

**EXERCISING WITH AND WITHOUT LUNGS**  
**II. EXPERIMENTAL ELIMINATION OF PULMONARY AND**  
**BUCCOPHARYNGEAL GAS EXCHANGE IN INDIVIDUAL SALAMANDERS**  
**(*AMBYSTOMA TIGRINUM*)**

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*Accepted 21 March 1988*

**Summary**

To ascertain whether the presence of lungs *per se*, or some other physiological feature, might account for the differences in oxygen consumption and stamina previously observed in an interspecific comparison (Full *et al.* 1988), individual salamanders (*Ambystoma tigrinum*) were exercised on a treadmill before and after their nares and mouth had been sealed. After airway closure, animals behaved normally and suffered no mortality. Airway closure reduced the routine  $\dot{M}_{O_2}$  (rate of oxygen consumption) by an average of 47% in six of seven individuals. Animals with open airways increased their  $\dot{M}_{O_2}$  2- to 4-fold during locomotion at  $11 \text{ cm s}^{-1}$ , and did not fatigue in 22 min of exercise at this speed. Animals with closed airways managed only small increases above the routine  $\dot{M}_{O_2}$  during exercise at  $11 \text{ cm s}^{-1}$ , and none could sustain activity for more than 10 min. Thus, exclusively skin-breathing *Ambystoma* cannot increase cutaneous gas exchange to compensate for the elimination of pulmonary and buccopharyngeal respiration; locomotor stamina suffers accordingly. Small salamanders can apparently increase cutaneous gas exchange during activity, although large salamanders cannot, because cutaneous diffusing capacity and the resting oxygen requirement approach one another with increasing body size; the skin of large salamanders apparently has a limited scope for aerobic activity.

**Introduction**

Amphibians respire through lungs and skin; gills and skin; lungs, gills and skin; or skin alone. A recurrent question in comparative physiology concerns the consequences of these various respiratory configurations for amphibians' ability to undergo sustained activity or to recover from non-sustainable activity (Bennett & Licht, 1973; Bennett & Wake, 1974; Feder, 1977; Boutilier *et al.* 1980; Withers, 1980; Quinn & Burggren, 1983; Feder & Burggren, 1985a; Full, 1986; Full *et al.* 1988). The general premise of these analyses has been that respiratory configurations that control the maximum rate of oxygen consumption during activity

Key words: cutaneous gas exchange, activity, amphibians.

( $\dot{M}_{O_2, \max}$ ) ought to limit both sustainable activity and recovery from non-sustainable activity (Feder, 1986, 1987). For example, a low  $\dot{M}_{O_2, \max}$  (Withers, 1980), a low maximum sustainable speed (Feder, 1986, 1987; Full, 1986) and slow recovery from activity-induced acidosis (Boutilier *et al.* 1980) might be expected of amphibians lacking both lungs and gills because of limitations associated with cutaneous gas exchange (Feder & Burggren, 1985a).

One approach to this issue has been to compare species, populations and developmental stages differing in respiratory configuration (see, for example, the studies cited above and in Full *et al.* 1988). Such studies have yielded a wealth of data that, by and large, accord with the above expectations of the consequences of cutaneous gas exchange for activity (reviewed by Feder & Burggren, 1985a). A general difficulty with the comparative approach is its assumption that variables other than the ones being studied (i.e. respiratory configuration) are themselves equivalent (the *ceteris paribus* assumption of Lewontin, 1978) and therefore do not confound the analysis. For example, a species with a locomotor musculature relatively undemanding of oxygen during activity (e.g. predominantly glycolytic) or one accustomed to moving at relatively slow speeds might well manage only a modest  $\dot{M}_{O_2, \max}$  and a moderate maximum sustainable speed, even though its skin could accommodate much greater rates of gas exchange. A species breathing with both lungs and skin might voluntarily avail itself of its lungs to meet an increased gas exchange requirement during activity, even though the skin is equally capable as a gas exchanger. In these examples, attribution of the  $\dot{M}_{O_2, \max}$  and the maximum sustainable speed to limitations of the skin would be unjustified. For example, Taigen & Wells (1985) found that during vocalization the  $\dot{M}_{O_2}$  of frogs (*Hyla versicolor*) was greater than the  $\dot{M}_{O_2, \max}$  during locomotion. Had Taigen & Wells limited their studies to locomotion, they would have reached very different conclusions regarding the gas exchange capacity of *Hyla*. Potentially confounding variables are numerous, and collectively pose an enormous challenge to the correct attribution of physiological limitation in comparative analyses.

