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Gas exchange potential in reptilian lungs: implications for the dinosaur–avian connection

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Abstract

The theory that birds evolved from a group of small terrestrial theropod dinosaurs has created much controversy. One argument proposed against this theory is that the lungs of early theropods were incapable of sustaining endothermic gas exchange requirements and could not have given rise to the lungs of birds. A reexamination of the comparative physiological and morphological literature combined with a theoretical analysis of gas exchange potential indicates that non-avian lungs would not constrain the gas exchange requirements of early endotherms. Furthermore, our analysis suggests that factors besides diffusive gas exchange were important in the evolution of the distinct morphology of the highly effective avian and mammalian lungs. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

A major controversy in paleontology, that has received considerable attention, concerns the evolution of birds and their relationship to theropod dinosaurs (Ruben et al., 1997; Padian and Chiappe, 1998; Unwin, 1998). Much of this debate results from the analysis and interpretation of anatomical features shared in both birds and theropods (reviewed in Ruben et al., 1997; Chen et al., 1998; Unwin, 1998). The description of a recently discovered fossil of a small theropod dinosaur, *Sinosauropteryx prima*, from northeastern China adds fuel to this debate (Chen et al., 1998). This fossil exhibits well preserved integumentary structures that may provide the first evidence of simple feathers (Chen et al., 1998; Unwin, 1998); suggesting an insulative function and an endothermic physiology (Unwin, 1998).

One requirement of endothermy is a continuous high rate of oxygen delivery to rapidly metaboliz-

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ing tissues, thus requiring a highly effective oxygen transport system. Ruben and colleagues (Ruben et al., 1997) examined photographs of *Sinosauropteryx prima* and noted the possible presence of a liver or liver-like structure. This observation combined with specific aspects of the pelvic structure lead them to suggest that theropod dinosaurs used a hepatic piston breathing mechanism similar to that found in extant crocodilians. These investigators concluded, therefore, that the lung of *Sinosauropteryx* was most likely a non-avian (reptilian) septate lung (Ruben et al., 1997). In addition, they proposed that such a lung would have been incapable of sustaining the high oxygen exchange rates associated with endothermy (Ruben et al., 1997).

More recently, an examination of the fossil theropod, *Scipionix samniticus*, lead these authors to suggest that the liver subdivided the visceral cavity into a thoracic and abdominal space (Ruben et al., 1999). This finding was purported to provide additional evidence that theropod dinosaurs may have used either a diaphragmatic or a hepatic piston breathing mechanism (Ruben et al., 1999). In response to Ruben and colleagues, we presented a preliminary analysis that argued that high gas exchange rates in theropods would not have been constrained by the presence of a non-avian septate lung (Hicks and Farmer, 1998).

In the present paper we present, in detail, our analysis of the gas exchange capacity of the non-avian septate lung and address whether the cardiopulmonary system of reptiles is capable of supporting the metabolic rates of active endotherms. This analysis used two approaches. First, we examined the comparative physiological literature and determined that the cardiopulmonary system of reptiles does not constrain endothermy because in some extant species the oxygen delivery rate is as great or even greater than in some endotherms. Second, we used an integrative oxygen transport model combined with morphological and physiological values from the literature to calculate the oxygen transport capacity of the reptilian cardiopulmonary system. Our theoretical analysis shows that conservative modifications at each step in the oxygen cascade results in gas exchange rates approaching ‘typical’ endothermic values. However, during the course of evolution natural selection gave rise to the morphologically distinct but functionally similar avian and mammalian lungs. It appears that the evolution of these distinct structures was not driven by gas exchange requirements alone, but was influenced by selection on other factors. The distinct morphology of the avian and mammalian lungs may reflect historical differences in ventilatory mechanics that were present in bipedal archosaurs and quadrupedal synapsids.

2. Overview of the oxygen transport cascade

Vertebrates meet their long-term energy demands by aerobic metabolism, dictating a continuous and adequate supply of oxygen. The transport of O_2 from the surrounding air to the sites of ATP production (mitochondria) results from the co-ordinated interactions of four transfer steps. These steps function in series and include lung ventilation, diffusion of O_2 from the lung gas into the pulmonary blood, bulk transport of O_2 to the tissues by the cardiovascular system and diffusion of O_2 from the tissue capillaries into the cells and ultimately the mitochondria (Fig. 1). The transfer rate of O_2 ($\dot{V}_{O_2}$) at each step is represented by two convective and two diffusive equations (Fig. 1). Each equation can be simplified by expressing the physiological variables necessary to produce a given $\dot{V}_{O_2}$ for a given partial pressure difference as a conductance (G). Consequently, the two diffusive steps express the diffusion capacity of the lung and the tissues ($D_{L_{O_2}}$ and $D_{M_{O_2}}$, respectively) as Gdiff. The products of convective flow rates (ventilation and cardiac output) and their respective capacitance coefficients for oxygen in the lung gas and blood (β_{gas} and β_{blood}) are expressed as Gvent and Gperf, respectively (Piiper and Scheid, 1975; Fig. 1).

