial membrane surface areas per cm^3 of tissue have been determined (see Methods Eq. 2) and these values are compared in Fig. 4 and the allometric equations for the tissues are given in Tables 1 and 2. All the mammalian tissues scale with negative slopes and those for liver, kidney, brain and heart tissues are significantly different from zero. None of the reptilian tissue show slopes significantly different from zero. All the mammalian and reptilian slopes are statistically parallel, with liver, heart and kidney all showing statistically different elevations between the mammals and reptiles. The differences in the mitochondrial membrane surface areas per cubic centimetre of tissue between the mammals and reptiles range from 10% greater in the brain to 110% greater in the liver.

The differences in the mitochondrial membrane surface area densities per gram of tissue between the mammals and reptiles are further increased when the effect of tissue size is included. Total tissue mitochondrial membrane surface area for the mammalian and reptilian tissues are compared in Fig. 5. The allometric equations are given in Tables 1 and 2. All slopes for both the mammals and the reptiles are positive and parallel and all significantly different from zero with the one exception of mammalian skeletal muscle. For the mammals the tissues which show exponents significantly less than one are liver, kidney, brain and heart, and for the reptiles kidney, brain and heart. Although the slopes are parallel for total tissue mitochondrial membrane surface area, the liver, kidney, brain and heart tissues all show statistically different elevations between the mammals and reptiles.

Discussion

As previously noted for mammals (Else and Hulbert 1985) the relationship between body size and oxygen consumption shows effects at many different levels of organization from ecological and physiological, through to cellular and subcellular levels. Similar allometric relationships between organismal metabolism and body size are also reflected at different levels within the biology of the ectothermic vertebrates. As a result of the phylogenetic differences between the mammals and reptiles the elevations or 'a' constants show phylogenetic related effects at the different levels of organization between the mammals and ectothermic vertebrates. For example, the field metabolic rates of lizards during the active season are allometrically correlated with body mass ($W^{0.80}$) but are twenty times lower than for similar sized mammals (Nagy 1983). Respiratory variables such as heart weight in mammals (Stahl 1967; Prothero 1979) and fish (Poupa et al. 1981) scale allometrically with similar slopes but the mammals have larger hearts as indicated by the 5 times higher value of their elevation constant. Similarly, the aerobic enzyme capacities of mammalian tissues have been shown to be greater than those for similar sized reptiles measured at the same temperatures (Bennett 1972; Else and Hulbert 1981).

In both mammals and reptiles the total mitochondrial membrane surface areas of the tissues show allometric exponents characteristic of those which describe metabolism of the whole animal. In the majority of tissues these exponents are made up of tissue weights with allometric slopes between 0.75 and 1.00 and weight specific tissue mitochondrial membrane surface area densities with slopes between −0.25 and zero. Although the slopes of the allometric equations describing total tissue mitochondrial membrane surface area are statistically the same, in the mammalian tissues the elevations are significantly higher, approximately 4 times higher in the liver, brain and kidney and 3 times higher in the heart. Also higher in the mammals are the skeletal muscle (2.2 times) and lung (1.4 times) total tissue mitochondrial membrane surface areas (Table 3).

The increased mitochondrial capacity of mammals compared to reptiles is not the result of any single 'quantum' factor but is primarily a result of the mammals having relatively larger tissues with a greater proportion of their volume occupied by mitochondria. Internal mitochondrial membrane surface area densities (i.e. per cm^3 of mitochondria) show no large differences between the mammalian and reptilian mitochondria and therefore are not major contributors to the observed differences. All differences measured for tissue sizes and mitochondrial parameters in mammalian and reptilian tissues regardless of how small the difference, are always to the increased metabolic advantage of the mammalian tissues (Table 3). The factors which contribute to the observed differences between the mammalian and reptilian total tissue mitochondrial membrane surface areas also vary in their relative contributions depending upon the species.