In the present case, companion comparative studies (Full, 1986; Full *et al.* 1988) have found that salamander species occurring naturally without lungs (plethodontids) had lower rates of oxygen consumption and lower sustainable speeds than species with lungs (ambystomatids). In the light of the potential difficulties of comparative studies, the present study was undertaken to demonstrate that the presence of lungs *per se*, and not some other physiological feature, was indeed responsible for the differences in oxygen consumption and stamina. Might, for example, a limited muscular capacity for exercise, and a morphology that compromises sustained activity, be responsible for the limited aerobic capacity of plethodontid salamanders, rather than their exclusive reliance on cutaneous gas exchange? To examine this, the gas exchange configuration of individual animals was manipulated, with each animal serving as its own control. The animals chosen were *Ambystoma tigrinum*, which ordinarily respire with lungs, skin and the buccopharyngeal lining, can sustain relatively high speeds, and have a relatively large oxygen requirement during activity (Full *et al.* 1988). If gas exchange by the

skin can increase during activity to meet the large oxygen requirement, then the elimination of alternative gas exchangers (e.g. the lungs and buccopharynx) in this species should have little effect on oxygen consumption and locomotor stamina. Alternatively, if cutaneous gas exchange cannot be increased during activity, then the elimination of alternative gas exchangers should markedly reduce both oxygen consumption and locomotor stamina. In the latter case, the conclusions of Full *et al.* (1988) would be corroborated.

### Materials and methods

All procedures were identical to those of Full *et al.* (1988) with the following exceptions. Seven *Ambystoma tigrinum* (mass 31–45 g) were chosen that could maintain locomotion at  $11 \text{ cm s}^{-1}$  for at least 22 min. This speed is slightly lower than that at which *A. tigrinum* attains  $\dot{M}_{\text{O}_2, \text{max}}$ . Individuals were placed in a treadmill respirometer at  $21^\circ\text{C}$ . The effective volume of the treadmill was 3623 ml; the track was 25.5 cm long and 12.5 cm wide. Animals were allowed at least 30 min to become accustomed to the chamber. The routine  $\dot{M}_{\text{O}_2}$  of each animal was monitored for 5 min, after which the treadmill was activated at  $11 \text{ cm s}^{-1}$  (approx.  $0.4 \text{ km h}^{-1}$ ) and the  $\dot{M}_{\text{O}_2}$  of each animal was monitored for 20 min while it walked. The 'instantaneous'  $\dot{M}_{\text{O}_2}$  was calculated for each 5-s interval (Fig. 1). After resetting the computer (which required approximately 2 min), the treadmill was inactivated and each animal's  $\dot{M}_{\text{O}_2}$  recorded for the next 20 min as it rested.

The animals were allowed to rest for 2–4 h. They were then anaesthetized in MS-222 (tricaine methanesulphonate, 1:1000 adjusted to pH 7.0), air was expressed from their lungs by gentle pressure on the thorax, and their nares and mouth were sealed with cyanoacrylate cement (WonderBond Plus, Borden Inc., Columbus, OH). This procedure eliminated pulmonary and buccopharyngeal gas exchange by sealing the airways. A complete seal was evident from the collapsed state of the buccopharynx and unusual jaw movements, as if the animals were vigorously attempting forced inspirations. Apart from these movements, the animals exhibited no ill effects. They showed normally low levels of activity in their cages after recovery from anaesthesia. The cyanoacrylate seals were lost 1–2 weeks after experimentation as the animals sloughed their skins. The animals then resumed normal breathing, and none died.