Generally, during resting conditions, $\dot{V}_{O_2}$ is independent of O_2 delivery. However, when tissue oxygen demands are increased, for example during activity, G at each step in the oxygen cascade is increased to meet the new energy demands. As metabolic demands continue to increase, this process continues until structural and functional constraints at each step limit continued increases and a maximum $\dot{V}_{O_2}$ ($\dot{V}_{O_2max}$) is reached. These constraints include convective transport by the lungs, the diffusive limitations in the lungs, convective transport by the cardiovascular system and diffusive limitations in the tissues.

3. Oxygen transport capacity of extant reptiles: does the reptilian cardiopulmonary system constrain endothermy?

The Mesozoic Era (240 to 65 million years ago) ancestors of birds and mammals most likely possessed a reptilian-like oxygen transport system (Fig. 1; Perry, 1983). Consequently, these animals are often considered to have been incapable of supporting endothermic rates of resting metabolism or activity metabolism (Ruben, 1995; Ruben et al., 1997). This idea was based, in part, on a purported unalterable constraint on the pulmonary anatomical diffusion factor of the non-avian septate lung. This constraint was suggested to be due to a large blood–gas diffusion barrier in septate lungs and the passive participation of ediculae or faveoli in lung ventilation (Ruben et al., 1997). However, in a number of active reptiles, the rate of respiratory gas exchange during activity surpasses the resting and activity V_{O_2} of several endotherms. For example, the monitor lizards (genus *Varanus*) are exceptionally active ectotherms with relatively complex lungs and a functional four-chambered heart (Bennett, 1978; Perry, 1983; Hicks, 1998). Measurements of $\dot{V}_{O_2}$ during treadmill exercise indicate that the cardiopulmonary system of these lizards is capable of supporting a $\dot{V}_{O_2}$, during exercise, equivalent to or greater than that found in several similar size mammals walking at similar speeds (Fig. 2). Other highly active reptiles with multicameral lungs (e.g.

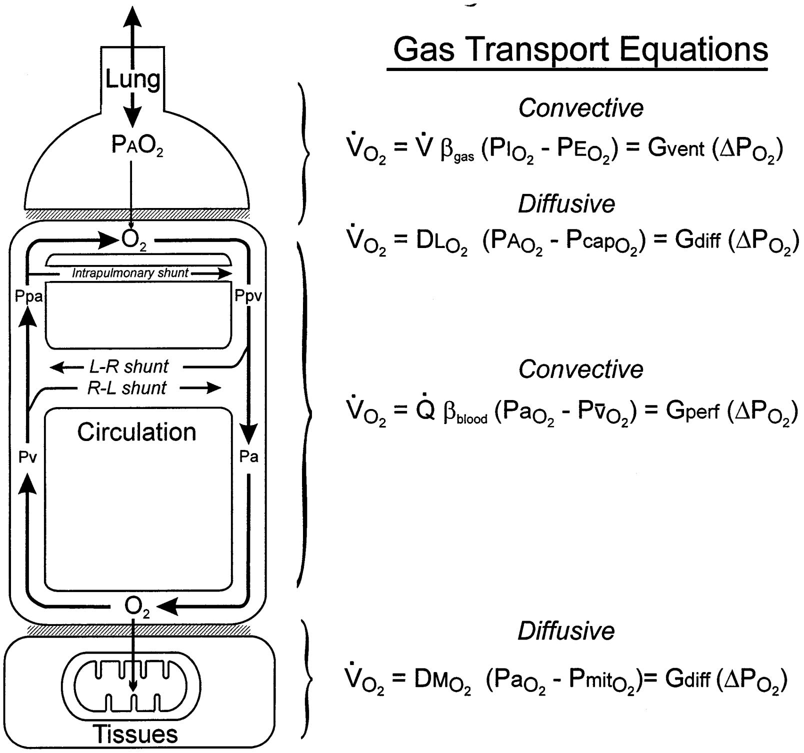

Fig. 1. Schematic of the four step process in oxygen delivery. Each step is represented by two transfer equations. The Fick Principle describes the movement of oxygen by the lungs and circulation. Fick's Law of Diffusion describes the diffusion of oxygen from air to blood or from the capillaries to the mitochondria. Modified from Wang and Hicks (1999).