Organismal metabolism is presumably a result of the cumulative metabolisms of the tissues. Considering the largest and most active organs (liver, heart, kidney and brain) to be major contributors to standard metabolism (Drabkin 1950) and summating the total tissue weights of those from each individual reptile and mammal measured the allometric equations described are given in Table 4. When the total mitochondrial membrane surface areas of the same four tissues are similarly treated the exponents from the allometric equations (Table 4) are 0.67 and 0.59 for the reptiles and mammals, respectively. Standard oxygen consumption for reptiles in general (Bennett and Dawson 1976) and for the mammalian species used in this study (Else and Hulbert 1985) show exponents of 0.77 and 0.62, respectively.

The elevation values for the allometric equations describing total mitochondrial membrane surface area for the same four organs are significantly different ($P<0.01$); the mammalian elevation value is 3.7-fold higher than the reptilian elevation value. The mammals appear to have a total

Table 3. Relative differences of mitochondrial parameters: mammals compared to reptiles

	Organ size (%)	Inner mitochondrial membrane surface area ($m^2 \cdot cm^{-3}$ of tissue) (%)	Cristae mitochondrial membrane surface area ($m^2 \cdot cm^{-3}$ of mitochondria) (%)	Mitochondrial volume density (% of cell volume)	Mitochondrial membrane surface area ($m^2 \cdot cm^{-3}$ of tissue) (%)	Total tissue mitochondrial membrane surface area (m^2) (%)
Liver	186	200	103	219	213	395
Kidney	253	123	106	156	156	404
Brain	374	116	–	133	107	439
Heart	165	142	–	166	174	288
Lung	84	156	111	160	148	141
Skeletal Muscle	129	197	119	140	172	223

Values are percentages with mammalian values expressed relative to a 100% reptilian value. Percentage differences calculated from common slopes (where slopes are statistically parallel) and adjusted mean scores

Table 4. The allometric equations for summated tissue weights and mitochondrial membrane surface areas in reptiles and mammals

	Reptiles			Mammals		
	n	Total tissue weight (grams)	Mitochondrial membrane surface area (m^2) per total of tissues	n	Total tissue weight (grams)	Mitochondrial membrane surface area (m^2) per total of tissues
Summated organs Liver Kidney Brain Heart	8	$0.14\ W^{0.75}$ * (±0.18, 0.97)	$0.55\ W^{0.67}$ * (±0.21, 0.96)	9	$0.18\ W^{0.83}$ * (±0.11, 0.99)	$3.04\ W^{0.59}$ * (±0.11, 0.98)
Summated tissues Liver Kidney Brain Heart Lung Skeletal-Muscle	6	$0.24\ W^{1.07}$ * (±0.34, 0.98)	$0.30\ W^{1.11}$ * (±0.36, 0.97)	7	$0.51\ W^{1.00}$ * (±0.31, 0.96)	$6.85\ W^{0.76}$ * (±0.73, 0.77)

n = number of animals
( ) Within the brackets firstly the ±95% confidence limit for each exponent and secondly the correlation coefficient
* Denotes exponents statistically significant from 0 ($P<0.05$)
W in grams

3–4-fold greater mitochondrial membrane surface area in these four organs.

Maximum oxygen consumption is presumed to be predominantly the result of muscle metabolism. If skeletal muscle and lung are combined with the organs already examined (liver, heart, kidney and brain) the allometric equations describing total tissue weight become as shown in Table 4. The exponents of these equations for both the reptiles and mammals are increased compared to those previously found for the four organs alone. This increase is carried over into the exponents describing the total mitochondrial membrane surface area of these tissue for both the reptiles and mammals (Table 4). The elevation values for the allometric equations describing the total mitochondrial membrane surface areas for skeletal muscle, lung and the four organs are 2–3-fold greater for the mammals than for the reptiles. This again shows that these particular mammals have 2–3 times more mitochondrial membrane surface area compared to the reptiles.

The exponents for maximum oxygen consumption for reptiles, 0.82 (Bennett and Dawson 1976) and mammals, 0.79 (Taylor et al. 1980) show in-