Each animal was housed individually so that its performance before and after application of cyanoacrylate could be compared. They were allowed 1–2 days to recover from the application of cyanoacrylate and anaesthesia before a second exercise/ $\dot{M}_{\text{O}_2}$  trial. Routine  $\dot{M}_{\text{O}_2}$  and  $\dot{M}_{\text{O}_2}$  during activity at  $11 \text{ cm s}^{-1}$  were again determined, as described above. In this second trial, however, no animal could sustain activity for 20 min. When animals were judged to be exhausted, according to the criteria of Full *et al.* (1988), the treadmill was inactivated; recording of  $\dot{M}_{\text{O}_2}$  continued for at least 20 min thereafter.

<sup>1</sup> In a control experiment, three animals were anaesthetized as described above and a patch of cyanoacrylate cement ( $2 \text{ cm}^2$ ) was applied to their dorsal surface

instead of their nares and mouth. Animals performed no differently after treatment in terms of routine  $\dot{M}_{O_2}$ ,  $\dot{M}_{O_2}$  during activity, and ability to sustain activity for 20 min. These results suggest that anaesthesia and application of cyanoacrylate do not affect  $\dot{M}_{O_2}$  or locomotor performance.

The re-analysis of Czopek's (1957, 1959, 1961, 1962, 1965) data (see Discussion) was based upon the largest individuals of 16 species for which complete data are available, plus a small *Aneides lugubris*. A list of these data is available from the author upon request. Relationships between  $\log_{10}$  diffusing capacity and  $\log_{10}$  body mass were determined with least squares linear regression.

### Results

Closure of the airways reduced the routine  $\dot{M}_{O_2}$  of salamanders in six of the seven subjects. In these individuals, the routine  $\dot{M}_{O_2}$  decreased by  $47 \pm 17\%$  (mean  $\pm$  s.d.) (Fig. 1).

In salamanders with open airways,  $\dot{M}_{O_2}$  increased 2- to 4-fold during locomotion at  $11 \text{ cm s}^{-1}$ . All seven subjects could sustain locomotion at this speed for at least 22 min. The exercise period was then ended, even though these animals were capable of additional locomotion. The pattern of oxygen consumption during activity was related to the pattern of locomotion. For example, the salamander whose record is depicted in Fig. 1C faltered between about 600 and 750 s after the start of exercise, and subsequently regained its stride. Changes in its  $\dot{M}_{O_2}$  paralleled the changes in locomotion.

Salamanders with closed airways managed only small increases in  $\dot{M}_{O_2}$  during activity at  $11 \text{ cm s}^{-1}$  (Fig. 1), and none could sustain activity for more than 10 min ( $\bar{x} \pm \text{s.d.} = 8.0 \pm 1.7 \text{ min}$ ). The experiment was intended to compare the kinetics of oxygen debt payment in animals with open and closed airways, but the oxygen debt of salamanders with closed airways was so small (Fig. 1) as to frustrate this comparison. Oxygen debt may have been reduced in the salamanders with closed airways, or the oxygen debt may have been repaid more slowly than in salamanders with open airways, or both.

### Discussion

#### *Experimental design*

Although repeated measurement of individuals before and after experimental alteration of the gas exchanger can eliminate the confounding effects of interspecific (and, indeed, interindividual) variation, the procedure is not without difficulties in design and interpretation. In amphibians, training can improve locomotor performance (Cummings, 1979; Miller & Camilliere, 1981). Also, both increased metabolic demands and hypoxaemia due to closure of airways might induce diverse acclimatory responses that facilitate oxygen transport, such as hypertrophy of cutaneous surface area, thinning of the epidermis and haematological adjustments (e.g. Noble, 1925; Bannikov, 1948; Burggren & Mwalukoma,

1983; Pinder & Burggren, 1983). These responses would tend to obscure any adverse effect of airway closure. In contrast, progressive systemic deterioration or retarded recovery from fatigue or anaesthesia, both possible consequences of airway closure, might in themselves reduce  $\dot{M}_{O_2}$  and stamina, apart from any limitation inherent in cutaneous gas exchange. In designing the experiment, we sought a middle ground in the time between experimental trials: sufficient time for recovery from application of cyanoacrylate and anaesthesia, but not so much time that acclimation, training or systemic deterioration could affect the results. In the trials after airway closure, salamanders were alert, responsive to stimuli and (apart from the reduction in  $\dot{M}_{O_2}$  and stamina) walked normally on the treadmill. All experimental animals were alive and healthy months after experimentation.