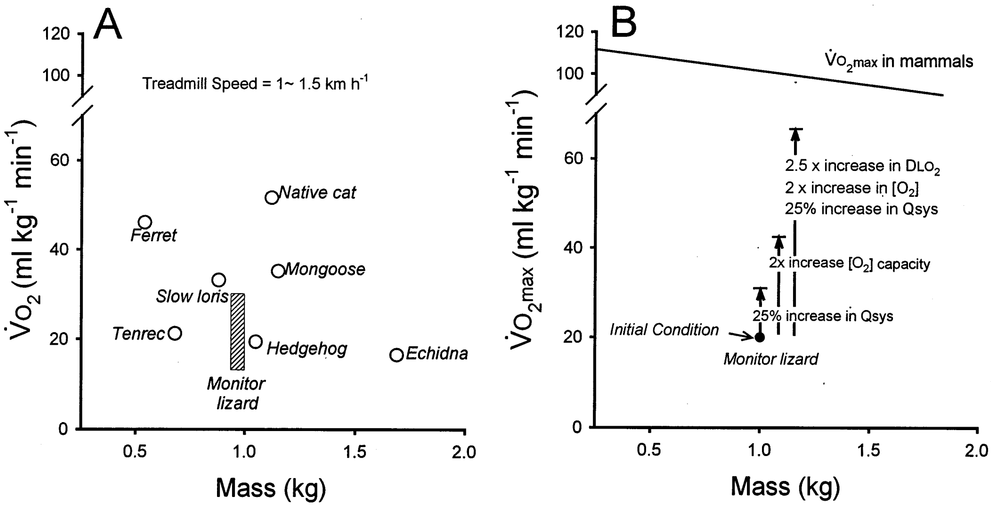

Fig. 2. (A) $\dot{V}_{O_2}$ in selected mammals walking at 1–1.5 km h^{-1}. Data for mammals from (Crompton et al., 1978; Taylor et al., 1980). Range of $\dot{V}_{O_2}$ values for monitor lizard walking at 1–1.5 km h^{-1} (hatched bar) from (Mitchell et al., 1981; Wang et al., 1997a; Owerkowicz et al., 1999). (B) $\dot{V}_{O_2max}$ in a hypothetical lizard calculated from the integrative oxygen transport model (see text for details). Regression line represents the predicted $\dot{V}_{O_2max}$ of mammals (Lindstedt and Thomas, 1994).

sea turtles) also have oxygen consumption rates similar to endothermic values during activity (Jackson and Prange, 1979; Paladino et al., 1990). Hence an explanation for the ectothermic physiology in these reptiles lies somewhere besides their lung morphology. Clearly if the cardiopulmonary system of the Mesozoic ancestor of birds and mammals was similar to that in extant reptiles, it cannot be concluded that it constrained them from achieving or supporting endothermic-like rates of gas exchange. However, there is a wide range in $\dot{V}_{O_2max}$ among endotherms and ectotherms of similar size at similar body temperatures (Bennett, 1978). For example a 1 kg banded mongoose has a $\dot{V}_{O_2max}$ of 117 ml kg^{-1} min^{-1} (Taylor et al., 1980) while a 1 kg monitor lizard has a $\dot{V}_{O_2max}$ of 20–30 ml kg^{-1} min^{-1} (Mitchell et al., 1981; Owerkowicz et al., 1999). Therefore, we addressed the question of what modifications in the oxygen delivery system of an ectotherm would be necessary to support higher rates of oxygen consumption.

4. Theoretical analysis of the reptilian oxygen transport system

The transfer potential of the oxygen transport system can be increased by modifications in the design properties or morphological features that determine each of the four conductances (Weibel, 1984); e.g. increasing stroke volume of the heart, oxygen carrying properties of the blood, diffusive capacity of the lungs and tissue). Recently, Wagner (1996) described an integrative model of oxygen transport that can be used to determine the effects of modifying each transfer step on $\dot{V}_{O_2max}$. An important aspect of this model is that it takes into account that P_{O_2} at any given point in the O_2 transport cascade is dependent on the O_2 transfer in the previous step. For example, at $\dot{V}_{O_2max}$, the P_{O_2} of the blood leaving the lung is determined by the $P\bar{v}_{O_2}$ entering the lung and the conductance ratio, Gdiff /Gperf (Piiper and Scheid, 1991). Simultaneously, the $P\bar{v}_{O_2}$ entering the lung is determined by the arterial P_{O_2} (Pa_{O_2}) entering the tissues and the diffusive and perfusive conductance ratio in the tissues. Thus, Pa_{O_2} is dependent on Pv_{O_2}, and$P\bar{v}_{O_2}$ is dependent on Pa_{O_2}. The analytical approach used in the Wagner model inherently satisfies the coupling and mutual dependency between gas exchange in lungs and tissues.

A detailed description of the integrative oxygen transport model is reported elsewhere (Wagner, 1996; Wang and Hicks, 1999). Three equations define this analytical approach. First is the standard mass conservation equation or Fick Principle. This principle states that the differences between the rates of O_2 inhaled and exhaled equals the product of cardiac output and arterio-venous O_2 concentration difference across the lung. Second, a differential equation, Fick's Law of Diffusion, represents O_2 flux from alveolar gas into pulmonary capillary blood. This equations takes into account diffusional conductance of the lung for O_2 ($D_{L_{O_2}}$), transient time available for O_2 diffusion, total pulmonary blood flow, alveolar P_{O_2} ($P_{A_{O_2}}$), and the profile of blood P_{O_2} along the pulmonary capillary. This second equation is integrated over the total capillary length to determine the end-capillary P_{O_2}, which is taken to equal Pa_{O_2} (Bohr integration). The third equation is analogous to the second and represents the unloading of O_2 by diffusion from the capillaries within the muscle to the site of aerobic metabolism, the mitochondria.

Briefly, the model simultaneously calculates the oxygen flux at three levels: (1) in the lungs between the inspired air and the lung gas; (2) between lung gas and pulmonary blood; and (3) between systemic blood and the tissues. At steady state, $\dot{V}_{O_2}$ is identical at all three steps. Many of the parameters used to calculate $\dot{V}_{O_2}$ at each step are determined by $\dot{V}_{O_2}$ at the two other steps. This coupling and mutual dependency between gas exchange in the lung and tissues requires that the solution to the equations are iterated by estimating and entering values for $P_{A_{O_2}}$, Pa_{O_2} and $P\bar{v}_{O_2}$ until a unique solution for all three compartments is achieved.

5. Oxygen transport potential of the reptilian cardiopulmonary system: results of the theoretical analysis

To address the question of what modifications in the oxygen delivery system of a reptile would be necessary to support higher oxygen consumption rates, we determined the effects of modifying several parameters in the oxygen cascade on $\dot{V}_{O_2max}$ in the monitor lizard *Varanus exanthematicus*. We chose this animal because the required input parameters for the model (initial conditions) have been experimentally determined at $\dot{V}_{O_2max}$ (e.g. cardiac output, hematocrit, lung P_{O_2} and P_{CO_2}, oxygen carrying properties of the blood, etc; Table 1). From these initial conditions (first column Table 1), we modified three basic parameters either separately or in combination. These included an increase in the maximum cardiac output, blood oxygen capacity and pulmonary diffusion capacity ($D_{L_{O_2}}$). We determined the $\dot{V}_{O_2max}$ that could be supported by increasing maximum cardiac output by 25% and examined a greater range of values for oxygen carrying capacity of the blood, with an upper limit set by values found in endotherms. Finally, it is important to note that because we wanted to gauge the gas exchange potential of the lung of a theoretical reptilian-like Mesozoic animal we constrained all pulmonary morphological modifications within a range of values measured in extant reptiles (Perry, 1983).

The analytical approach was straightforward; increasing the diffusional conductance of the muscle ($D_{L_{O_2}}$) simulated an increase in tissue oxygen demand. In response to the increased oxygen flux rate we adjusted the various parameters at each transfer step so that gas exchange in the lungs and tissues were matched. The individual parameters were adjusted to maintain arterial oxygen saturation above 95%. The assumptions for the analysis were similar to those previously described (Wagner, 1996; Wang and Hicks, 1999), and included no ventilation/perfusion inhomogeneity, no perfusion/metabolism inhomogeneity in the muscle, steady state at all points in the O_2 pathway, and the P_{O_2} in the mitochondria is zero at $\dot{V}_{O_2max}$. We also assumed that during intense activity the lung ventilation increased to maintain a lung P_{O_2} of 127 torr (Mitchell et al., 1981; Hopkins et al., 1995), and that no significant intracardiac mixing of oxygenated and deoxygenated blood occurred during exercise (Mitchell et al., 1981; Wang et al., 1997b; Hicks, 1998).