#### *Effects of airway closure*

Unlike that of anurans the skin of salamanders lacks a discrete conduit of blood from the right ventricle, and is instead supplied exclusively by the usual systemic arterial circulation. Normally this circulatory pattern works to the disadvantage of cutaneous gas exchange: blood that supplies the skin has in part already passed through the lungs, and blood that is arterialized in the skin mixes with venous blood in the right atrium. After airway closure, however, the skin is no longer supplied with any blood that has first been arterialized in the lungs (although arterialized venous return from the skin still mixes with deoxygenated venous blood in the heart). Thus, after airway closure the decreased  $P_{O_2}$  of blood supplying the skin should favour diffusion of oxygen across the skin. Moreover, physical activity should exacerbate this effect. Increased tissue utilization of oxygen during activity should increase the  $P_{O_2}$  gradient across the skin, and increased cardiac output should lessen any perfusion limitation. These effects should jointly increase cutaneous uptake of oxygen if the skin is capable of supporting such an increase (i.e. if the diffusive conductance of the skin is adequate).

The results of the present study strongly suggest, however, that the skin of *A. tigrinum* is incapable of supporting large increases in  $\dot{M}_{O_2}$ , and cannot compensate for the elimination of pulmonary and buccopharyngeal respiration. The routine  $\dot{M}_{O_2}$ , the  $\dot{M}_{O_2}$  during activity, and locomotor stamina all declined markedly within individuals upon airway closure. In effect, airway closure transforms *A. tigrinum* into the equivalent of a normally lungless salamander of similar size. *Desmognathus quadramaculatus*, a large (28 g) normally lungless salamander, can manage at best a 60% increase in  $\dot{M}_{O_2}$  during activity and can sustain locomotion at  $11 \text{ cm s}^{-1}$  for less than 5 min (Full *et al.* 1988). Thus, the present study corroborates the conclusions that Full *et al.* (1988) drew from interspecific comparisons, and illustrates the value of pursuing comparative and intra-individual approaches in tandem (see also Bennett, 1987).

In the present study, airway closure eliminated buccopharyngeal gas exchange whereas, in the comparative study of Full *et al.* (1988), buccopharyngeal gas exchange was present in both lungless and lunged salamanders. This discrepancy