Table 1
The effects of modifying oxygen delivery system on V_{O_2max} in a 1 kg lizard, *Varanus exanthematicus* at 35°C[a]

Physiological variable	Initial condition	25% increase in cardiac output	Doubling oxygen carrying capacity of blood	Increase DL_{O_2} oxygen carrying capacity and cardiac output
Ventilation (L kg^{-1} min^{-1})	0.683	1.24	1.47	2.3
Cardiac output (L kg^{-1} min^{-1})	0.350	0.438	0.350	0.438[b]
PA_{O_2} (torr)	127	127	127	127
PA_{CO_2} (torr)	23	23	23	23
Pa_{O_2} (torr)	95	105	98	97
$P\bar{v}_{O_2}$ (torr)	34	24	24	20
$[O_2]$cap (vol.%)	10	10	20	20
Hills n	3.5	3.5	3	3
P50 (torr)	40	40	30	30
DL_{O_2} (ml min^{-1} $mmHg^{-1}$ kg^{-1})	0.42	0.42	0.59*	1.06[c]
DM_{O_2} (ml min^{-1} $mmHg^{-1}$ kg^{-1})	0.42	0.81	0.94	2.02
Arterial (Sat%)	96	96	97	97
(a–v)O_2 (vol.%)	5.8	7.3	12.3	15
Temp	35	35	35	35
$\dot{V}_{O_2max}$ (ml kg^{-1} min^{-1})	20	32	43	67

[a] Physiological parameters: initial conditions are from measured values in this species at V_{O_2max} (Gleeson et al., 1980; Mitchell et al., 1981); DL_{O_2} are estimated from morphometric data (Perry, 1983) and assumed to double during heavy exercise.

[b] DL_{O_2} increases from the effects of hemoglobin concentration (Marrades et al., 1997).

[c] DL_{O_2} estimated from modifications of multicameral lung. Ventilation calculated by assuming a gas exchange ratio (RE) of 1.1 at V_{O_2max} (Mitchell et al., 1981; Wang et al., 1997a). V_{O_2max} calculated after model from (Wagner, 1996).

5.1. Increasing the maximum cardiac output

We first determined that a $\dot{V}_{O_2max}$ of 32 ml $kg^{-1}min^{-1}$ could be supported by increasing maximum cardiac output by 25%. This V_{O_2max} is approximately 30% of the value usually quoted for a 'typical' 1 kg active endotherm ($\dot{V}_{O_2max} =$ 100 ml kg^{-1} min^{-1}; (Bennett, 1978). Intuitively, to support the typical $\dot{V}_{O_2max}$ of a 1 kg endotherm, the maximum cardiac output could have been increased 5–10-fold. This modification in maximum cardiac output is appealing for its simplicity. The Fick principle indicates that for a given oxygen extraction, higher levels of oxygen transport will be supported by higher cardiac outputs. Furthermore, higher cardiac outputs are usually correlated with higher a $\dot{V}_{O_2max}$ in all tetrapods. However, as previously discussed (Ruben et al., 1997), increasing the maximum pulmonary blood flow 5–10-fold above normal ectothermic values, without additional modifications of the pulmonary vasculature, would increase the possibility of pulmonary capillary stress failure (West and Mathieu-Costello, 1995). In addition, such high blood flows would significantly decrease the transit time of blood through the lung, allowing less time for diffusion of oxygen and resulting in desaturation of arterial blood. For example, using the input values for *Varanus exanthematicus* and the integrative oxygen transport model, we predict that increasing maximum cardiac output 10-fold results in a reduction in the arterial oxygen saturation to values below 80%. Since arterial desaturation does not normally occur at $\dot{V}_{O_2max}$ in lizards, we concluded that a 10-fold increase in maximum cardiac output, without modifications of the other transfer steps, would not have occurred.

5.2. Increasing the maximum oxygen carrying capacity

Second we determined that a $\dot{V}_{O_2max}$ of 43 ml $kg^{-1}min^{-1}$ could be supported by only modifying the oxygen carrying properties of the blood from the values normally measured in varanid lizards to those more typical of endotherms. We doubled the oxygen carrying capacity from 10 to

20 vol.% and changed the shape and position of the oxygen equilibrium curve (Hill's n decreased from 3.5 to 3 and P50 decreased from 40 to 30 torr to insure adequate O_2 loading in the lung; Table 1). In our theoretical approach, the parameters describing the oxygen dissociation curve are within the range measured in extant reptiles (Wood and Lenfent, 1976). The larger oxygen carrying capacity could be achieved either by doubling hematocrit from the typical ectothermic values of 20% to the values normally measured in extant endotherms or by increasing mean cell hemoglobin values. Hematocrits approaching 40% and hemoglobin concentrations of 12.5 g/100 ml blood have been reported in extant reptiles (Garland, 1993).