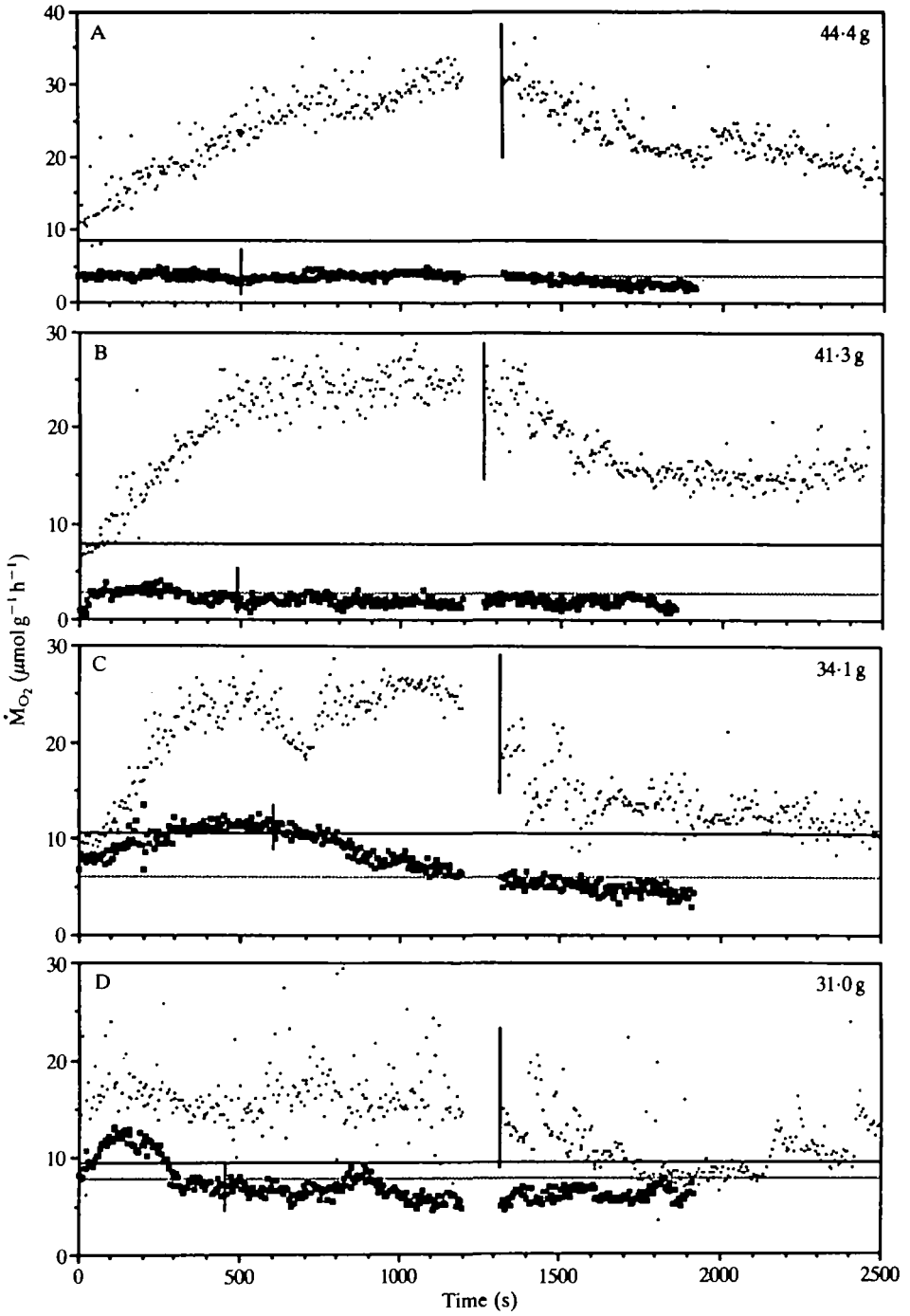


Fig. 1A-D

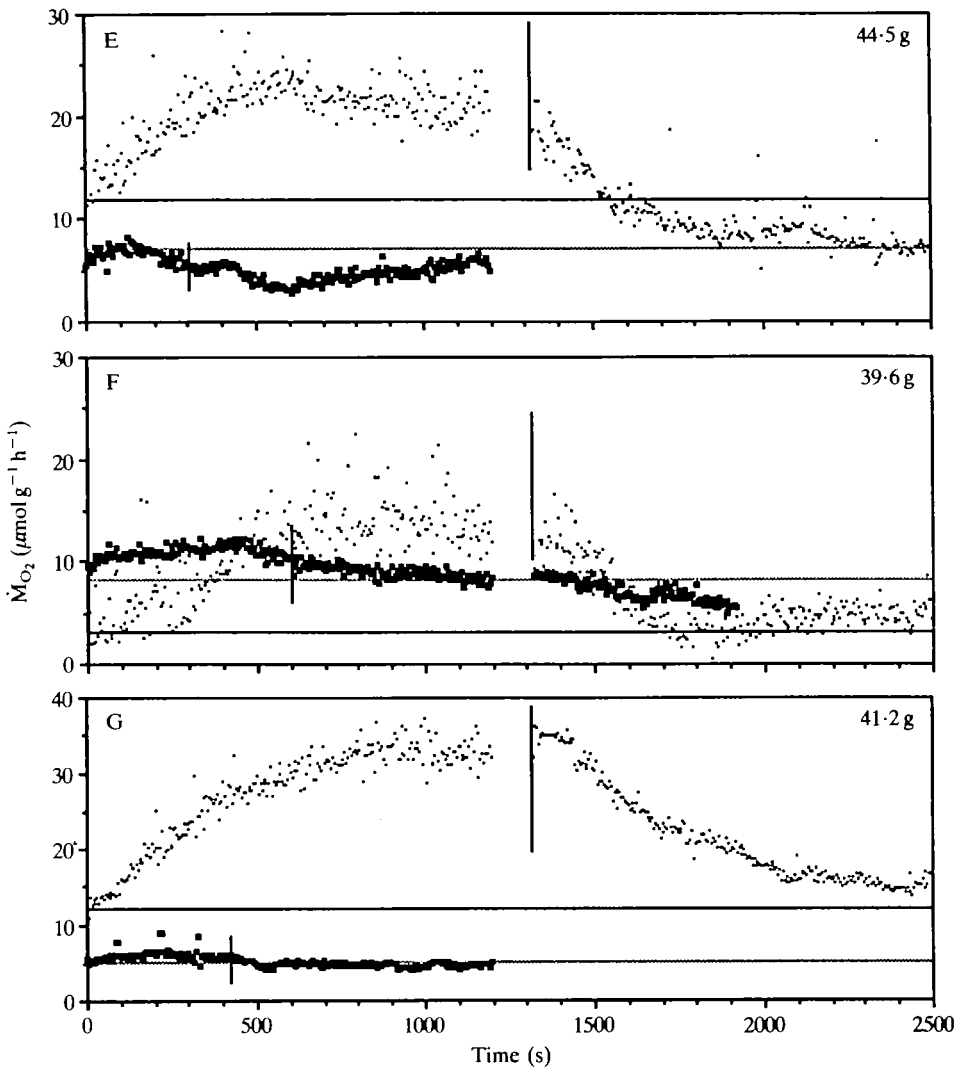


Fig. 1. Effect of airway closure on the routine rate of oxygen consumption ( $\dot{M}_{O_2}$ ),  $\dot{M}_{O_2}$  during treadmill exercise and locomotor stamina in seven (A–F) *Ambystoma tigrinum*. The horizontal lines indicate routine  $\dot{M}_{O_2}$  before exercise in individuals with airways open (solid line) and closed (shaded line). Dots (open airways) and squares (closed airways) indicate the  $\dot{M}_{O_2}$  in each 5-s interval during and after walking at  $11 \text{ cm s}^{-1}$ . Corresponding vertical lines indicate when the experimenter ended the exercise period at about 22 min (open airways) or when animals fatigued (closed airways). Gaps in the record indicate times at which data were not recorded. The body mass of each individual is given in the upper right-hand corner of each graph.

probably has little effect on the interpretation of these studies. Czopek (1965) and Whitford & Hutchison (1965) showed in morphometric measurements and direct determinations of gas exchange, respectively, that buccopharyngeal respiration

accounts for only a small fraction of total gas exchange. This fraction is too small to account for the differences between lunged and lungless salamanders observed in either this study or that of Full *et al.* (1988).

That airway closure should also reduce the routine  $\dot{M}_{O_2}$  in all but one animal was unexpected. Ultsch (1976) reported a similar finding for amphibious salamanders (*Siren*) that were prevented from breathing air. This may be because the 'lungless' salamanders are spared the energetic cost of lung ventilation, or that they underwent less spontaneous activity.