5.3. *Modifying the oxygen cascade*

Finally, we considered the effects of simultaneously modifying several components in the oxygen cascade, increasing oxygen carrying properties of the blood, increasing maximum cardiac output, and modifying two parameters in lung morphology; surface area and diffusion barrier.

Three basic lung types occur in the reptiles: unicameral, paucicameral (transitional) and multicameral (Perry, 1983; Dunker, 1989). The multicameral lung is the most complicated, with the central lumen divided into numerous smaller chambers (Perry, 1983). Reptiles do not necessarily have a thicker air to blood gas barrier than mammals, as has been claimed (Ruben et al., 1997); the barrier to diffusion between air and the capillaries in the lung is, on average, about the same for mammals and many reptiles. In reptilian lungs, the harmonic mean thickness (τht) ranges from 0.46 to 1.0 μ compared to a range of 0.26 to 0.62 μ in mammals (Perry, 1983). Consequently, the higher diffusive conductance of the lungs of mammals is primarily due to a vastly greater surface area ($\approx$ 10-fold) for gas exchange (Perry, 1983; Glass, 1993).

It has been suggested that multicameral lungs were present in the Mesozoic reptilian ancestors of birds and mammals (Perry, 1983), thus our analysis focused on this lung type. In the multicameral lung the respiratory gas exchange area, located in the dorsal region, could be increased through elaboration of the intercameral septa while maintaining a membranous region in the ventral portion of the lung (Perry, 1983). This modification could be achieved without significant changes in total lung volume, producing a highly effective gas exchange organ characterized by a higher $D_{L_{O_2}}$, high compliance and low work of breathing (Perry, 1983).

Our theoretical modification of the multicameral lung and calculation of the resulting diffusion capacity required the following steps. In the lizard *Varanus exanthematicus*, the parenchymal volume (that volume of the lung devoted to respiratory function) represents 29% of the total lung volume (displacement volume, $V_L = 307$ ml kg^{-1}; Perry, 1983). However, in multicameral lungs of other reptiles (turtles and crocodilians) this value can be as high as 45% of V_L. Using this upper value for percent parenchyma increases the total parenchymal volume from 83 to 138 ml kg^{-1}. Assuming that the surface area available for gas exchange remains a constant fraction of the total parenchymal volume, then the respiratory surface area (RSA) will nearly double, increasing from 5.43×10^3 to 9.01×10^3 cm^2 kg^{-1}. The anatomical diffusion factor (ADF) represents the mass specific value for the ratio of RSA to τht (Perry, 1983). In multicameral lungs, τht ranges from 0.46 to 1.0 μ (Perry, 1983) and if we use the lower value of 0.46 μ, then ADF increases almost 3-fold to 19.6×10^3 cm^2 μ^{-1} kg^{-1}. Morphometric diffusion capacity of the lung (Dt_{O_2}) is the product of ADF and Krogh's diffusion constant for tissue (3.1×10^{-8} cm^2 min^{-1} torr^{-1}; Perry, 1983) and, in this case, is equal to 6.5 ml min^{-1} mmHg^{-1} kg^{-1}. The Dt_{O_2} is always considerably higher than physiological estimates of resting $D_{L_{O_2}}$, with the ratio $Dt_{O_2}/D_{L_{O_2}}$ ranging from 6 to 25 depending on the species (Perry, 1983). In varanids, this ratio is 12 (Perry, 1983) and consequently we estimate a $D_{L_{O_2}}$ of 0.53 ml min^{-1} mmHg^{-1} kg^{-1} at rest. Measurements of $D_{L_{O_2}}$ during exercise have not been made in reptiles, however in mammals and birds, exercise increases $D_{L_{O_2}}$ 2–4-fold (Piiper and Scheid, 1980). If we assume that $D_{L_{O_2}}$ doubles in reptiles during heavy exercise, then the modified multicameral lung would have a $D_{L_{O_2}}$ of 1.06 ml min^{-1} mmHg^{-1} kg^{-1}.

Using this modified $D_{L_{O_2}}$ and combining it with an increase in oxygen carrying capacity and an increase in maximum cardiac output our hypothetical reptilian oxygen delivery system supports a $\dot{V}_{O_2max}$ of nearly 70 ml kg^{-1} min^{-1} (Table 1; Fig. 2). Our analysis indicates that modifying several steps in the oxygen transport system, within a range of values measured in extant reptiles, results in an increase in the transport capacity to levels approaching a typical 1 kg active endotherm (Fig. 2).

Our analysis included three major modifications. First, we increased the oxygen carrying capacity of the blood from 10 to 20 vol.%. We can see no reason why reptiles would be constrained from synthesizing more red blood cells to produce a hematocrit equivalent to that of extant endotherms. In fact, in examining hematocrits and hemoglobin content in 39 species of extant lizards, Garland (1993) reports the highest values for hemoglobin of 12.5 g/100 ml blood and hematocrits of 35%. Second, we increased the cardiac output from 350 to 440 ml kg^{-1} min^{-1}. Because cardiac output is the product of stroke volume and heart rate small changes in either or both of these parameters could achieve our predicted value. For example in a 1 kg varanid lizard, the new maximum cardiac output could be achieved by a 10% increase in maximum heart rate (HR increases from 100 to 110 beats min^{-1}) and a 14% increase in stroke volume (stroke volume increases from 3.5 to 4.0 ml kg^{-1}). Third, we increased the parenchymal volume in the lung by 50% and reduced the mean harmonic thickness 16%. This values for surface area and mean harmonic thickness have been measured in multicameral lungs from several extant reptiles (Perry, 1983) so these changes also seem reasonable. Taken together, these modifications support a 235% increase in $\dot{V}_{O_2max}$.

6. Conclusion

Mesozoic ancestors of birds and early theropods may or may not have approached the intense levels of aerobically sustainable activity seen in extant birds and mammals. However, our examination of the comparative physiological literature and our theoretical analysis do not support the hypothesis that non-avian multicameral lungs constrain endothermy. Nonetheless, the question still remains, if the multicameral lung could be reasonably modified into an highly effective gas exchange organ, why has this option not been realized and what factors drove the evolution of the avian parabronchial lung and the mammalian alveolar lung? Theoretically, the avian parabronchial lung is a more effective gas exchange organ than the alveolar lungs of mammals (Piiper and Scheid, 1975). This is evidenced by calculations that show in the parabronchial lung the arterial P_{O_2} obtains values that are significantly higher than expired P_{O_2} (Piiper and Scheid, 1975), a result that is not possible in the alveolar lung. However, the actual differences in gas exchange efficacy in real organs under physiological conditions are relatively small and probably not a significant determinant in the evolutionary development of the particular gas exchange organs (Scheid, 1982). Instead, other factors, such as the mechanics of ventilation may have played an important role in the evolution of the distinct avian and mammalian lungs.

7. Speculations on the evolution of avian and mammalian lungs

In our analysis, conservative modifications at several steps in the oxygen transport system result in supporting a large increase in O_2 flux from air to mitochondria. However, this higher $\dot{V}_{O_2}$ requires a significantly large increase in lung ventilation. Consequently, in our analysis a $\dot{V}_{O_2max}$ of 67 ml kg^{-1} min^{-1} requires a lung ventilation of 2.3 L kg^{-1} min^{-1}. This value is 237% greater than maximal levels of ventilation measured in *Varanus exanthematicus* (Table 1). This lung ventilation rate may represent an unreasonably high maximum rate of ventilation for a 1 kg lizard. Extant lizards have a mechanical constraint on simultaneous running and breathing that arises from the design of the axial musculoskeletal system (Carrier, 1987b). Consequently, even if Mesozoic reptiles modified the lungs and cardiovascular system