### General conclusion

In view of the evident ability of smaller salamanders to increase cutaneous oxygen uptake during activity (Hillman *et al.* 1979; Withers, 1980; Feder, 1986, 1987; Full, 1986; Full *et al.* 1988) and the burgeoning evidence for regulatory mechanisms in cutaneous gas exchange (Feder & Burggren, 1985*b*; Feder *et al.* 1988), why might large salamanders such as *D. quadramaculatus* and 'lungless' *A. tigrinum* be so deficient in these respects? Earlier studies (reviewed by Feder & Burggren, 1985*a*), often reasoning from simple correlations among body size, cutaneous surface area and oxygen consumption (but see Ultsch, 1973), typically invoked the unfavourable scaling of cutaneous surface area with body size to explain such a result. Because cutaneous gas exchange is potentially limited by many variables in addition to cutaneous surface area, I re-examined this hypothesis.

Although both diffusion and perfusion contribute to the skin's resistance to gas exchange in salamanders, diffusion accounts for the bulk of the resistance. This conclusion is supported by analysis of inert gas elimination in both small (Gatz *et al.* 1975; Piiper *et al.* 1976) and large (Feder *et al.* 1988) lungless salamanders, measurements of blood  $P_{O_2}$  and  $P_{CO_2}$  (Piiper *et al.* 1976) and morphological estimates of diffusing capacity (Piiper *et al.* 1976). Thus, the cutaneous diffusing capacity should constitute an important limitation to cutaneous gas exchange.

According to Malvin (1988), the morphological variables that jointly determine cutaneous diffusing capacity ( $D_{\text{skin},O_2}$ ) are the skin's diffusion coefficient ( $K$ ), skin area ( $A$ ), the thickness of the barrier between the respiratory medium and underlying capillaries ( $x$ ), capillary radius ( $R$ ), and the distance between adjacent capillaries ( $S$ ), as follows:

$$D_{\text{skin},O_2} = \frac{2\pi KA}{\ln[(S/\pi R)\sinh(2\pi x/S)]S}$$

This formulation extends earlier analyses by accounting for the spacing and radius of cutaneous capillaries. Fortuitously, Czopek (1957, 1959, 1961, 1962, 1965) determined each of these morphological variables in a variety of salamanders. I have used these measurements, and the  $K_{O_2}$  calculated by Piiper *et al.* (1976), to examine the relationship of  $D_{\text{skin},O_2}$  (in  $\text{nmol O}_2 \text{ min}^{-1} \text{ mmHg}^{-1}$ ;  $1 \text{ mmHg} = 133.3 \text{ Pa}$ ) and body mass in salamanders (Fig. 2). For salamanders  $<100 \text{ g}$  body mass,  $D_{\text{skin},O_2}$  scales as the 0.57 power of mass (Fig. 2A). Thus,  $D_{\text{skin},O_2}$  fails to



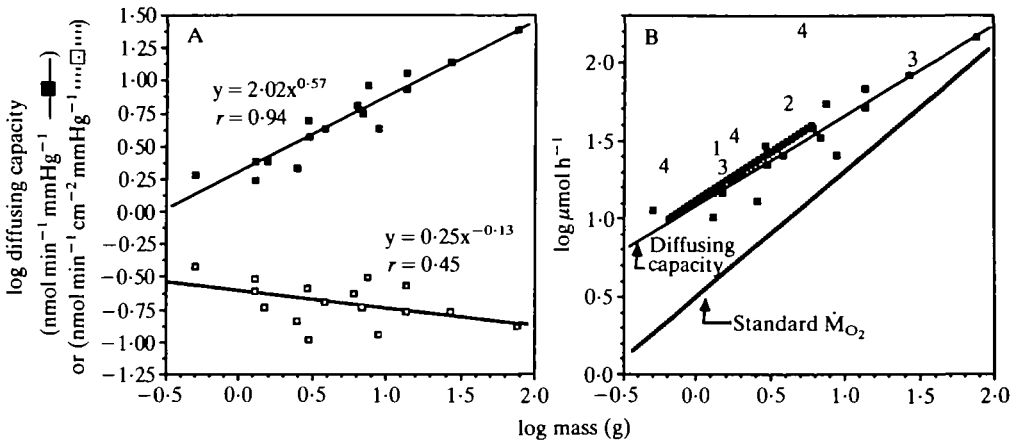


Fig. 2. Scaling of cutaneous diffusing capacity and the rate of oxygen consumption ( $\dot{M}_{O_2}$ ) in salamanders weighing less than 100 g. Cutaneous diffusing capacity was calculated from the data of Czopek (1957, 1959, 1961, 1962, 1965) according to Malvin (1988). (A) Scaling of cutaneous diffusing capacity for intact salamanders ( $\text{nmol O}_2 \text{ min}^{-1} \text{ mmHg}^{-1}$ , solid squares and solid line) and per unit surface area ( $\text{nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1} \text{ mmHg}^{-1}$ , open squares and broken line). (B) Comparative scaling of standard  $\dot{M}_{O_2}$ , maximum  $\dot{M}_{O_2}$  during exercise, and cutaneous diffusing capacity. Diffusing capacity (from Fig. 2A) has been multiplied by 100 mmHg, an estimate of the  $P_{O_2}$  gradient between the cutaneous microcirculation and ambient air (Piiper *et al.* 1976), and thus represents a putative 'cutaneous diffusing limit' based on morphological measurements. Values for maximum  $\dot{M}_{O_2}$  of exclusively skin-breathing salamanders are superimposed: (1) Feder (1987); (2) Full (1986); (3) Full *et al.* (1988); (4) Hillman *et al.* (1979); shaded line, summary regression of Withers (1980). The broken line is the standard or minimum  $\dot{M}_{O_2}$  expected for salamanders at 21°C.

increase isometrically with body size. The allometric scaling of  $D_{\text{skin},O_2}$  is not entirely a function of the scaling of surface area with body mass (although  $A \propto \text{mass}^{0.67}$  in Czopek's measurements). The  $D_{\text{skin},O_2}$  per unit surface area decreases with increasing size (Fig. 2A), reflecting the scaling of diffusion barrier thickness ( $x$ ), capillary spacing and capillary radius.

Some important implications of this allometry emerge from a comparison with metabolic rates. The  $D_{\text{skin},O_2}$  multiplied by the  $P_{O_2}$  gradient between the respiratory medium and blood within the cutaneous capillaries is the maximum cutaneous oxygen uptake that is physically permissible, assuming no perfusion limitation. Only a single estimate of the  $P_{O_2}$  gradient is available for salamanders, 100 mmHg (Piiper *et al.* 1976). Nonetheless, in view of the assumptions inherent in such estimates, the product of  $D_{\text{skin},O_2}$  and this  $P_{O_2}$  gradient across the skin (expressed in  $\mu\text{mol O}_2 \text{ h}^{-1}$ ) corresponds remarkably closely with the maximum  $\dot{M}_{O_2}$  previously reported for exclusively skin-breathing salamanders (Fig. 2B). The relationship between standard (i.e. minimum)  $\dot{M}_{O_2}$  and body mass at 21°C was estimated from the 'lunged and lungless' salamander equation of Feder (1976) with a  $Q_{10}$  of 2.6 (Feder, 1976). As is evident from Fig. 2B, the standard  $\dot{M}_{O_2}$  of

small salamanders is so low that they may increase their cutaneous oxygen uptake many-fold during activity before encountering the 'cutaneous diffusing limit'. Thus, the superior ability of small lungless salamanders to increase cutaneous gas exchange during activity is apparently due not only to the scaling of  $D_{\text{skin},\text{O}_2}$ , but also to the impressively low resting metabolism of small salamanders. In contrast, the  $\dot{M}_{\text{O}_2}$  of large salamanders is already so close to the cutaneous diffusing limit when these animals are resting that little scope is available for increase during activity.

I thank Bruce Anderson and David Liefer for technical assistance, and Robert Full for his thoughtful comments on several drafts of the manuscript. At various times, Norbert Heisler, Johannes Piiper, Alan Pinder and Dana Quinn were instrumental in focusing my attention on the contradiction between the large diffusion limitation and the ability to increase oxygen consumption during activity in lungless salamanders. Juan Markin originally suggested the use of cyanoacrylate cement, and George Bartholomew subsequently recommended control experiments for its use. This research was supported by NSF grant DCB84-16121.

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