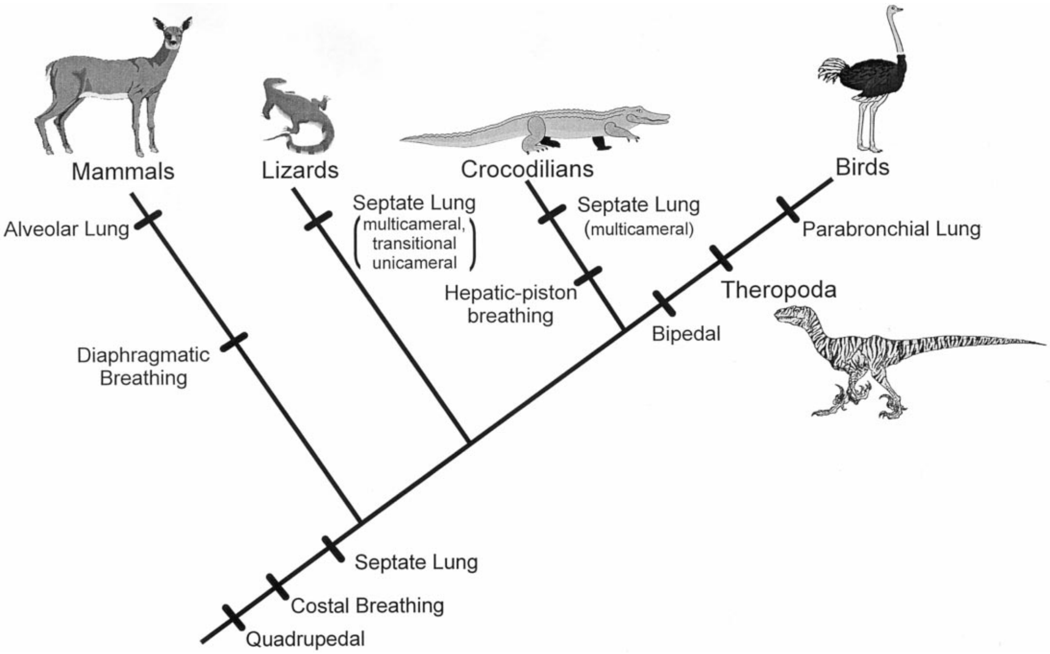

Fig. 3. A hypothetical cladogram illustrating the relationship of posture, gait, ventilatory mechanics with different lung morphologies in terrestrial vertebrates.

to support higher tissue gas exchange rates, they still would have been constrained by the inability to ventilate the lung adequately. Much of the axial musculoskeletal system of early tetrapods (e.g. *Ichthyostega* and *Eryops*) can be deduced from studies of their fossils and it seems probable that they too were constrained from simultaneous running and exclusively costal breathing (Carrier, 1987a). This constraint has been circumvented in the lineages that gave rise to birds and mammals by the evolution of novel ventilatory and locomotor mechanics (Carrier, 1987a; Bramble and Jenkins, 1989), and to varying degrees in some extant lizards (e.g. the use of the gular pump to assist costal ventilation; Owerkowicz et al., 1999). The evolution of both dinosaurs and mammals involved a change in limb posture from the sprawling configuration of early tetrapods to a more parasagittal arrangement in which the limbs were positioned under the body. One lineage, the archosaurs, were unique among early reptiles in that many of them tended toward a bipedal (Romer, 1966) in which the entire weight of the body was supported by the hips. Furthermore, avian archosaurs evolved powered flight. In contrast, mammal-like reptiles (*Thrinaxodon*, *Cynognathus*, *Lycaenops*) retained a quadrupedal stance and evolved a bounding gait in which the trunk flexes and extends in the sagittal plane. It has been proposed that these postural and gait transformations facilitated increased rates of ventilation in the archosaur and synapsis lineages (Carrier, 1987a).

We speculate that the distinct morphology of the avian and mammalian lungs reflects not only an increased demand for gas exchange, but is historically correlated with these divergent modes of locomotion that facilitated higher rates of ventilation (Fig. 3). In addition, novel ventilatory mechanics arose in these groups. Mammals and crocodilians both evolved a diaphragm. Whether or not dinosaurs also had a diaphragm is unknown, but some may have used the abdominal cuirassal basket to supplement costal ventilation (Perry, 1983; Claessons, 1996, 1997). These mechanical factors could have provided a selective pressure during the avian and mammalian radiation that contributed to their divergent lung morphology. Selection for higher metabolic rates mandated additional respiratory surface area and greater rates of lung ventilation. However, the additional surface area was not randomly scattered about the lung but was organized into the parabronchial and alveolar geometry perhaps because these structures functioned in harmony with the locomotor mode. Gas flow patterns within the mammalian lung have been shown to be affected by locomotion, and it has been suggested that the unique lobar structures of these lungs is due to tissue stresses as well as gas distribution requirements (Bramble and Jenkins, 1989). Furthermore, mechanical factors such as peak ventilatory flows and tracheal resistance influence lung morphology (Leith, 1983). Pulmonary parenchymal cells and connective tissues change their geometry when distorted by altered inflation in extant mammals (Rannels, 1989). If the genetic mechanisms that are responding to mechanical stresses in the lungs of extant mammals are primitive features of amniotes, it is possible that the mechanical stresses associated with bipedal locomotion in archosaurs, or with flight in avian archosaurs, gave rise to a different array of lung morphologies than were present in quadrupedal mammals. Natural selection would have then favored the morphologies that functioned for each locomotor mode to support increase oxygen flux.

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